

**Ant assemblages in a Southern African savanna: local processes and
conservation implications**

by

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**Live as if you were to die tomorrow,
Study as if you were to live forever.**

St. Edmund of Abingdon

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Ant assemblages in a Southern Africa savanna: local processes and conservation implications

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Abstract

The structuring of ant assemblages in a Southern African savanna was investigated using data from the only long-term, large-scale savanna fire experiment in Africa. A comprehensive survey of three habitats in the Kruger National Park (KNP) revealed a total of 169 ant species from 41 genera. The sampling efficiency and consistency of pitfall traps and Winkler samples for inventory, bioindicator and ecological studies in savanna habitats was compared using ants. Pitfall traps were more efficient and productive than Winkler sampling for epigeaic ants, with a greater total species richness and higher abundance of ants recorded. Suggestions were made to improve Winkler sampling output, and to allow quantitative data to be collected. With the structuring of local assemblages, competition was the most significant local factor tested. The relationship between ant dominance and ant species richness was consistent across three continents. A model developed to test mechanisms that could be responsible for the form of this relationship supported the hypothesis that competitive exclusion by dominant ants at least partially reduces species richness. Stress was only partially responsible for low dominance and low species richness, while scatter in the data points is related to patchiness of ants at baits. These findings contrast strongly with previous claims regarding the relationship

between richness and dominance. Habitat complexity was not found to play an important role in determining ant assemblage body size in this savanna system. The size-grain hypothesis (Kaspari & Weiser 1999) which predicts that environmental rugosity results in positive allometric scaling of leg length on body length because of changes in locomotion costs, was tested by comparing the body sizes of ants from areas of contrasting habitat complexity. No support for the hypothesis was found. Phylogenetic independent contrast methods did however support the allometric relationship found by Kaspari and Weiser (1999). Ant assemblages in KNP exhibited a remarkable degree of resistance, and in some cases resilience, to burning. Species richness or abundance did not vary with different burning treatments, although ant assemblage composition was sensitive to burning treatment. This difference, however, was only pronounced between burnt and unburnt plots, not between burning treatments. The degree of response of ant assemblages is likely to be related to two main contributory factors: mean annual rainfall and changes in vegetation structure with burning, and the assemblage's history of association with fire. An overview of published research on the effects of fire on fauna in Southern Africa was undertaken. Few studies have examined the effects of fire on amphibians or reptiles and few experimental studies have been undertaken using an experimental fire regime applied over appropriately long time intervals. Most studies provided no information on the scale of the study. Replication was often not reported, and was generally inadequate. Information on the effects of fire on fauna in Southern Africa is fragmentary, and consequently informed management decisions regarding the consequences of burning policies on the conservation of biodiversity both within and outside protected areas are problematic. Recommendations and suggestions for improving fire research are given.

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Chapter 1: General Introduction

Anthropogenic transformation of the landscape through continuing habitat loss and degradation (Soulé 1991; Ehrlich 1995; Tilman & Lehman 2001; Travis 2003), invasive species introductions (Lodge 1993; Williamson 1999; Cook 2003; Rouget et al. 2003; Sanders et al. 2003) and climate change (Hughes et al. 1997; Van Jaarsveld & Chown 2001; McLaughlin et al. 2002; Travis 2003), is contributing to rapid loss of biodiversity. As a consequence, effective conservation is becoming ever more important. In Southern Africa, typically the focus of conservation efforts has been on specially designated protected areas or national parks, although increasingly conservation in the matrix outside reserves is receiving attention (see Scholtz & Chown 1993; Clark & Samways 1996; McGeoch 2002; Fabricius et al. 2003). Regardless of whether conservation is targeted within or outside reserves, the principal aim of most conservation agencies is the maintenance of biodiversity and ecosystem functioning (see for example: Nott et al. 1985; Mentis & Bailey 1990; Richards et al. 1999; Brockett et al. 2001; Armstrong 2002). In South Africa this includes the Kruger National Park, the largest conservation area in the country, which has as its mission statement “To maintain biodiversity in all its natural facets and fluxes...” (Braack 1997).

Recognising that management of protected areas is goal-orientated, and that the maintenance of biodiversity is a key objective, there are several tools managers can use to meet these objectives. These include manipulations of animal and plant numbers through removals and introductions, and manipulation of resource availability for example through the provision of water and the alteration of fire regimes (see Collinson 1983; Bailey et al. 1993; Bothma 1996; Braack 1997; Thrash 1998; Hoffmann et al. 1998). In Southern Africa, conservation has traditionally focused on large mammals, and as a consequence has been rather agriculturally biased. Management aims have included focusing on the improvement of grazing swards, and control or reduction of woody biomass (Stander et al. 1993). As a result of the focus on large mammals and vegetation, there has generally been very little management and research interest in invertebrates in savanna systems, with the exception of disease vectors (Miller et al. 2000; Miller & Rogo 2001).

This early lack of attention to invertebrates is surprising. Invertebrates dominate terrestrial systems being the most diverse and numerous of all living things (Wilson 1988;

Groombridge 1992; Kim 1993; Kremen et al. 1993). Estimates of global insect species richness range from about 3.5 million to over 10 million (Gaston 1991; Stork 1993; May 2000; Alroy 2002), while for Africa, conservative estimations suggest approximately 600 000 species (Miller & Rogo 2001). Because of their huge biomass, large diversity, and extensive range of ecological roles (including pollinators, decomposers, predators, herbivores and scavengers) invertebrates are integral to the structure and functioning of biotic systems (Fisher 1998).

Ants are important in many systems as ecosystem engineers (Jones et al. 1994), and play an important role in the maintenance of system productivity and functioning, and in the structuring of communities. Occurring in a diverse range of habitats across the globe, ants are functionally important at all trophic levels, as predators, herbivores and scavengers (Hölldobler & Wilson 1990; Folgarait 1998). Furthermore, many species have evolved close relationships with plants, such that they protect plants against herbivory or play a crucial role in the dispersal and germination of seeds (e.g. in the fynbos of South Africa) (Bond & Slingsby 1983; Andersen 1991; Christian 2001; Heil et al. 2001; Ness 2003). However, ants not only influence biotic components of the ecosystem, but they are also responsible for altering the structure and composition of soil, which affects above ground vegetation and microclimate properties (Lobry de Bruyn & Conacher 1990; Elmes 1991; Dean & Yeaton 1993; Lobry De Bruyn 1994). Ants are highly abundant and diverse in savanna systems, and their wide distribution throughout the world in diverse habitats, make ants strong indicators of biological diversity (Roth et al. 1994; Folgarait 1998). As indicators of ecosystem condition and because of their sensitivity to system structure, ant assemblages often reflect the degree of habitat disturbance or succession in a community (Majer 1983, 1985; Andersen 1990; Vanderwoude et al. 1997; Peck et al. 1998). Furthermore, ants are easily sampled, and in Southern Africa at least, are relatively well known taxonomically (Robertson 2000), and thus sorted to morphospecies level with comparative ease.

Pattern and Process

For conservation to be effective, it is important not only to know what species are present, but also to have some understanding of the processes that generate and maintain diversity (Pickett et al. 1992). The mechanisms responsible for local species richness have been widely

discussed, and although there is now general agreement that both local and regional factors are important (Ricklefs & Schluter 1993; Gaston 2000; Godfray & Lawton 2001), the relative importance of these factors is still unclear (Ricklefs 1987; Cornell & Lawton 1992; Huston 1999). Local processes regulating species richness, such as competition (McLaughlin & Roughgarden 1993), disturbance (Huston 1994) or parasitism (Belkessam et al. 1997), are considered relatively deterministic, and can limit the number of species co-existing locally irrespective of regional diversity. In contrast, regional processes are more stochastic and focus on evolutionary causes such as speciation, extinction and migration (Srivastava 1999; Shurin & Allen 2001).

In the context of ants, competition is considered the key process structuring local ant assemblages (Savolainen & Vepsäläinen 1988; Hölldobler & Wilson 1990; Retana & Cerdá 2000). Supporting evidence is diverse, and includes territoriality (Fox et al. 1985; Andersen & Patel 1994), spatial ant mosaics (Room 1971; Majer et al. 1994), behavioural dominance hierarchies (Savolainen & Vepsäläinen 1988), and antagonistic behaviour (Andersen et al. 1991). Other local processes such as parasitism (LeBrun & Feener 2002) and disturbance (Perfecto & Snelling 1995; Hoffmann 2000; Watt et al. 2002; Bruhl et al. 2003) also play a role in determining local species richness. Furthermore, regional scale processes have also been shown to determine local ant species richness. For example, Kaspari et al. (2000) found that local species richness was strongly correlated with net primary productivity. Thus, while the relative importance of any one process is not known, it is likely that these processes are not mutually exclusive. Therefore, this thesis investigates the roles that competition, habitat structure and disturbance (specifically fire), play in the structuring of local ant assemblages in a South African savanna.

Fire

Although fire is generally considered a key determinant of the structure and function of Southern African savanna systems (Walker 1987; Scholes & Walker 1993; Van Langevelde et al. 2003), its use in protected area management remains highly contentious (see Biggs & Potgieter 1999). As a result, over time a range of burning policies have been applied in conservation areas. These have varied enormously from *laissez-faire* to strictly controlled, prescribed fire regimes where the frequency and seasonality of fires is standardised (Mentis

& Bailey 1990; Van Wilgen et al. 1998). The changes in fire policy and attitudes to burning in Southern Africa have also been paralleled to some degree in the United States of America and in Australia (Pyne 1991).

In Kruger National Park, fire policy has tended to reflect general trends in burning elsewhere in the country and sub-region. Following the proclamation of Kruger National Park in 1902, burning policy was quite relaxed with deliberate burning of the vegetation frequent. Burning was also carried out towards the end of the wet season in Autumn (February to May) to provide grazing for animals through the winter (Brynard 1964). Fires were often extensive because the low number of staff, and lack of fire-breaks meant effective control was not possible (Braack et al. 1999).

However, general sentiment towards fires became increasingly negative, with fire regarded as having a detrimental effect by upsetting the natural balance of an area (Mentis & Bailey 1990). Largely as a result of the lack of understanding and concern over the effects of fire, controlled burning was almost completely abandoned in the early 1940s with the introduction of the Soil Conservation Act. Under these strict regulations land managers were forced to seek permission from the Department of Agriculture in order to burn, and as a result controlled burning in arid savannas was virtually eliminated (Trollope 1984). In Kruger National Park, controls to eliminate accidental fires were introduced later with the adoption of a policy which limited burning to once every five years, but then only after the first good spring rains (Mentis & Bailey 1990).

Due to several very large fires in 1954, covering more than 500 000 ha (approximately a quarter of the park), an extensive network of fire-breaks was established across the park, dividing it up into a series of management blocks. A new burning policy of three-year rotational burns was also adopted. This was applied until the early 1990s when concerns over a change in the dominant grass types, apparent declines in tree densities, and lack of variation in burning lead to the adoption of a lightning fire policy (Van Wilgen et al. 1998). This policy allowed all lightning fires to burn unchecked, but all human-induced fires were to be suppressed (Braack 1997). While this was initially seen as a more flexible and natural approach, the extensive, intense fires of 1996 and 2001 caused by a large build up of biomass and extreme weather conditions, precipitated a re-think of burning policy. Today, management in Kruger National Park is in the process of developing a new fire policy. It is

envisaged that this will incorporate greater flexibility in burning to include both lightning and human-induced fires. Fires will be spread throughout the year, with more being set earlier in the year (at the end of the wet season or beginning of the dry season). The rationale here is similar to that used by fire managers in Australia, where many small fires early in the dry season break up the fuel in a patchwork, and reduce the probability of large fires later in the year towards the end of the dry season (see Russell-Smith et al. 1997).

Kruger National Park: Experimental Burn Plot Trial

The Experimental Burn Plots (EBPs), situated in Kruger National Park, represent a unique experiment in savanna Africa. The EBP trial was set up as a large field-scale experiment in 1954, following the appointment of a botanist to the park and continuing concern about burning policy. Given the emphasis placed on large mammals and grazing quality, the EBPs were originally designed to test the effects of fire on plant communities. In addition, it was realised that results from agricultural burning experiments were not directly relevant or applicable to managers in the park, especially given that in the park no effective control could be exercised over where animals could graze (Brynard 1964).

The EBP trial was laid out to cover four major vegetation types of the Park, in each of which four separate replicates were placed. Originally each replicate had 12 treatments (season-frequency combinations, and a control which has remained unburned) applied to plots of approximately 7 ha. The organisation of the plot treatment sequences was randomised. Fire frequency is defined as the reciprocal of the time between fires, and season refers to the time of year fires occur. The experiment was expanded in 1979 to include quadrennial and sexennial October burns, thus increasing the number of fire treatment plots to 14.

This study focuses primarily on the Satara plots which are situated in a mixed Knobthorn (*Acacia nigrescens* Oliv.)/Marula (*Sclerocarya birrea* Hochst) dominated landscape, the Mopane plots which are situated in a Mopane (*Colophospermum mopane* J.Kirk) dominated veld, and the Pretoriuskop plots situated in the Lowveld Sour Bushveld (Trollope et al. 1998) (see Fig. 1). This study concentrates on all burn frequencies for April (autumn burns at the end of the wet season) and August (winter burns in the dry season) seasons and the control plot.

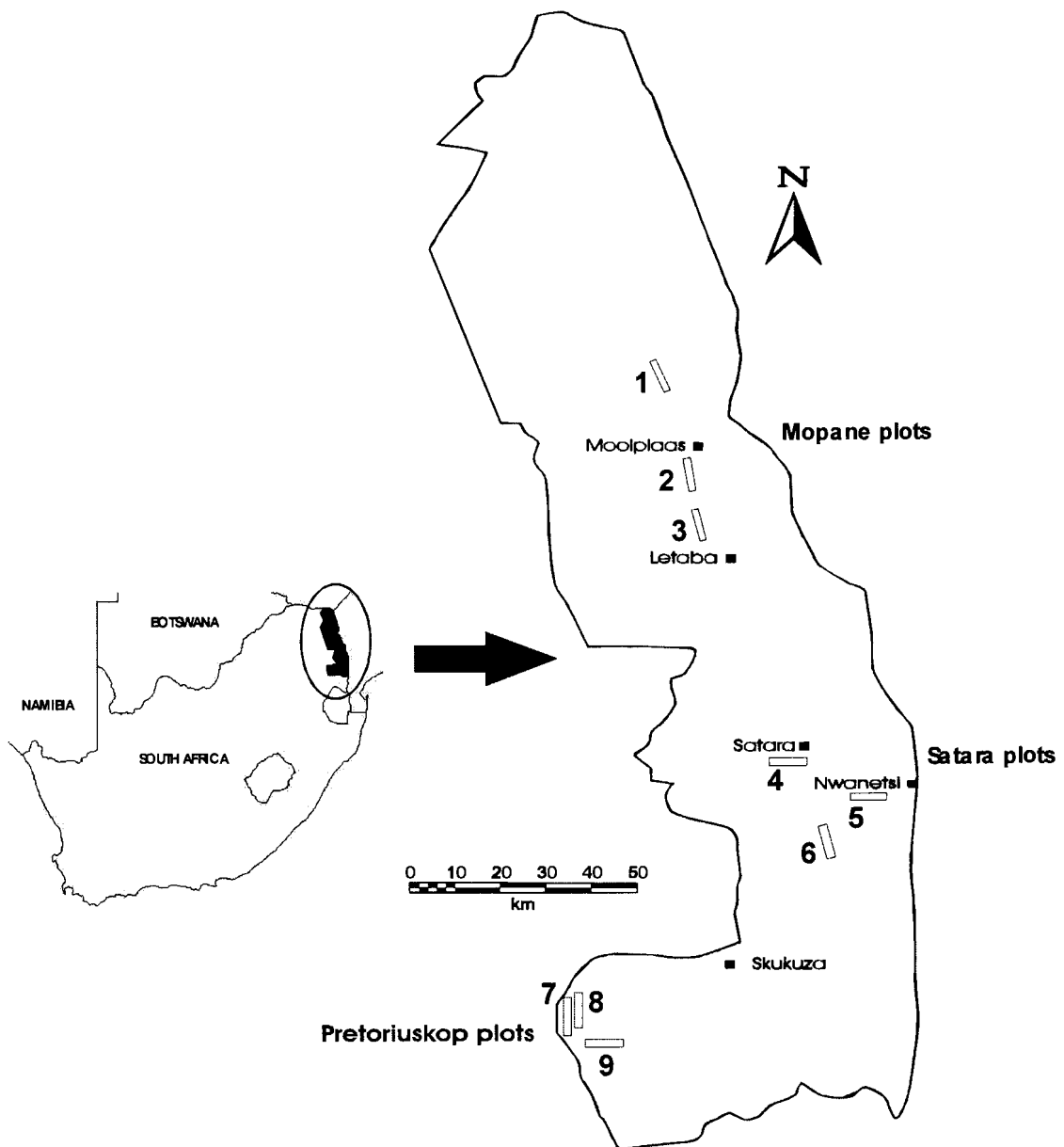


Figure 1. Map showing location of Kruger National Park within South Africa. The approximate position of the experimental burn plot replicates used for this study, are shown for Mopane, Satara and Pretoriuskop areas. Replicates are as follows: 1 = Dzombo, 2 = Mooiplaas, 3 = Tsende, 4 = Satara, 5 = N’wanetsi, 6 = Marheya, 7 = Numbi, 8 = Shabeni, 9 = Kambeni.

Three replicates at each site are used to avoid problems of pseudoreplication (Hurlbert 1984); the fourth replicate being excluded because it is considered unrepresentative of the other three (Venter 1999) (see Fig. 1 for replicates).

The 1997 revision of the Kruger National Park Management Plan made provision for Thresholds of Potential Concern (TPCs) which are defined as ‘those upper and lower levels along a continuum of change in a selected environmental indicator which, when reached prompt an assessment of the causes which led to such an extent of change, and results in either (a) management action to moderate such causes, or (b) re-calibration of the threshold to a more realistic or meaningful level’ (Anon 1997). The goals of maintaining diversity require fire management goals to be framed in terms of a range of fire return periods and seasons. It is therefore important to understand the implications of applying fires at different times of the year, and with differing frequency.

Thus, this study focuses on the Satara area of the park because managers have expressed concerns that TPCs may have been exceeded in this area. In addition, the Satara area appears highly productive, supporting high numbers of large mammals, yet virtually nothing is known about the insects occurring in the same area. Furthermore, park managers are interested in using bioindicators to identify habitat changes caused by fire. Thus, the potential use of ants as bioindicators to fire are assessed in Satara, Mopane and Pretoriuskop. The Mopane area has been identified as an important focus for understanding savanna woodland dynamics and the effects of human use on woodlands. Outside conservation areas, Mopane woodlands are being subjected to increasingly levels of human use, and this is the source of considerable conservation concern in southern Africa (Rebe 1999).

Thesis structure

Despite the importance of invertebrates in ecosystem processes, baseline data as to what invertebrates occur in reserves is frequently unavailable, and thus the degree to which these areas successfully conserve invertebrates remains unclear (McGeoch 2002). Therefore, there is a pressing need to improve understanding of the structure and functioning of invertebrate communities in savanna conservation areas, particularly if the goals of conservation are to be met (Fisher 1998; Miller & Rogo 2001). With this in mind, this thesis focuses on ants (Hymenoptera: Formicidae) in Kruger National Park, South Africa.

Previous collecting of ants in Kruger National Park was carried out by Prins (1963, 1964, 1965, 1967) who made several survey trips through the park during Spring 1960, and early Winter 1961 and 1962. In a revised list of the ants of the Kruger National Park (Prins 1964), 22 genera (recent revisions taken into account) and 79 species were recorded (species not verified with present nomenclature). However, apart from ants not being most active at this time of the year, no information was given as to how sampling was conducted. These reports suggest that surveys were not conducted in a systematic way with ants collected opportunistically by hand sampling. Therefore, at best these surveys represent a cursory, qualitative and incomplete record of the ants of Kruger National Park. Thus this thesis aims to address some of these issues, and by carrying out intensive, systematic, quantitative sampling focusing in detail in two savanna habitat types of the park, provide Kruger Park management with more detailed information of the epigaeic ant species occurring in these areas.

The primary goals of this research are therefore to investigate both pattern and process in relation to ant community structuring a South African savanna system. This thesis examines the relative importance of different factors in structuring local ant assemblages using the Experimental Burn Plot trial as the basis for the study. In doing so, much needed information is provided for conservation managers in the region, especially in the context of fire management.

Chapter 2 of the thesis explores methods of collecting ants in savanna systems to increase sampling efficiency: a factor that is crucial for biodiversity surveys, and particularly for park managers whose task it is to monitor biodiversity. The importance of local processes in structuring ant assemblages is examined in the following three chapters with Chapter 3 focusing on competition, Chapter 4 investigating whether habitat structure determines ant body size by empirically testing the Size-Grain Hypothesis, and Chapter 5 exploring the effects of fire on ant diversity. Finally, Chapter 6 presents a critical assessment of faunal fire studies in Southern Africa, highlighting potential experimental problems, but also suggesting ways of improving future studies and indicating possible new research directions.

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Chapter 2

Testing pitfall and Winkler methods with ants in a South African savanna

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Introduction

Insects are recognised as important components of global biodiversity in terms of their considerable biomass (Groombridge 1992), species richness (Erwin 1991; Gaston 1991), and significant role in ecosystem functioning (Kim 1993; Jones et al. 1994; Folgarait 1998; McGeoch 1998). In consequence, their conservation requirements are being increasingly investigated (e.g. Samways 1994). Although formal conservation areas clearly contribute to the conservation of insects, the extent to which these animals are represented in such areas is not well known (Koch et al. 2000). Likewise, investigations of the extent to which different kinds of habitat transformation affect insects outside protected areas are recent (Scholtz & Chown 1993; Samways 1994). Thus increasing attention is being paid to inventorying and understanding patterns of insect diversity both inside and outside of formal conservation areas (see Brown 1991; Lawton et al. 1998; Balmford & Gaston 1999; Van Rensburg et al. 1999). Like inventories for all other taxa, those undertaken for insects should be designed so that they are as realistic, rapid, repeatable, quantitative and cost-effective as possible (Margules & Austin 1991; Kim 1993; Oliver & Beattie 1996; Fisher 1999).

Insects are also being used increasingly as bioindicators in a variety of roles (Noss 1990; Cranston & Trueman 1997; McGeoch 1998; Hilty & Merenlender 2000). Not only are they being used as valuable indicators of the effects of changes in the environment on local communities (ecological indicators, e.g. Van Rensburg et al. 1999; McGeoch & Gaston 2000), but they may also be used to detect changes in environmental condition (environmental indicators), and more broadly as indicators of diversity as a whole (biodiversity indicators, see McGeoch 1998 for additional discussion). Initial quantitative studies are essential to establish the utility of insects in these roles. As with inventorying, the techniques employed for such work should ideally be realistic, rapid, repeatable, and cost-effective.

To address these inventory and bioindicator survey requirements, the most appropriate sampling technique (or techniques) should be identified for the area or taxon in question. In addition to the requirements mentioned above, this technique should also seek to reduce problems associated with both the analysis and interpretation of data with many zeros, and low species abundances (see Clarke & Warwick 1994; Hilty & Merenlender 2000). Often, when time and finances are limited, only one sampling method may be employed. Because

methods differ in their efficacy, efficiency and repeatability, the optimum method for the study must therefore preferably be selected *a priori*.

For sampling epigeic ant species, the most commonly employed method is pitfall trapping. Pitfall traps provide a relatively simple, quick and cost-effective sampling method for collecting epigeic ants, and allow for continuous day and night sampling (Southwood 1978; Andersen 1991; Majer 1997). There are, however, several disadvantages to this method (Luff 1975). Pitfall trapping is most productive in open habitats because catch can be compromised by vegetation complexity (Greenslade 1964; Majer 1997; Melbourne 1999). Pitfall size influences catch in terms of species caught (for example, small traps may undersample large ants (Abensperg-Traun & Steven 1995)), and abundances. The clumped nest distribution of ants may also pose problems for pitfall sampling because pitfalls adjacent to nests or foraging trails can lead to distorted results (Andersen 1983). Furthermore, ants may be differentially susceptible to capture (Marsh 1984). For example, fast moving ant species have been over-recorded in open habitats (Greenslade 1973; Andersen 1983). Certain species of ants may also be deterred from traps, while others may be attracted to them (Marsh 1984). Sampling with pitfall traps is also affected by 'digging in' effects (Greenslade 1973) where catches are generally greatest immediately after traps have been dug.

Winkler sampling is an alternative collection method for surface and litter-dwelling ants, and has been shown to render pitfall sampling of epigeic ants redundant in areas of high litter loads (Fisher 1999). The Winkler method involves collecting leaf-litter from within a 1m² quadrat, and sifting this material through a coarse sieve (1cm² mesh size). The collected leaf litter is then placed into a mesh bag, which is vertically suspended inside a cotton enclosure. The leaf litter usually amounts to approximately 2 litres. Where leaf litter is scarce, less may be used, and where it is extremely plentiful, a maximum of 2 litres is used. Over a period of at least 48 hours, ants and other invertebrates work their way out of the drying litter, and are collected in a small cup partially filled with ethanol, suspended at the bottom of the bag (Besuchet et al. 1987; Nadkarni & Longino 1990; Fisher 1996, 1998, 1999; Didham et al. 1998).

The Winkler method is particularly useful for collecting litter and soil fauna that are not caught as readily with pitfall traps and is highly recommended for use in forested habitats where litter is plentiful (Nadkarni & Longino 1990; Olson 1991; Fisher 1996, 1999). Previous

sampling using the Winkler method in rainforest habitats has proved very successful, yielding significantly better results than pitfall trapping alone (e.g. Olson 1991; Fisher 1999). Nonetheless, few studies have tested Winkler sampling in drier systems where litter levels are lower and more patchily distributed. Although traditionally used in forest systems, the Winkler method could be used in savannas where a litter layer also accumulates. The relative efficiency of Winkler extractors compared to other sampling methods in such habitats still requires investigation.

Furthermore, the rationale underlying the choice of 1 m² as the preferred quadrat size is not well documented. Most studies simply state that a 1m² quadrat was chosen for the collection of leaf litter (e.g. Fisher 1996, 1999; Longino & Colwell 1997; Didham et al. 1998; Lawton et al. 1998; Bestelmeyer et al. 2000). Although this might be the most appropriate quadrat size for habitats with high litter loads (e.g. rainforests), it is not clear why this should be the most efficient quadrat size for determining the species richness and relative abundance of insect species in such habitats, or in those where litter is less abundant and more patchily distributed. Rather, it appears that this quadrat size was chosen because it yields sufficient, but not too much, litter for extraction. Thus, there appear to be considerable grounds for also assessing the relative merits of the quadrat size and number used for each Winkler sample to improve the efficiency of this method. In the case of ants, such an assessment is particularly important given the influence that clumped nest distributions are likely to have on the outcome of the sampling.

Hence, the aims of the current study were to test the relative merits of pitfall traps and Winkler sampling for assessing the diversity (richness and abundance, and size composition of catch) of ants in a savanna ecosystem, and to assess the effects of differences in quadrat size and number on the efficacy of the Winkler sampling method. In so doing, recommendations for the most appropriate sampling technique(s) for inventories and for other quantitative studies in savannas are made.

Study Site

Sampling of ants was undertaken on a long-term field experimental area in the central Satara area of the Kruger National Park, South Africa. The study was carried out on an experimental control plot (7 ha) that constitutes part of a long-term burning experiment (Experimental Burn

Plot Trial), and has remained unburned since 1954 (Trollope et al. 1998). As a consequence of no burning, the plot is densely vegetated, comprising moribund grass, bushes and trees. The vegetation of the area is classified as a Knobthorn (*Acacia nigrescens* Oliv.)/ Marula (*Sclerocarya birrea* Hochst) savanna in the Sweet Lowveld Bushveld (Low & Rebelo 1996). Litter load and cover on the plot was patchy, being thick (up to 20 cm deep) in some areas, while almost non-existent in other areas. Mean annual rainfall in this area is approximately 550 mm (Gertenbach 1983). The site is on basalt-derived clay soils.

Methods

A total of 30 pitfall traps (fifteen 62 mm diameter (large), and fifteen 18 mm diameter (small)) were set at 5 m intervals along six randomly placed transects, covering an area of approximately 2 ha. Each transect consisted of five traps, with large and small traps alternating. Each trap contained a 50% propylene glycol solution, and was open for three days from 4-7 December 1999. Propylene glycol is non-toxic to larger animals, and is not known to significantly attract or repel ants (Adis 1979). Vegetation around the pitfall traps was not cleared.

Following the pitfall trapping, Winkler litter samples were collected in the same area (13-19 December 1999). Fifteen samples were collected for each of the following Winkler quadrat combinations: 1m² (total 15 m²), ½ m² (total 7 ½ m²), ¼ m² (total 3 ¾ m²), 2 × ½ m² (total 15 m²) and 4 × ¼ m² (total 15 m²). Collection quadrats were spaced at 2 m intervals along randomly placed transects. Where more than one quadrat was used per Winkler sample, the litter from all quadrats was mixed and sieved together, and then 2 litres taken for hanging. Each set of Winkler samples was suspended for 48 hours; this being the hanging time in many other studies (e.g. Olson 1991, Fisher 1998, 1999). It is unlikely that earlier removal of ants with pitfall trapping would affect numbers caught with Winkler sampling because the pitfall samples were not sufficiently numerous, or open for a pre-longed period of time, and the collection area was large.

Ant samples collected with both techniques were stored in 80% alcohol. All ant samples were sorted and identified to morphospecies level on the basis of characters previously established to be important at the species level for each genus. Where possible,

species names were assigned. Voucher specimens were mounted, and a representative set stored at the South African Museum, Cape Town.

The maximum head width of each species was measured to 0.01 mm with an ocular micrometer mounted on a dissecting microscope. Head width provides a standard and accurate measure of overall body size (Hölldobler & Wilson 1990; Kaspari 1993). For each species, and where possible, several individuals were measured. In order to provide an indication of the body size frequency distribution for each sampling method, ant species were placed into 0.2 mm size classes based on head size: 1 = 0.30-0.50 mm, 2 = 0.51-0.70 mm, 3 = 0.71-0.90 mm, 4 = 0.91-1.10 mm, 5 = 1.11-1.30 mm, 6 = 1.31-1.50 mm, 7 = 1.51-1.70 mm, 8 = 1.71-1.90 mm, 9 = 1.91-2.1 mm, 10 = 2.11-2.30 mm. The mean abundance of ants/ sample and standard error for each size class were calculated.

To assess and compare pitfall and Winkler sampling completeness, species accumulation curves for each sampling method were plotted. Species accumulation curves were extrapolated to estimate expected species richness with different sample numbers. Since the shape of species accumulation curves is influenced by the order in which samples are added to the total (Colwell & Coddington 1994), sample order was randomised 100 times with the program EstimateS to produce smooth curves (R.K. Colwell, Version 5, <http://viceroy.eeb.uconn.edu/estimates>).

The incidence-based coverage estimator (ICE) provided in EstimateS is a robust measure for indicating completeness of sampling. However, where the number of rare species does not decrease with increased sampling effort, ICE does not perform well (Colwell & Coddington 1994). In this study, singletons (species that only occur in one sample) did not decrease with sampling for all sampling methods, and in consequence ICE could not be reliably used. Therefore, smoothed, observed species accumulation curves were fitted using a logarithmic model: $S(t) = \ln(1 + zat)/z$, where t is the measure of sampling effort (sample number), and z and a are curve-fitting parameters (Fisher 1999, see also Soberón & Llorente 1993). Non-asymptotic functions were used for the extrapolation. Although extrapolation may result in enhanced bias of data (Colwell & Coddington 1994), this method provides a suitable alternative to a non-parametric estimator such as ICE.

Results

A total of 34 ant species comprising 16 genera was recorded with pitfall traps and Winkler samples combined (Table 1). Species richness was greatest with pitfall trapping. A total of 25 ant species was recorded from pitfall trapping alone, with the richest genera being *Monomorium* (5 species), *Pheidole* (4 species), and *Tetramorium* (3 species). The most abundant species was *Pheidole* sp. 1, representing 74.0 % of all ants found in pitfall traps. A total of 22 ant species was recorded from Winkler samples, with the richest genus being *Tetramorium* (5 species). The most abundant species were *Plagiolepis* sp. 1, representing 38.7 % of all ants found in Winkler samples, and *Pheidole* sp. 1 representing 37.2 %. Not all Winkler samples contained ants (11 of the 75 samples did not; Table 2).

In all of the Winkler sampling protocols, with the exception of the 1 m² quadrats, the mean number of ants per sample was lower than that found in both the large and small pitfalls (Table 2). Total species richness was greatest for large pitfall samples (20 species), and lowest for Winkler quadrat size ¼ m² (7 species). Moreover, there were 12 species of ant unique to pitfall sampling, and seven species unique to Winkler sampling. The mean number of ants per sample and mean number of species per sample was highest for large pitfall traps (44.0 ± 10.0, mean ± S.E., and 5.2 ± 0.4, respectively) (Table 2).

Comparisons of extrapolated species accumulation curves as a function of the number of stations sampled (Fig. 1) showed that large pitfall traps had a higher rate of species accumulation than did small pitfall samples, and all Winkler samples. For Winkler samples, 2 × ½ m² quadrats showed the highest rate of species accumulation (Fig. 1).

Completeness of collection methods was assessed by estimating the effect of additional sampling. Based on the extrapolation of observed curves using the logarithmic model, a doubling of sampling effort (an additional 15 samples) would achieve a 18-22 % gain in species richness at sites with an initial 15 samples (Table 3). The addition of 15 samples from 45 to 60 samples would achieve a 7-8 % gain in species richness.

Frequency distributions for abundance and species richness per sample (Figs. 2a and 2b) were used to compare the collecting efficiency and consistency of pitfall and Winkler sampling (data from the different protocols were combined). Mann-Whitney U tests performed on frequency distribution data for both abundance and species richness revealed

Table 1. List of species collected in pitfall traps and Winkler samples. Data are numbers of ants per species for each sampling method. Species codes only apply to this study.

Species	Pitfall samples		Winkler samples				
	Large	Small	1m ²	½ m ²	¼ m ²	2 x ½ m ²	4 x ¼ m ²
Dolichoderinae							
<i>Tapinoma</i> sp.2	-	1	-	-	-	-	-
<i>Technomyrmex</i> sp.1	3	1	7	1	-	-	-
<i>Technomyrmex</i> sp.2	1	-	-	-	-	1	2
Formicinae							
<i>Anoplolepis</i> sp. 1	13	10	-	-	-	-	-
<i>Camponotus cinctellus</i>	10	-	2	-	-	-	1
<i>Camponotus vestitus</i> (F. Smith)	2	-	-	-	-	-	-
<i>Camponotus</i> sp. 2	1	-	-	-	-	1	-
<i>Lepisiota</i> sp. D	1	-	-	-	-	-	-
<i>Lepisiota</i> sp. 1	-	1	-	-	-	-	-
<i>Plagiolepis</i> sp. 1	1	1	185	17	60	20	100
<i>Plagiolepis</i> sp. 2	-	-	-	-	-	1	-
<i>Polyrhachis</i> sp. 1	-	-	-	-	-	1	-
Myrmicinae							
<i>Meranoplus</i> sp.1	-	-	-	1	2	-	1
<i>Messor</i> sp. 1	2	-	-	-	-	-	-
<i>Monomorium albopilosum</i> Emery	10	3	2	-	-	-	-
<i>Monomorium</i> sp. 2	40	21	-	-	1	-	-
<i>Monomorium</i> sp. 3	6	7	-	-	-	-	-
<i>Monomorium</i> sp. 4	1	-	-	-	-	-	-
<i>Monomorium</i> sp. 5	14	1	6	-	-	1	6
<i>Monomorium</i> sp.8	-	-	6	-	-	4	6
<i>Ocymyrmex</i> sp. 1	28	21	-	-	-	-	-
<i>Oligomyrmex</i> sp. 1	-	-	14	5	28	25	5
<i>Pheidole</i> sp. 1	471	382	168	16	38	39	106
<i>Pheidole</i> sp. 3	4	-	-	-	-	-	-
<i>Pheidole</i> sp. 5	-	2	-	-	-	-	-
<i>Pheidole</i> sp. 6	-	2	-	-	-	-	-
<i>Tetramorium frigidum</i> Arnold	3	-	62	3	3	10	10
<i>Tetramorium sericeiventre</i> Emery	53	30	29	-	-	2	2
<i>Tetramorium</i> sp. 4	-	1	4	1	-	1	-
<i>Tetramorium</i> sp. 5	-	-	2	8	-	4	2
<i>Tetramorium ?setigerum</i> Mayr	-	-	26	-	-	42	3
Ponerinae							
<i>Hypoponera</i> sp. 1	-	-	1	-	2	-	2
<i>Pachycondyla</i> sp. 1	1	3	2	1	-	-	-
<i>Pachycondyla</i> sp. 2	-	-	2	-	-	2	1
Total no. of ants	665	487	518	53	134	154	247

Table 2. Species richness and abundance (total and mean with standard error (SE)) for pitfall traps (62mm and 18mm diameter) and Winkler samples.

Winkler and pitfall sizes	Number of samples	Mean no. ants/ sample (\pm SE)	Total no. of species (unique species)	Mean no. species/ sample (\pm SE)
1 m²	15	34.5 \pm 7.1	16	4.5 \pm 0.5
½ m²	11	4.8 \pm 1.3	9	2.4 \pm 0.4
¼ m²	11	12.2 \pm 4.6	7	1.9 \pm 0.2
2 x ½ m²	13	11.8 \pm 2.7	16 (2)	3.9 \pm 0.5
4 x ¼ m²	14	17.6 \pm 4.4	14	3.2 \pm 0.4
62 mm	15	44.0 \pm 10.0	20 (5)	5.2 \pm 0.5
18 mm	15	32.0 \pm 7.3	16 (4)	3.9 \pm 0.4

significant differences between sampling methods (2 tailed test, $p = 0.001$, and $p < 0.001$ respectively).

Pitfall sampling was more consistent and less variable than Winkler sampling for both number of ants/ sample (Coefficient of Variation (CV %) for pitfalls was 90% while Winklers was 130%), and number of species/ sample (CV % = 39 % for pitfalls, and 73 % for Winkler samples). The majority of pitfall samples had >11 ants/ sample, while the Winkler samples were highly inconsistent (Fig. 2a). Fifty percent of Winkler samples contained five or fewer ants, while there were no pitfall samples with five or fewer ants. This emphasises the relative inefficiency of Winkler sampling where a high effort, yields low output. Pitfalls were highly productive and efficient with 70 % of samples containing >21 ants/ sample.

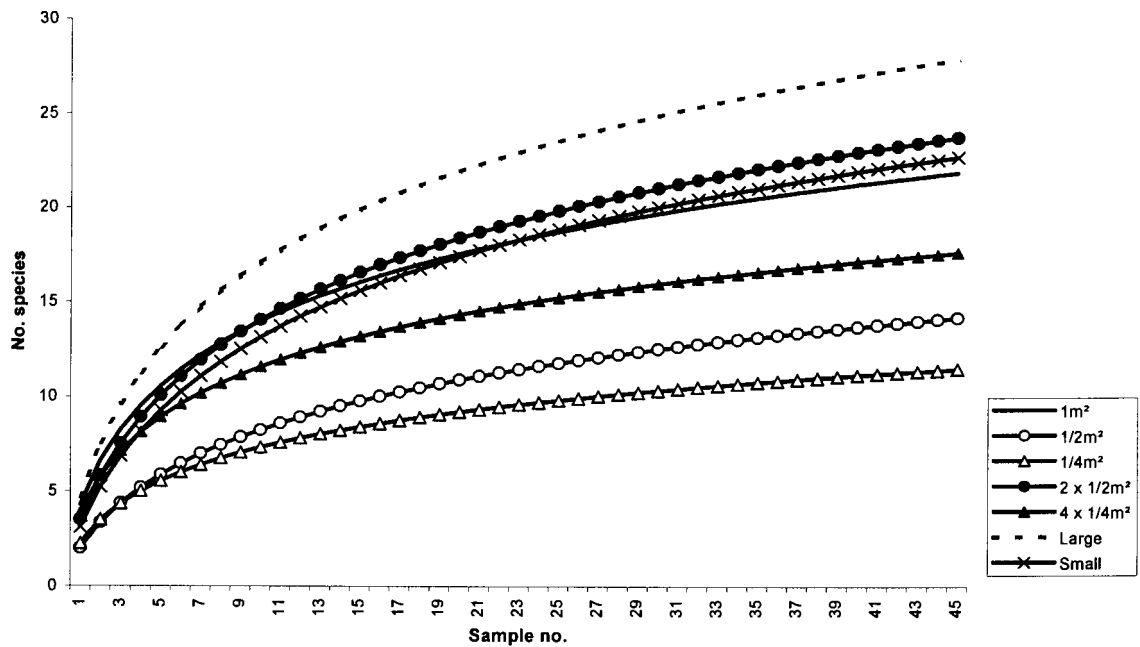


Figure 1. Projection of species accumulation curves for 45 samples using the logarithmic model (Soberón & Llorente 1993) for each sampling technique ($r^2 > 0.996$). Winkler quadrat sizes: 1m^2 , $\frac{1}{2}\text{m}^2$, $\frac{1}{4}\text{m}^2$, $2 \times \frac{1}{2}\text{m}^2$, $4 \times \frac{1}{4}\text{m}^2$. Pitfall sizes: large (62 mm), small (18 mm).

Table 3. The observed number of species for 15 samples and projected species richness at 30 and 45 samples. Projected species richness is based on extrapolation of observed species accumulation curves using the logarithmic model. Pitfall traps: 62 mm and 18 mm diameter.

Winkler and pitfall sizes	Obs. at 15 samples	Extrap. at 30 samples (% increase from <i>15 samples</i>)	Extrap. at 45 samples (% increase from <i>30 samples</i>)
1 m²	16	19.7 (18.6)	21.9 (10.0)
½ m²	9	12.5 (21.9)	14.2 (11.7)
¼ m²	7	10.4 (18.5)	11.5 (9.9)
2 x ½ m²	16	21.1 (21.4)	23.8 (11.4)
4 x ¼ m²	14	16.0 (17.5)	17.6 (9.4)
62 mm	20	24.9 (20.0)	27.9 (10.7)
18 mm	16	20.1 (22.2)	22.7 (11.8)

In the case of species richness/sample there were large differences between the sampling methods (Fig. 2b). More than a quarter of the Winkler samples (28 %) contained one or no species, and more than 50% only had two or fewer species. No pitfall samples contained fewer than two species. Conversely, >50 % of pitfall samples were found to contain more than four species, whereas this was the case in only 22 % of the Winkler samples.

The body size frequency distributions suggested that the mean number of ants/sample for different size classes differed with sampling method. The mean number of ants/sample for size classes 1 and 3 was greatest for 1 m² quadrat Winklers, while pitfall traps had the highest mean number of ants/ sample for size class 4. Only pitfall traps and Winkler 2 × ½ m² quadrats collected ants in size class 7, and the largest ants (classes 8 and 10) were found exclusively in large pitfalls (Table 4). Nonetheless, frequency-size distributions were not significantly different when tested in a pairwise fashion for distributions (Kolmogorov

Smirnov two sample test, $p > 0.05$ in all cases), although this may be a result of small sample sizes.

The number of species in each size class was also determined for each sampling method. Large pitfall traps performed most efficiently; catching a wider range of sizes, and generally more species per class than did the other sampling techniques (Fig. 3). Trends for pitfall sampling and Winkler $2 \times \frac{1}{2} \text{ m}^2$ quadrats were similar, with species richness being greatest in size classes 1-3.

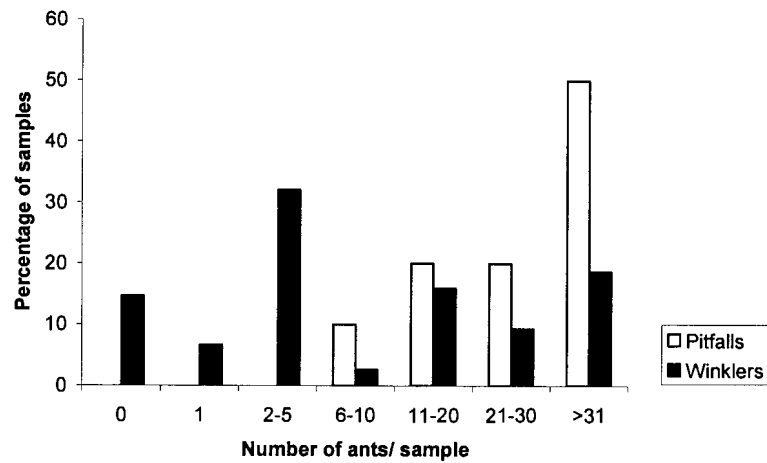
From class 4 onwards, ant species richness was low. Although the mean abundance of ants/ sample for class 1 was greatest with 1 m^2 quadrat Winklers (see above), when the number of species/ size class is considered, pitfall samples contain more species in class 1 than did any of the Winkler samples.

Discussion

In this savanna system, pitfall traps proved more efficient and consistent than Winkler sampling in collecting epigeic ants. Even with a relatively short pitfall sampling period (3 days), dense ground cover on the control plot, and fewer samples (Winkler samples: $n = 75$, pitfall samples: $n = 30$) pitfall traps produced a higher total species richness. More pitfall samples contained ants than Winkler samples, and a greater proportion of pitfall samples contained higher ant abundances, and species richness than Winkler samples. With extrapolation and equal sample sizes, large pitfalls were consistently more effective than all other sampling methods. The $2 \times \frac{1}{2} \text{ m}^2$ quadrat Winklers performed more efficiently than all other Winkler combinations. The fact that large pitfalls performed better than small pitfalls indicates that although pitfall traps may be used in preference to Winkler samples in savanna habitats, they must be of a sufficiently large diameter to allow for good catch.

Pitfall trapping is thought to favour large, mobile ants, while Winkler sampling should be more efficient at collecting smaller, more cryptic ants. This is because small ants are likely to be slower moving due to the nature of their foraging habits (Kaspari & Weiser 1999), and hence more likely to be caught with Winkler litter sampling. This study showed that although there was no significant difference in ant size frequency distribution with the different sampling techniques, some trends could be discerned.

a)



b)

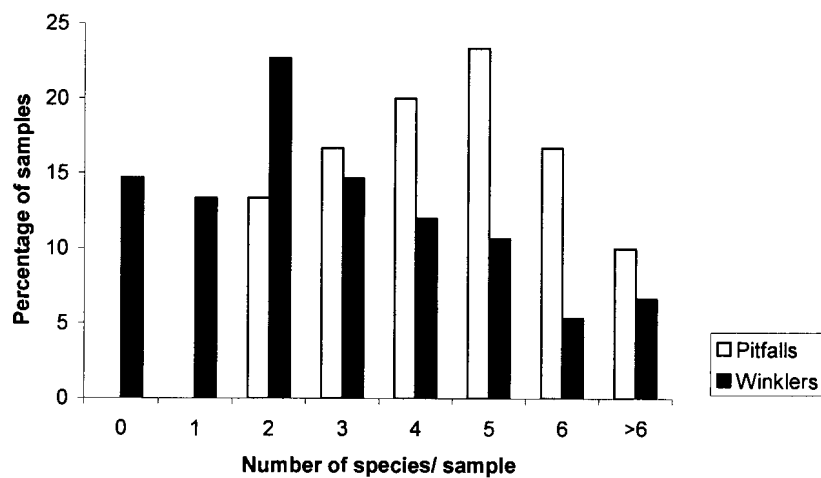
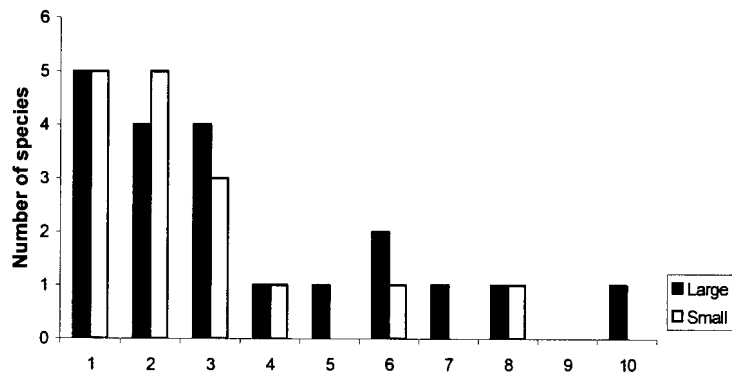


Figure 2. (a) Frequency histogram for the number of ants/ sample for pitfall and Winkler sampling as a percentage of the total samples (Mann- Whitney U 2 tailed-test, $p = 0.001$), (b) Frequency histogram for the number of species/ sample for pitfall and Winkler sampling as a percentage of the total samples (Mann- Whitney U 2 tailed-test, $p < 0.001$).

Table 4. Number of ants/ sample (mean and SE) for each size class for pitfall (62mm and 18mm diameter) and Winkler samples. Size classes (based on head size): **1** = 0.30-0.50 mm, **2** = 0.51-0.70 mm, **3** = 0.71-0.90 mm, **4** = 0.91-1.10 mm, **5** = 1.11-1.30 mm, **6** = 1.31-1.50 mm, **7** = 1.51-1.70 mm, **8** = 1.71-1.90 mm, **9** = 1.91-2.1 mm, **10** = 2.11-2.30 mm.

Size Class	Pitfall and Winkler sizes						
	62mm (n = 15)	18mm (n = 15)	1 m ² (n = 15)	½ m ² (n = 11)	¼ m ² (n = 11)	2 x ½ m ² (n = 13)	4 x ¼ m ² (n = 14)
1	4.13 ± 0.92	2.07 ± 0.56	13.73 ± 5.8	1.47 ± 0.65	6.07 ± 2.65	3.13 ± 1.22	7.53 ± 2.65
2	1.80 ± 0.66	1.20 ± 0.48	0.53 ± 0.4	0	0	0.33 ± 0.16	0.40 ± 0.27
3	4.00 ± 0.95	2.13 ± 0.38	8.67 ± 3.2	0.40 ± 0.34	0.33 ± 0.16	3.80 ± 1.35	1.27 ± 0.33
4	31.40 ± 9.77	25.47 ± 7.28	11.20 ± 2.4	1.07 ± 0.38	2.53 ± 1.19	2.60 ± 0.78	7.07 ± 2.64
5	0.67 ± 0.60	0	1.87 ± 0.6	0.53 ± 0.53	0	0.27 ± 0.15	0.20 ± 0.14
6	0.13 ± 0.09	0.20 ± 0.14	0.13 ± 0.1	0.07 ± 0.07	0	0.07 ± 0.07	0
7	0.13 ± 0.13	0	0	0	0	0.07 ± 0.07	0
8	1.87 ± 0.66	1.40 ± 0.57	0	0	0	0	0
9	0	0	0	0	0	0	0
10	0.13 ± 0.09	0	0	0	0	0	0

a)



b)

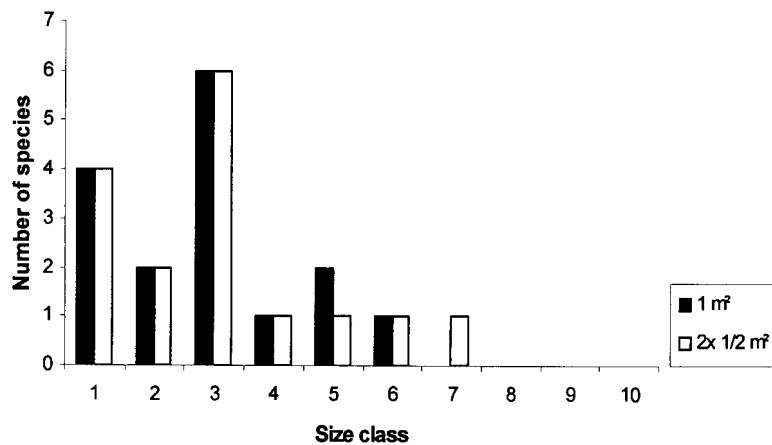


Figure 3. Ant species richness for different size classes: (a) Pitfall traps (62 mm and 18 mm diameters), (b) Winkler sampling. Size classes (based on head size): **1** = 0.30-0.50 mm, **2** = 0.51-0.70 mm, **3** = 0.71-0.90 mm, **4** = 0.91-1.10 mm, **5** = 1.11-1.30 mm, **6** = 1.31-1.50 mm, **7** = 1.51-1.70 mm, **8** = 1.71-1.90 mm, **9** = 1.91-2.1 mm, **10** = 2.11-2.30 mm. Results from Winkler sampling with $\frac{1}{2}$ m², $\frac{1}{4}$ m² and $4 \times \frac{1}{4}$ m² quadrats are not shown.

Thus, in terms of relative abundances of ants, Winkler sampling catches greater numbers of smaller ants than pitfall trapping, and pitfall trapping catches more, larger ants (particularly, in this case, size class 4). Olson (1991) also found that litter samples contained a greater proportion of smaller species.

Winkler sampling was much more time-consuming, and labour intensive than pitfall trapping since samples had to be collected in the field, and processed to extract the ants. Collection of the 75 Winkler samples took approximately six to seven times longer than the digging-in of the 30 pitfall traps. Although the hanging time for the Winklers (48 hours) was less than that for the pitfall sampling (72 hours), it took a total of 6 hours to prepare the bags before hanging. It was expected that the Winkler method would yield different ant species to pitfall sampling because the former method is designed primarily for surveying litter and soil-dwelling species. It was, thus, expected that Winkler sampling would contribute additional information to pitfall sampling through the sampling of different ant communities. However, this was not the case. Firstly, species richness was greater using pitfall traps, even though the total number of pitfall samples was less than the total number of Winkler samples. Secondly, although Winkler sampling is designed primarily for litter sampling and not exclusively for epigeic ants, the catch did not reflect a greater proportion of litter and soil species. There was significant overlap in species caught with the two methods: the number of unique species being much higher with pitfall traps. It is possible that more soil/litter dwelling and cryptic species could be recorded in pitfall traps given a longer sampling period.

When considering Winkler sampling alone, the standard 1 m² quadrat size was not the most efficient and productive (in terms of species richness). Instead, the 2 × ½ m² quadrat collection per Winkler sample was the most productive. By using litter from two quadrats per Winkler sample some of the problems associated with the clumped nest dispersion of ants are addressed. Although the total litter collecting area is kept constant (2 × ½ m² = 1 m²), a wider sampling area is covered and spatial variation is incorporated. The wider range of ant sizes (classes 1-7) collected with 2 × ½ m² quadrats (Table 3) compared to other Winklers lends further support to the use of this Winkler quadrat combination. The 4 × ¼ m² quadrat collection method did not perform as well as the 2 × ½ m² quadrat collection, possibly due to edge effects when collecting litter; total quadrat edge increases as more, smaller quadrats are used which could result in incomplete litter collection.

In addition to the number and size of quadrat used, Winkler sampling could be improved by increasing the number of samples. Furthermore, there appears to be some confusion with the Winkler technique; some studies did not disturb the bags during the hanging period (Didham et al. 1998; Fisher 1998), while others particularly emphasise that contents of the bag should be mixed on at least a daily basis (Besuchet et al. 1987). Mixing and disturbance of the litter material could be important to ensure all ants are active, and improve chances of them falling into the collecting cup, and not remaining within the litter. In this study, the samples were not disturbed and re-mixed daily. The extraction efficiency for Winkler samples should also be determined for the typical hanging period of 48 hours. It is possible that extraction efficiency is affected by length of the hanging period, and other factors such as litter moisture (see Southwood's 1978 discussion on behavioural extraction methods).

Finally, it is worth considering that while Winkler sampling is typically viewed as a qualitative 'relative' method of sampling, useful primarily for inventory-type studies (e.g. Didham et al. 1998; Fisher 1999), it can also be used to produce quantitative results once the extraction efficiency has been determined. Although the present method of collecting Winkler samples cannot be used directly for quantitative purposes, it could be modified slightly to produce quantitative results. Estimates of local densities (animal numbers expressed as a density per unit area of the ground of the habitat (Southwood 1978)) are often used in ecological studies of species abundances (Gaston et al. 1999). Since quadrats of a known size are used to collect litter, Winkler sampling could be used to provide an indication of ant density.

One way that this could be done is to use all the litter collected within the quadrat, instead of only using a maximum of 2 litres of litter in each sample. This would provide an absolute measure of density, since the quadrat size is fixed. There are some practical problems with this approach though. For example, some vegetation types produce vast quantities of leaf litter, and fitting it all in a Winkler bag would be impossible. This could be overcome by increasing the bag size, or putting the litter into several Winkler bags for hanging. An alternative approach is to measure all the leaf litter collected in each quadrat, and calculate what proportion the 2 litres used in the Winkler bag is of this total. Results from the 2 litres could then be used to extrapolate back to determine total ants in the whole litter sample, and

density of ant species. This method assumes that the litter is mixed and homogeneous; something which is particularly difficult to ensure. Since this method depends on evenly mixed litter, it could potentially be quite unreliable.

Many studies using Winkler sampling have been carried out in forests, particularly rainforests (see Olson 1991; Didham et al. 1998; Fisher 1999) where leaf litter typically forms a very thick and continuous ground layer. In such areas, vegetation complexity is likely to influence pitfall catch negatively (Greenslade 1964; Majer 1997; Melbourne 1999), making Winkler sampling the more efficient method of collection for both surface-active and cryptic, hypogaeic ant species. Some rainforest studies have demonstrated that Winkler sampling can replace pitfall trapping entirely (e.g. Fisher 1999). In contrast, in more open, patchy and less complex environments, that have variable litter loads, such as savannas, it appears that pitfall traps perform better, and reduce the usefulness of Winkler sampling in adding new species. It is also worth noting that studies comparing pitfall and Winkler sampling efficiencies (e.g. Olson 1991; Fisher 1999) use only small pitfall sizes (18mm diameter). It is highly probable that with a larger pitfall diameter, sampling efficiency would have increased. Moreover, if the sampling period for pitfalls is short (e.g. 48 hours, Olson 1991), catch will be affected.

In summary, pitfall sampling alone is more efficient, productive and consistent than Winkler sampling for epigaic ants in this savanna system. Where constraints limit sampling to one technique, the most appropriate method for ant collection in such habitats is pitfall trapping. When using Winkler sampling alone, we suggest collecting litter from several quadrats for each sample (e.g. $2 \times \frac{1}{2} \text{ m}^2$) instead of 1 m^2 may reduce the problem with clumped ant dispersions. Winklers may be used quantitatively to provide some indication of density, although it must be recognised that extraction efficiency and the exact number of quadrats required for a particular area should be determined in a pilot study.

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Chapter 3

Competition and dominance in savanna ants

The important thing in science is not so much to obtain new facts as to discover new ways of thinking about them.

- Sir William Bragg

Introduction

Although it is now widely appreciated that regional scale processes determine the potential membership of local assemblages (Ricklefs 1987; Gaston 2000; Godfray & Lawton 2001), how membership of an assemblage is finally determined remains contentious. Membership may be a consequence of highly stochastic processes such as random colonisations (see Gaston 2000), or it may be the outcome of more deterministic processes such as the operation of a set of assembly rules (Weiher & Keddy 1999). Depending on the taxon and system concerned, interspecific competition may be an important local process structuring the assemblage, may be negligible relative to other processes, or may simply not occur (see Connell 1983; Gurevitch et al. 1992). In ants, interspecific competition is thought to be a key mechanism structuring local assemblages, and it has been referred to as the ‘hallmark of ant ecology’ (Hölldobler & Wilson 1990). Support for interspecific competition includes spatial ant mosaics (Room 1971; Majer et al. 1994), behavioural dominance hierarchies (Savolainen & Vepsäläinen 1988), territoriality (Fox et al. 1985; Andersen & Patel 1994), antagonistic behaviour (Andersen et al. 1991), and spatial and temporal changes in ant co-occurrence patterns (Sanders et al. 2003) (but also see Ribas & Schoereder 2002; Gibb 2003).

The ‘dominance-impoverishment rule’ (Hölldobler & Wilson 1990) describes the relationship between ant species richness and dominant species in an assemblage: the fewer ant species in a local assemblage, the more likely it is to be behaviourally dominated by one or two species with large, aggressive colonies. In many studies, however, the direction of this causality has been reversed, and emphasis has been placed on the effect dominants have on species richness, not *vice versa* (e.g. Andersen 1992; Andersen & Patel 1994; Morrison 1996; Retana & Cerdá 2000; Farji-Brener et al. 2002). The effect of dominance on species richness was examined in detail by Andersen (1992), who suggested that at baits, the full relationship between species richness and dominance is unimodal. With a unimodal relationship, species richness is low at very low levels of dominance, and as dominance increases species richness

also increases until a point is reached after which species richness declines. The ascending portion of the curve is thought to correspond to increasing habitat favourability for ants: in conditions considered marginal (or stressful) for ants, species richness and the abundance of dominant ants are low. As conditions begin to improve, the abundance of all ants begins to increase, and so does species richness (see also Andersen 1995, 1997a). The descending part of this relationship is generally attributed to an increase in the abundance of dominant ants to such an extent that they reduce species richness via competitive exclusion (Andersen 1992; Morrison 1996).

Although Andersen (1992, 1997a) suggested that the form of the dominance-species richness relationship is unimodal, to our knowledge there has only been one other study (Morrison 1996) explicitly exploring this pattern at baits. Morrison (1996) used removal experiments to demonstrate that the presence of dominant ants at baits decreased species richness. However, only the descending part of the unimodal relationship was evident. Thus, the question of whether this pattern applies generally at baits remains unclear.

While a unimodal or negative monotonic decline might indicate competition (see Andersen 1992; Morrison 1996), the question of whether other mechanisms can give rise to the unimodal pattern has not been addressed. First, with the ascending portion of the curve, an alternative explanation to that of stress is that high species richness and low dominance are only possible with a completely even abundance frequency distribution. With an even abundance frequency distribution, individuals would be distributed evenly amongst species, which would result in low dominance, since all species would have similar abundances. Put simply, area A on Figure 1 might only be filled if the assemblage has an abundance frequency distribution which is unrealistic (see for example Gaston & Blackburn 2000). Thus, the observed ascending part of the unimodal relationship is constrained to assume that form irrespective of the influence of habitat adversity or stress. Second, although competition has been assumed to reduce species richness at high dominance levels, an alternative explanation for this pattern is that high dominance and high species richness (Fig. 1, area B) are only possible with a very highly skewed abundance frequency distribution, which is again generally considered unrealistic in most natural communities, but particularly for insects (Halley & Inchausti 2002). This is because if one species is highly abundant and the others have very low abundances, over time it is very probable that species with low abundances

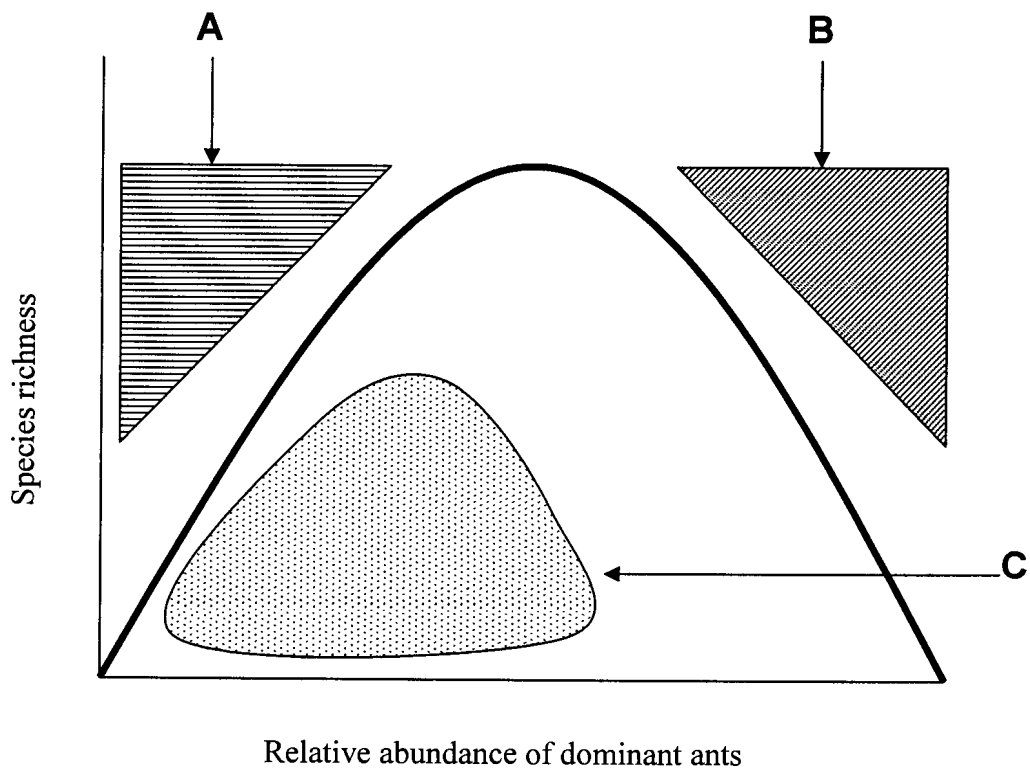


Figure 1. Graphical representation of the unimodal relationship between dominance and species richness: A) Low dominance and high species richness, B) High dominance and high species richness, C) Low to intermediate dominance and low species richness.

would go extinct (for discussion of abundance-extinction relationships see Gaston & Chown 1999).

Finally, none of the studies concerned with the unimodal relationship have considered variability about this pattern (Fig. 1, area C), and in consequence the cause of scatter around the unimodal pattern is not known. A potentially important factor that has received little attention in relation to ant dominance-species richness relationships is environmental patchiness. This omission is surprising given that natural systems are typically patchy, and environmental heterogeneity has been shown to be important in structuring communities (e.g. Kolasa & Rollo 1991; Li & Reynolds 1995; Wiens 2000).

Although interference competition might be responsible for setting limits to species richness at baits, it is not clear whether this is also the case at the whole assemblage level. That is, whether interspecific competition from dominant ants also translates to the control of resources and the regulation of richness at the assemblage level (Andersen & Patel 1994; Sanders & Gordon 2000; Ribas & Schoereder 2002; Gibb 2003). However, if interspecific competition, via behavioural dominance, is an important factor regulating 'momentary diversity' at baits (see Andersen 1992), it might be expected that competition also has a large influence on the whole assemblage level pattern.

Here we explore each of these issues in turn by 1) examining dominance-species richness patterns across a range of baiting trials on three continents (including within- and between-habitat comparisons), 2) modelling the distribution of ants amongst baits using a variety of realistic and unrealistic assemblage scenarios, and 3) comparing patterns at baits with those at the assemblage level for a system where dominance at baits has been established.

Methods

Study sites

South Africa

Baiting and pitfall data were collected in the Kruger National Park (KNP), South Africa in three savanna habitat types along a rainfall gradient: *Mopane* woodland (Mopane area, 23°33'S 31°26'E), *Acacia* savanna (Satara area, 24°26'S 31°46'E) and *Terminalia* woodland (Pretoriuskop area, 25°12'S 31°23'E). Mean annual rainfall is lowest in the Mopane area (450-

500 mm), intermediate in the Satara area (550 mm), and highest in the Pretoriuskop area (700 mm) (Gertenbach 1983).

Ant sampling was carried out on experimental burn plots that form part of a long-term burning experiment initiated in 1954; unburned plots have had no fires since then. Plots are approximately 7 ha in size, and are separated by fire-break roads (Trollope et al. 1998). Within each habitat type, seven treatment plots representing a range of burn histories (including the two extreme treatments, unburned and annually burned) were replicated twice. Unburnt plots are densely vegetated with moribund grass, and a well-developed litter layer, whereas annually burned plots are more open, with reduced ground cover and fewer trees (see Parr & Chown 2001; Parr et al. in press).

Australia and North America

In Australia, baiting data were collected at sites varying in structural complexity of the vegetation, and included sites in tropical savanna woodland (Darwin, Northern Territory, 12°40'S 131°00'E), and in open semi-arid savanna (Kidman Springs Research Station, Northern Territory, 16°18'S 133°48'E). The mean annual rainfall for Darwin is 1700 mm, while at Kidman Springs it is 650 mm (Commonwealth Bureau of Meteorology). In North America, baiting was carried out at sites centred in the Chiricahua Mountains of south eastern Arizona (31°52'N 109°15'W), situated along an elevation gradient (1400-2600 m a.s.l.), covering a variety of habitats from desert scrub to fir forest. Results from this latter study are published in Andersen (1997b).

Field sampling

South Africa

Both baiting and pitfall trapping fieldwork in South Africa were conducted in the summer months of late November 2001– early February 2002. In the summer rainfall region of South Africa, ants are most active and abundant at this time (e.g. Swart et al. 1999; Lindsey & Skinner 2001). Ant baiting was carried out on unburnt and annually burned plots, replicated twice in each of the three savanna habitats. The relative behavioural dominance of species was quantified using observations of ants at fish baits (see Fellers 1987; Savolainen &

Vepsäläinen 1988; Andersen 1992). Baiting was conducted in the early morning, midday and late afternoon, and for each time period was repeated at least three times.

For each bait session, fifteen bait stations were set out at 5 m intervals along a 70 m transect. A teaspoon of cat food (≈ 10 g, pilchard fish) was placed on a small white piece of paper (to aid observations at the bait), and all species present at each bait after 60 minutes were recorded. Following Andersen (1997b), abundances of ants were scored according to a six point scale: 1 = 1 ant, 2 = 2-5 ants, 3 = 6-10 ants, 4 = 11-20 ants, 5 = 21-50 ants and 6 = >50 ants. A species' abundance per baiting session was defined as the total of its abundance scores summed across the 15 baits. The total abundance (all species combined) during a baiting session was the sum of each species' total abundance for each bait station. Because dominants do not co-exist at baits, the total maximum abundance of dominants per baiting session was 90 (abundance score of 6 \times 15 baits). For all other ants combined, it is possible to have a total maximum abundance per baiting session of >90 because each species' abundance was scored separately, and often there was more than one subordinate species at a bait.

Pitfall trapping was also carried out in each savanna type. In addition to the annually burned and unburnt plots, pitfall sampling in Satara and Mopane was carried out on the five other burn plot types (replicated twice). In Pretoriuskop, pitfall trapping was only carried out on annually burned and unburned plots. On each plot, a total of 20 pitfall traps was laid out in a grid (5 \times 4) with 10 m spacing. All grids were situated at least 50 m from the plot edge to reduce the possibility that ants from adjacent areas were collected in the traps. Pitfall traps had a diameter of 62 mm, and contained 50 ml of a 50 % solution of propylene glycol. Propylene glycol has been shown to neither attract nor repel ants (Adis 1979). All traps were left open for a period of five days. A pilot study indicated that this period of time is sufficient for reasonably complete sampling, and avoids the problem of collecting excessively high numbers of ants. Although the study was conducted during the rainy season, there was no rain while the pitfall traps were open, and the weather was hot and humid. Voucher specimens of South African ants collected with baiting and pitfall trapping are held at the Iziko South African Museum.

Australia

In Australia, sampling was carried out during the build-up to the wet season (November 2002), a period when most ants are highly active (Andersen & Patel 1994). The relative behavioural dominance of species was quantified using observation of ants at fish baits (canned fish-based cat food). Baiting was conducted in the morning and late afternoon avoiding extreme midday temperatures, following the same method as described above. Pitfall trapping was not carried out. Voucher specimens of Australian ants are held at CSIRO, Tropical Ecosystems Research Centre, Darwin.

North America

Baiting was carried out in July 1993. The baiting protocol involved using tuna fish baits arranged in a grid (5 × 3) with 10 m spacing, and all species at the bait after 60 minutes were recorded according to the same abundance scores described above. A detailed description is provided in Andersen (1997b).

Data analysis

Although there are no standard criteria for identifying dominant ants, dominance is usually either defined in terms of ecological dominance (a higher number of individuals), or behavioural dominance (displays of aggression towards other species such that they exhibit avoidance behaviour) (see Andersen 1992, Cerdá et al. 1997). This study focused on ecological dominance to define dominant ants. Thus, dominant ant species are considered those that occurred at a large proportion of baits, numerically dominated and monopolised many of the baits where they occurred, and had high mean abundance scores (see Andersen 1992; Morrison 1996; Cerdá et al. 1997). Although behavioural dominance was not explicitly tested for using observations of interspecific interactions at baits to produce a dominance index (see Fellers 1987), any interspecific aggression that was observed was noted. Dominant species were identified, and general dominance levels for each area were determined using the following criteria (see Andersen 1992, 1997b; Morrison 1996; Cerdá et al. 1997): 1) number of baits monopolised with >20 individuals of a species, and 2) high mean abundance score. Pitfall dominance per plot type was calculated by summing the abundances of those species identified from the baiting trials as dominants.

To determine the relationship between species richness and dominance, linear ($y = ax + b$) and quadratic regressions ($y = ax^2 + bx + c$), where y is species richness and x is the relative abundance score of dominants) were fitted to the data. Where both regressions were found to fit the data, the regression model with the best fit (determined by R^2 value) was chosen.

Modelling ants at baits

A model was developed using VisualBasic to simulate the distribution of ants at baits, and to determine what conditions are necessary to generate different dominance and species richness combinations. The model consisted of two parts: a null model where there is no competitive exclusion at baits (i.e. the mechanism being tested is deliberately excluded, see Gotelli 2001), and a second model incorporating some degree of competitive interaction between ant species. Both model types (hereafter referred to as Null and Competitive), used 14 ant species, and up to 15 baits. These values were chosen because in KNP the maximum number of species recorded during a baiting session was 14, and 15 baits were deployed. The total abundance of ants in the model starting pool (a) ranged from 50-2500.

Numerically dominant ant species were identified either as those that had high mean abundance scores, or those that monopolised a high percentage of the baits at which they occurred, or both, depending on the model specifications (see also Andersen 1992, 1997b; Morrison 1996; Cerdá et al. 1997). For a species to monopolise a bait it had to be the only species at the bait, and there had to be >20 individuals of that species at the bait (i.e. score of >4 in the system developed by Andersen 1997b). Both measures were calculated only for baits where species are recorded, and thus zeros (species absences) in the data were excluded. This is common practise in ant studies, and therefore importantly enables direct comparison of the results from this modelling exercise with studies that have investigated dominance-species richness patterns (e.g. Andersen 1992; 1997b, Cerdá et al.1997).

For each species, a mean abundance score was calculated by dividing the sum of the abundance scores for the species at all baits by the number of baits at which the species was present. For each species, the percentage of baits monopolised (excluding zeros) was calculated. Dominant species were classified as those with a mean abundance of >3.21, or that

monopolised >21.9% of baits, or both depending on model specifications. These values were based on thresholds from field baiting data (see Table 1).

Each individual in the starting pool was randomly assigned to one of the 14 species based on a specified abundance frequency distribution. The three different abundance frequency distributions used for the models were: 1) an ecologically unlikely *even* distribution: all ants had an equal probability of being assigned to any species, 2) a more likely, but somewhat unusual (see Gaston & Blackburn 2000), highly *skewed* distribution: most of the ants in the starting pool were assigned the same species, whilst a very small number of ants were assigned equally to the other 13 species, 3) a *realistic* distribution: ants were assigned to species according to a Poisson distribution (most species are not highly abundant, with most being much less abundant than the most abundant species). This distribution was derived from an abundance frequency distribution for pitfall trap data from all areas sampled in KNP combined. Because abundance frequency distributions for each area were similar, this represents an abundance frequency distribution that is realistic for the assemblages in the field.

Once an individual from the pool had a species identity, this individual was then assigned to a bait. Depending on the model specifications, to assign individuals to baits either a random, even distribution (equal chance of being assigned to any bait), or a weighted random distribution (chance of being assigned to a bait is not equal because some baits are more likely to attract ants than others due to factors such as differing proximity of baits to nests) was used. Both bait distributions also incorporated a variable number of baits that could be occupied (see Table 2). Aggregated distributions, which are common in nature, are often best described by the negative binomial distribution (NBD) (see Pielou 1977, Taylor et al. 1978, Warren et al. 2003). The parameter k of the NBD was calculated to determine if the abundance scores of ants at real baits (using KNP field data for each area separately and combined) were aggregated (i.e. where abundance at one bait is high, whether surrounding baits are also likely to have high abundance scores). All values for k were, however, relatively high (3.8 - 6.14) (see Warren et al. 2003), which indicated abundance scores at baits were more random than aggregated. Moreover, because the frequency distribution for abundance scores did not differ significantly from a Poisson distribution, this distribution was used for the weighted assignment of ants to baits.

Table 1. Occurrence of dominant and subordinate ants at baits in KNP (Data are for morning and afternoon readings only). M = Mopane, S = Satara, P = Pretoriuskop (Total number of baits (n) = 1485: Mopane n = 510, Satara n = 525 and Pretoriuskop n = 450)

	% Baits recorded			% Baits monopolised			Mean abundance score*		
	M	S	P	M	S	P	M	S	P
Dominant									
<i>Pheidole</i> spp.	27.5	53.0	17.8	35.7	60.8	40.0	3.80	4.06	3.21
<i>Crematogaster</i> spp.	6.9	1.1	30.0	54.3	50.0	23.0	4.09	4.93	3.62
<i>Myrmecaria natalensis</i>	11.2	14.5	19.3	64.5	33.3	33.3	3.36	4.22	3.30
<i>Anoplolepis custodiens</i>	-	1.7	5.1	-	88.9	26.1	-	3.93	4.06
<i>Monomorium emeryi</i>	8.8	-	-	55.6	-	-	3.88	-	-
Non-dominant									
<i>Camponotus</i> spp.	11.8	5.1	14.0	3.3	0	1.6	1.45	1.53	1.55
<i>Polyrhachis</i> spp.	5.9	11.0	18.7	0	0	0	1.46	1.52	1.39

* Mean abundance scores range from a possible minimum of 1 (always a single ant recorded whenever the species occurred) to a possible 6 (always > 50 ants whenever the species occurred)

Table 2. Dominance measures, and degree of patchiness used in each of the models.

Model	Dominance measure			Patchiness type		
	Mean abundance ONLY	Monopolisation ONLY	Mean abundance AND monopolisation	Bait distribution - even	Bait distribution - weighted	Number of baits limited (2-15 baits)
<i>Null 1</i>			X	X		
<i>Null 2a</i>	X			X		
<i>Null 2b</i>		X		X		
<i>Null 3</i>	X				X	X
<i>Competition 1</i>			X	X		
<i>Competition 2</i>			X	X		X
<i>Competition 3</i>			X		X	X

Once all ants in the starting pool had been assigned to baits, raw abundances for each species at each bait were transformed to abundance scores based on the same scoring system (0-6) used in Andersen (1997b). The abundance scores of all species meeting the specified criteria for dominance were summed (total abundance score for dominants), and species richness was determined for all baits occupied. To explore a reasonably broad range of outcomes possible for each model, each simulation was iterated 100 times. All dominance and species richness values obtained from the 100 iterations were then plotted to determine how the relationship varied; these values often converged on the same value, although this was not always the case.

Null Model

In these models there were no rules restricting the number of ants at baits, thus no structuring mechanism is implied. Individuals were assigned to species using all three abundance frequency distributions. In model *Null 1*, for a species to be classified as dominant, it was required to meet both the abundance and monopolisation dominance criteria. In *Null 2a* and *Null 3*, a species was classified as a dominant based only on the mean abundance threshold (i.e. a species was classified as dominant if it had a mean abundance score of >3.21 , but monopolisation was not considered). In *Null 2b*, a species was classified as a dominant based only on the percentage of baits that were monopolised (i.e. a dominant species had to monopolise $>21.9\%$ of baits where it occurred, but the mean abundance score was not considered). Ants were assigned to baits using either an even or a weighted bait distribution (Table 2). Model *Null 2a* had an even bait distribution, while *Null 3* had a weighted bait distribution, and the number of baits occupied was limited.

Competitive Model

Competition was incorporated into the model using two rules. First, the number of species that could co-occur at a bait was restricted to four (based on the maximum number of species found at a bait during field baiting in KNP), and second, if the abundance of a species at any bait was >20 (i.e. abundance score of >4), no other species were allowed to co-occur at the bait. All ants from other species at that bait were removed, and returned to the pool to be re-allocated to species and baits. The model did not allow for insinuator, that is, subordinate species that are able to co-exist at baits with high numbers of dominants (see Wilson 1971).

In all competitive models, dominance was determined using both mean abundance and monopolisation dominance measures. In model *Competition1*, all 15 baits were occupied according to an even distribution across baits. Patchiness was introduced into the model in two stages. First, model *Competition2* limited the number of baits that could be occupied (2-15 baits depending on the model specification), whilst keeping the distribution at baits uniform, and second, additional patchiness was introduced in model *Competition3*, such that the number of baits that could be occupied was limited (2-15 baits) and ants were assigned to baits using a weighted distribution (Table 2). Although competition, which can create monopolisation at baits, is factored into these models by setting the threshold for the abundance at which species cannot co-occur to >20 individuals (abundance score of 4), highly aggressive species at the top of the dominance hierarchy may only require a few individuals to effectively control a bait. Thus the final model, *Competition4*, was based on *Competition3*, but simulated the effect of increasing competition by using a threshold of >10 ants/ bait (rather than >20) to limit co-occurrence for the monopolisation rule. Decreasing the threshold for abundance of ants necessary for monopolisation thus simulates the effect of increased competition.

Sensitivity analyses were performed using *Competition 1*, and the model re-run with mean abundance score thresholds of 2.8 and 3.8, and monopolisation percentage threshold set at 15 and 30%.

Results

Field data: Baiting

A total of 69 ant species was recorded at the baits in South Africa with 38, 36 and 49 species occurring in the Mopane, Satara and Pretoriuskop areas of KNP respectively. *Pheidole* (including *P. megacephala*), and *Crematogaster* spp., *Myrmecaria natalensis*, *Monomorium emeryi*, and *Anoplolepis custodiens* fulfilled the criteria for dominants: they were responsible for most of the monopolisation at baits and had the highest mean abundance scores per area (Table 1). In addition, *Pheidole* and *Crematogaster* spp. were observed aggressively displacing other ants from the baits in all areas, but the opposite was never found. Thirty-three species of ants were recorded at baits in Australia, and 83 species in North America.

Using baiting data, the dominance-species richness relationship was unimodal at all levels: within and between habitats, and between continents (Fig. 2). In Satara, dominance was higher on annually burned plots (open habitat) than unburnt plots. Species richness generally increased with increasing dominance on unburnt plots, but decreased with a continued increase in dominance on annually burned plots (representing the descending side of the pattern) (Fig. 2a). When all three habitats were combined, the upper bound was unimodal, but when species richness was low, dominance levels were highly variable ranging from very low to very high, and variation in species richness was greatest at intermediate levels of dominance. The upper bound also indicates a threshold (abundance score of dominants between 30-40), beyond which species richness declined as dominance increased (Fig. 2b).

Although the dominance-species richness relationship is unimodal when baiting data from South Africa, Australia and North America are combined (Fig. 2c), the relationship is similar to Fig. 1b, with a distinct unimodal upper bound, and considerable variation in richness for a given dominance level, especially at intermediate dominance values.

Field data: Pitfall trapping

A total of 164 species was collected with pitfall trapping in South Africa with 69, 111 and 89 species recorded in the Mopane, Satara and Pretoriuskop areas of KNP, respectively. Dominant species were based on results from baiting (see above for species descriptions). Data from pitfall trapping in KNP shows a clear unimodal pattern (Fig. 3). Mopane data points cluster to the left-hand side of the graph, and those for Pretoriuskop are slightly left of centre, but suggestive of a positive relationship, and those of Satara appeared humped with several data points on the far right hand side, indicating high dominance.

Model results

Null

Random, unrestricted assignment of ants to baits means that monopolisation of baits (according to the threshold specified in the model) does not occur (there will either always be at least one other species present at any given bait, or abundance will be so low that the threshold of >20 individuals set for monopolisation will not be reached). Hence, in models

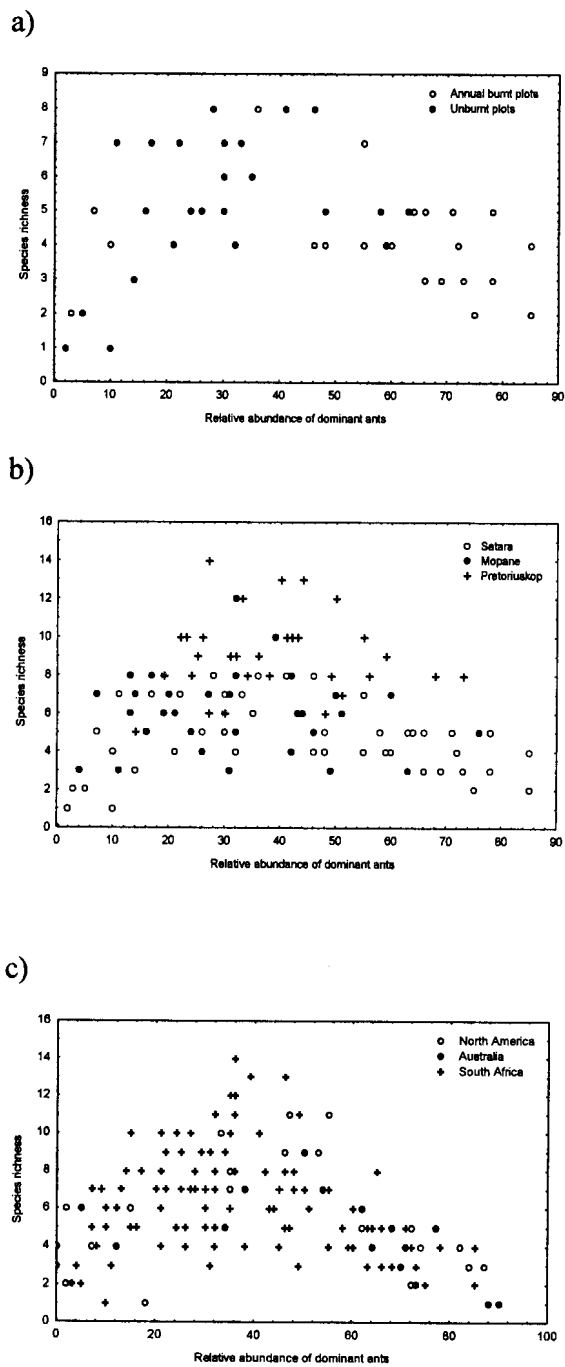


Figure 2. Relationship between species richness and the abundance score of dominants at baits for (a) within habitat at Satara (Quadratic regression; $y = -0.003x^2 + 0.21x + 1.63$, $R^2 = 0.49$, $p < 0.001$), (b) between habitat using all three habitat types in KNP (Quadratic regression: $y = -0.003x^2 + 0.27x + 2.25$, $R^2 = 0.33$, $p < 0.001$), and (c) continental comparison of Southern Africa, Australia and North America (Quadratic regression: $y = -0.003x^2 + 0.22x + 3.37$, $R^2 = 0.39$, $p < 0.001$). Each data point represents total species richness and total dominance for 15 baits.

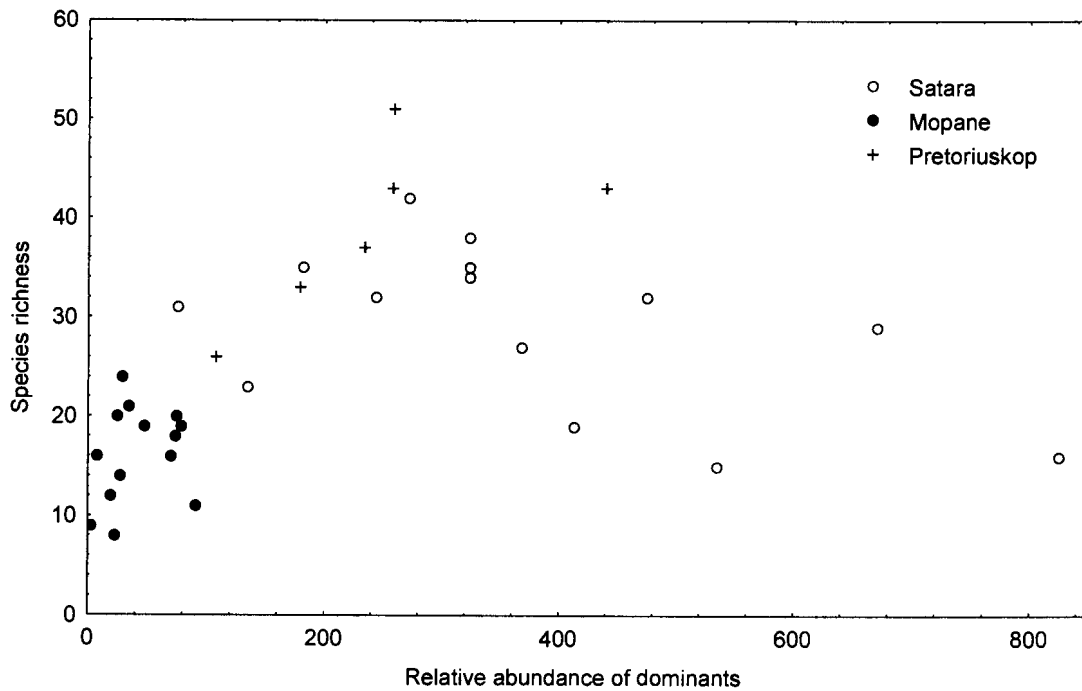


Figure 3. Relationship between species richness and abundance of dominant ants across three habitat types in KNP, using pitfall trap data (based on grid of 20 pitfalls per plot) (Quadratic regression: $y = -0.0001x^2 + 0.12x + 12.8$, $R^2 = 0.55$, $p < 0.001$).

Null 1, and *Null 2b*, there is no dominance. Thus, when there are no competitive rules, dominance can only be quantified using mean abundance score. Therefore, only models using mean abundance score are considered below.

For all frequency distributions and null model scenarios, because there are no rules limiting dominance levels, the maximum dominance attainable is dependent on the starting abundance (and the number of baits). This is because at lower abundances, there are insufficient ants (once distributed among species and baits) for any ant species to be classified as dominant based on mean abundance score. When the abundance of ants (a) is sufficiently large, dominance can be attained, but it is unrealistically high. With an even distribution and 15 baits occupied dominance is only achieved when the starting abundance of ants is very large (when a threshold abundance of approximately 2000 is reached) (Fig. 4a). When individuals are assigned to species using skewed (Fig. 4b) and realistic distributions (Fig. 4c), the outcome is high species richness (13-14 species), and a range of dominance values from the minimum to very high (>90). As the abundance of ants increases, dominance also increases.

There was much greater variation in species richness with the null model which incorporated both types of patchiness (*Null 3*). With an even distribution, the abundance of ants required for dominance is low when there are a small number of baits occupied (e.g. for dominance with 5 baits occupied, the minimum a value required for dominance is approximately 500). However, if all baits are occupied dominance is only possible with very high abundances (Fig. 5a and b). While dominance varies however, species richness does not, and remains at 14 species regardless of abundance of ants, or number of baits occupied.

When the number of baits that can be occupied is held constant, the effect of decreasing a is reduced dominance and lower, more variable species richness (Fig. 5c-f). For both a skewed and realistic abundance frequency distribution, as the number of baits increases, dominance also tends to increase (Fig. 5c and e). In addition, as the abundance of ants decreases (Fig. 5d and f), species richness becomes lower, and a wider range of values is produced, although this is more pronounced for a skewed distribution.

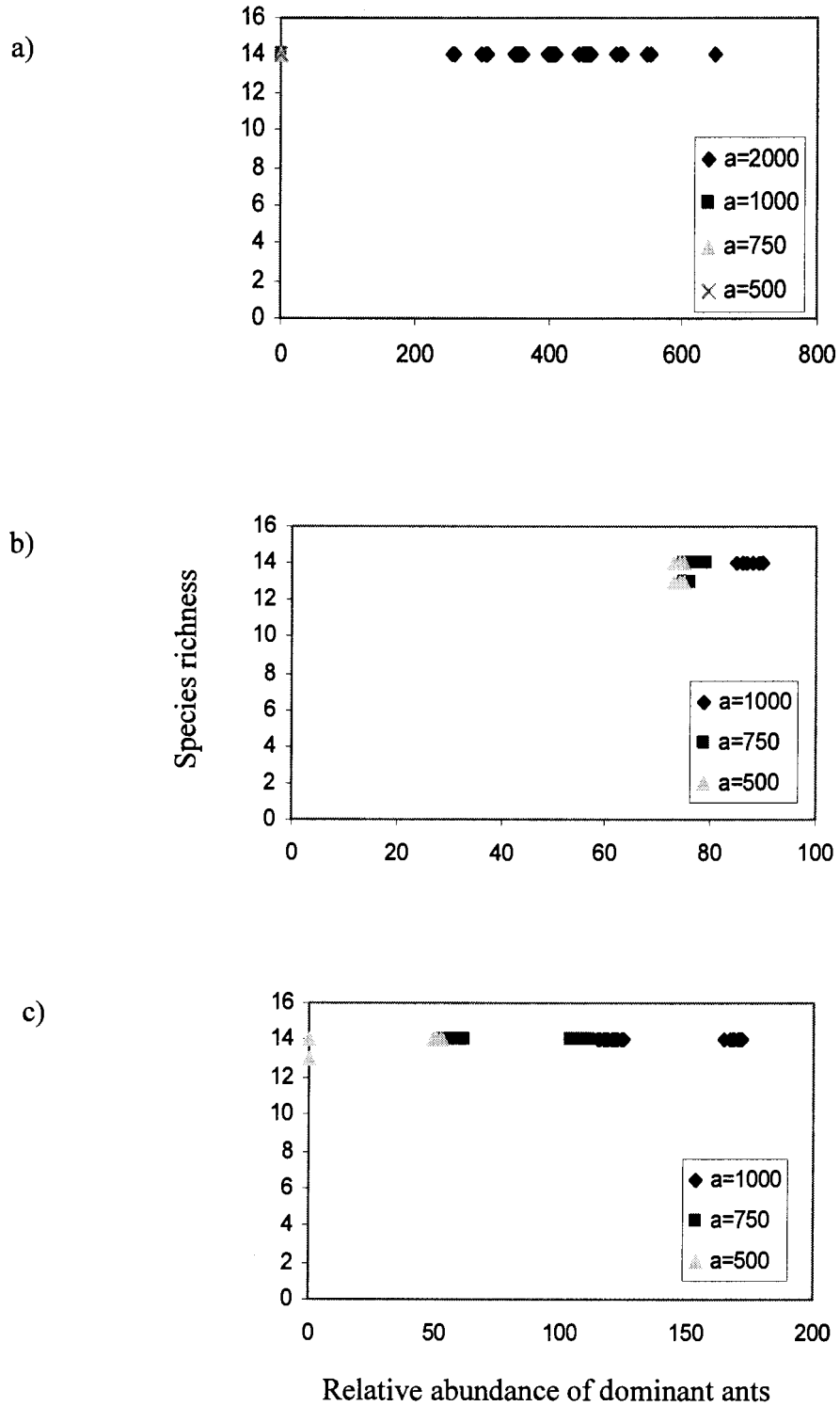


Figure 4. Relationship between species richness and abundance score of dominant ants for three species abundance frequency distributions using a null model where dominance is based on mean abundance score only: (a) even distribution, (b) skewed distribution, (c) realistic distribution. Data points are the results from 100 iterations for a particular starting abundance (a), and number of baits occupied. Starting values for a ranged from 500-2000.

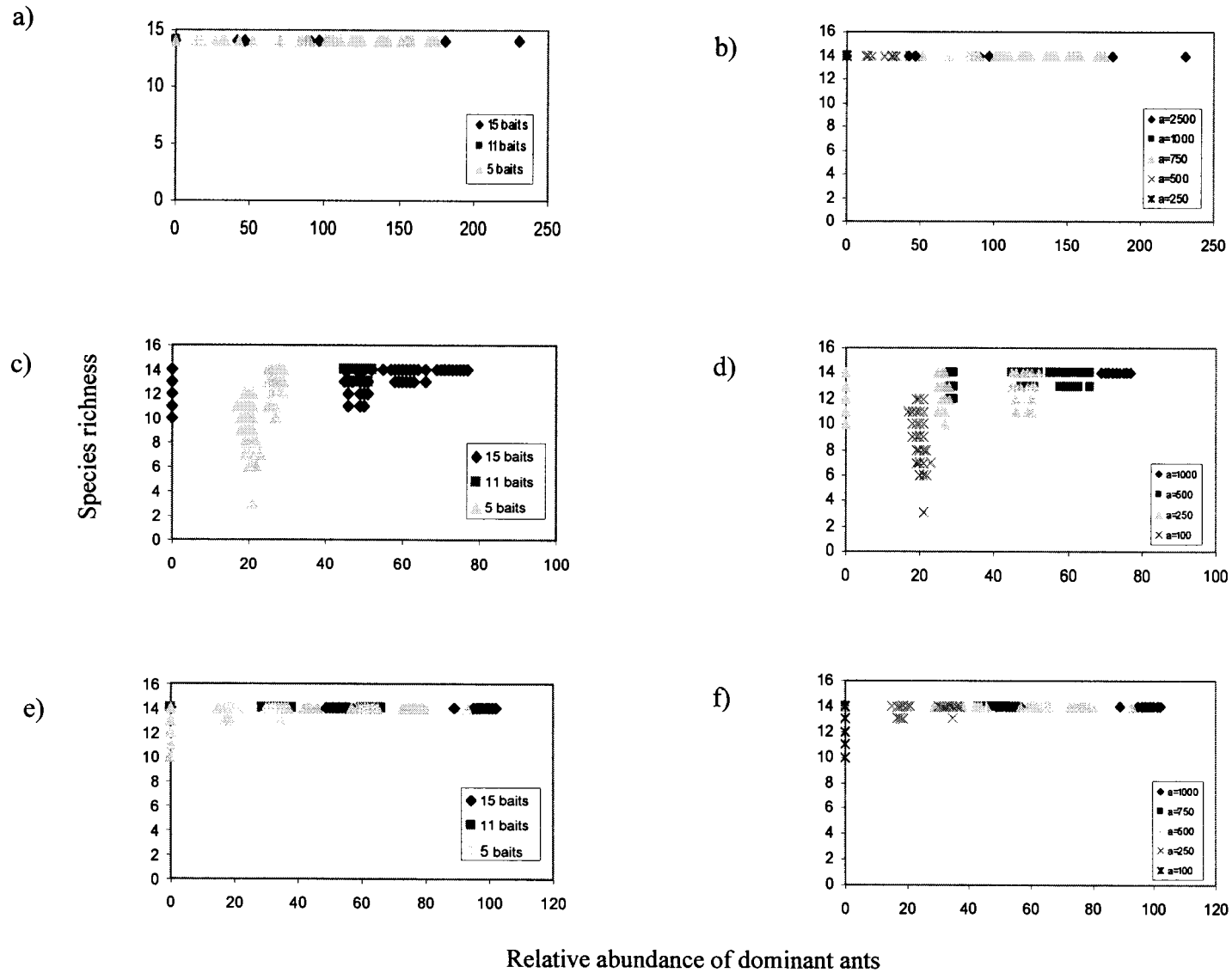


Figure 5. Relationship between species richness and abundance score of dominant ants for three species abundance frequency distributions using a null model, which includes patchiness within baits, and alters the number of baits that are occupied. For each frequency distribution the same data are presented first as number of baits occupied (variable a) (Figs a, c, e), and second, as starting abundance, a , (with variable number of baits occupied) (Figs b, d, f). Even distribution = a and b; skewed distribution = c and d; realistic distribution = e and f. Number of baits occupied: 5, 11 and 15 baits. Starting values for a ranged from 100-2500.

Competition 1

When all 15 baits are occupied, the three frequency distributions produce quite different results (Fig. 6). As with subsequent models, dominance values of zero are possible with any frequency distribution. Zero dominance values are a function of the size of a ; when a low starting abundance of ants is specified, there are not enough individuals, for the mean abundance score to be >3.21 , and for a species' score at a bait to be >4 (necessary to meet monopolisation rule) and thus, dominance values >0 are impossible because the dominance criteria are not met.

For all frequency distributions, the effect of varying the abundance of ants was that dominance tended to increase with increasing abundance (Fig. 6a-c) (although there was sometimes considerable variation in species richness and dominance values for a given a). With an even distribution, it appears that either dominance is low and richness high, or both richness and dominance are high (Fig. 6a). The latter was a function of excluding the zeros when analysing the dominance measures per species. Because species absences were excluded from the analyses when calculating dominance, a situation may occur with an even distribution where all or the majority of species, are classified as dominants. In such instances, these data points can effectively be discounted because in reality it is extremely unlikely that all species would be equally dominant. If all species are equally dominant, there is in effect, no dominance (rather there is a high level of equality). Dominance was high, and species richness low with a skewed distribution (Fig. 6b). The range of dominance values was much wider for a realistic distribution (Fig. 6c), and species richness ranged from low to the maximum (14 species). Species richness also decreased with increasing abundance.

Competition 2

Using the above versions of the model it is possible only to place data points on the periphery of the unimodal dominance-species richness distribution found with field baiting data (Fig. 2a-c), and it is not clear what process is driving the variation in species richness at intermediate dominance levels that is typical of the field data.

Thus, patchiness was incorporated in this version of the model, first by limiting the number of occupied baits. With an even distribution, high species richness and low dominance is one possible outcome (where increasing the number of baits occupied and

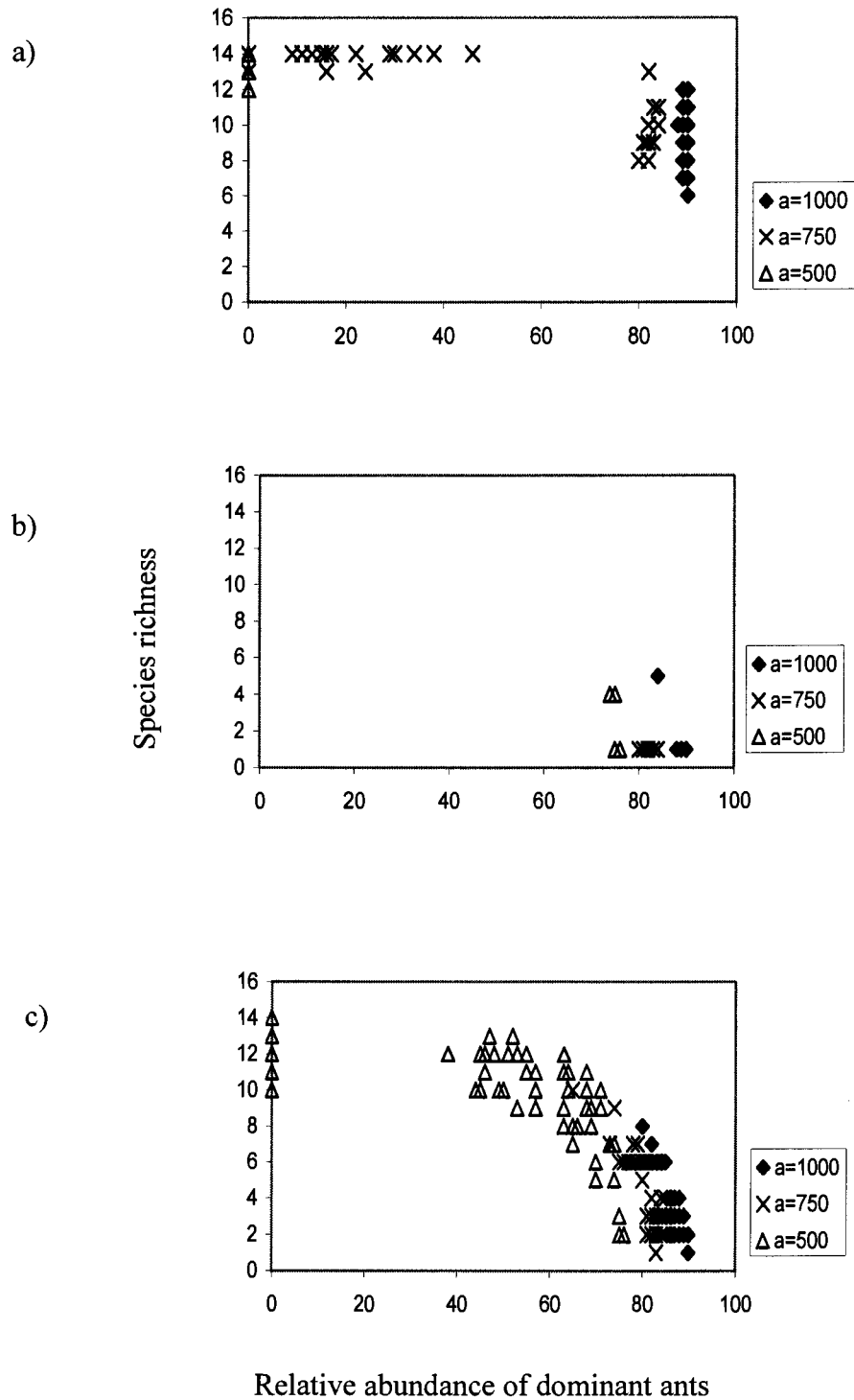


Figure 6. Relationship between species richness and abundance score of dominant ants for three species abundance frequency distributions using a competitive model in which all 15 baits are occupied, and the starting abundance (a) of ants is altered: (a) even distribution, (b) skewed distribution, (c) realistic distribution. Starting values for a ranged from 500-1000.

abundance of ants also increases dominance and species richness, but reduces variability in species richness) (Fig. 7a). This outcome is reached because only a very low number of baits are ever monopolised (usually only one bait). This results in low dominance, and a high number of species. Another outcome using an even distribution is that with a low number of baits occupied, dominance and species richness are also low, and as successive baits are occupied, dominance and species richness increase. Thus with all 15 baits occupied dominance is high, and species richness ranges from 6-13 species. For a given number of baits that are occupied, species richness values are always more variable than those for dominance, and the range of species richness values increases as the number of baits increases. This outcome is achieved because each bait is monopolised by one species, and this reduces species richness. With an even distribution however, as with *Competition1*, data points indicating high dominance are unrealistic because the number of ant species is similar to the number of dominant ants, and is always relatively high.

With both a skewed and realistic distribution, high levels of dominance are only possible when the majority of the baits are occupied (e.g. 14 or 15 baits have ants present at them) (Fig. 7c and 7e), and the starting abundance is high (e.g. $a = 1000$) (Fig. 7b, d and f). Furthermore, the overall outcome using both skewed and realistic distributions is a unimodal pattern similar to that produced with field baiting data.

Competition 3

Both patchiness measures (number of baits that are occupied, and differential chance of these baits attracting ants) are used in this version of the model. As with previous models, as more baits are occupied (simulating less environmental patchiness), dominance increases, and to a lesser degree species richness increases (most noticeable with an even distribution, Fig. 8a). None of the three abundance frequency distributions were able to produce an outcome of high dominance and low species richness. An even distribution produces a graph with no data points representing intermediate to high dominance and low species richness combined (Fig. 8a). When dominance is low, the full range of species richness values is possible, but as dominance increases, the range of species richness values becomes narrower, with an increase in the number of species. High dominance and high species richness is the outcome produced when most or all species are dominant, which is highly unlikely in reality.

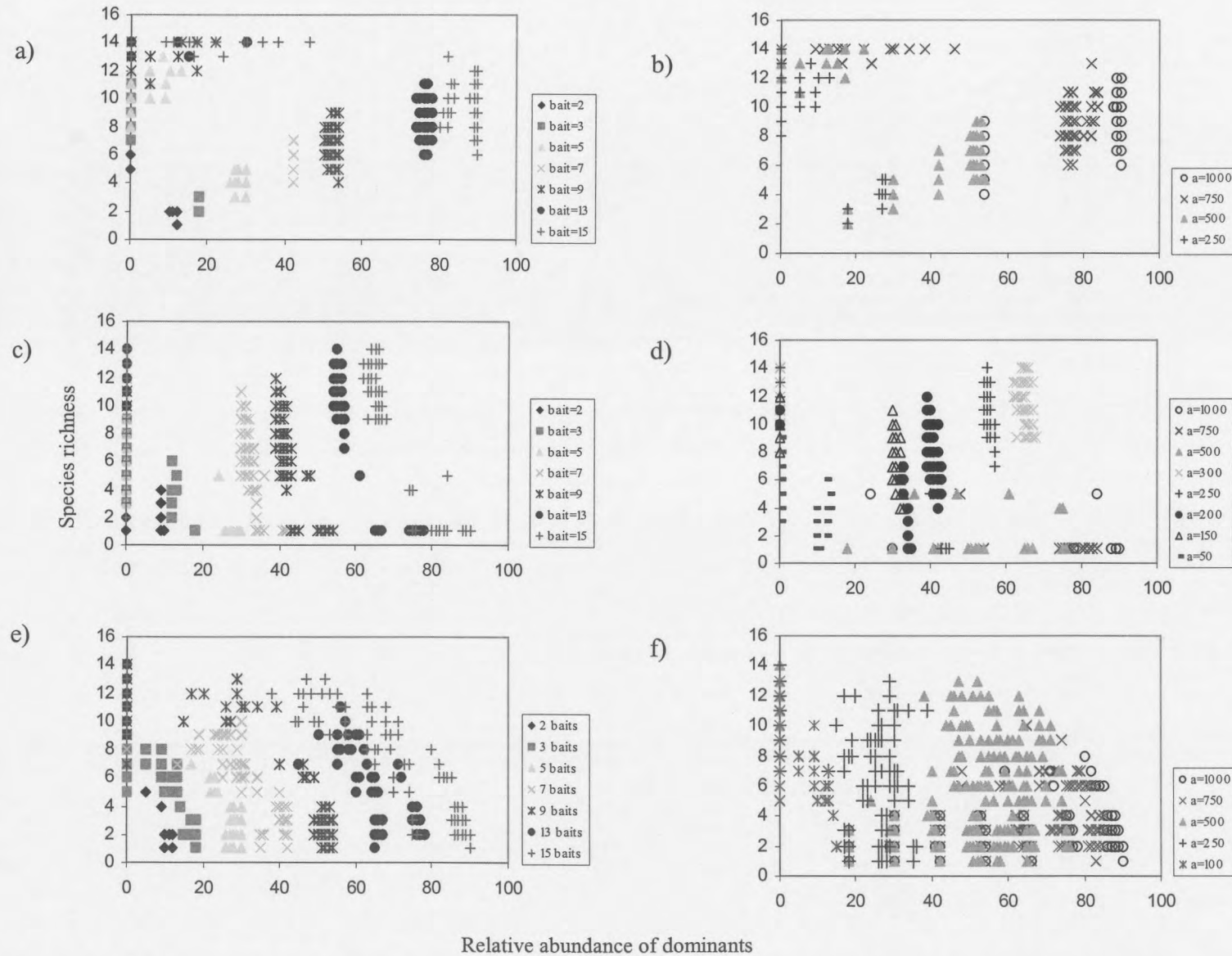


Figure 7. Relationship between species richness and abundance score of dominant ants for three species abundance frequency distributions using a competitive model which simulates the effect of changing the number of baits that are occupied. For each frequency distribution the same data are presented first according to number of baits occupied (variable a) (Figs a, c, e), and second, according to starting abundance, a , (with variable number of baits occupied) (Figs b, d, f). Even distribution = a and b; skewed distribution = c and d; realistic distribution = e and f. Number of baits occupied ranged from 2 – 15 baits. Starting values for a ranged from 50-1000. Each data point represents the result of 100 iterations of the model.

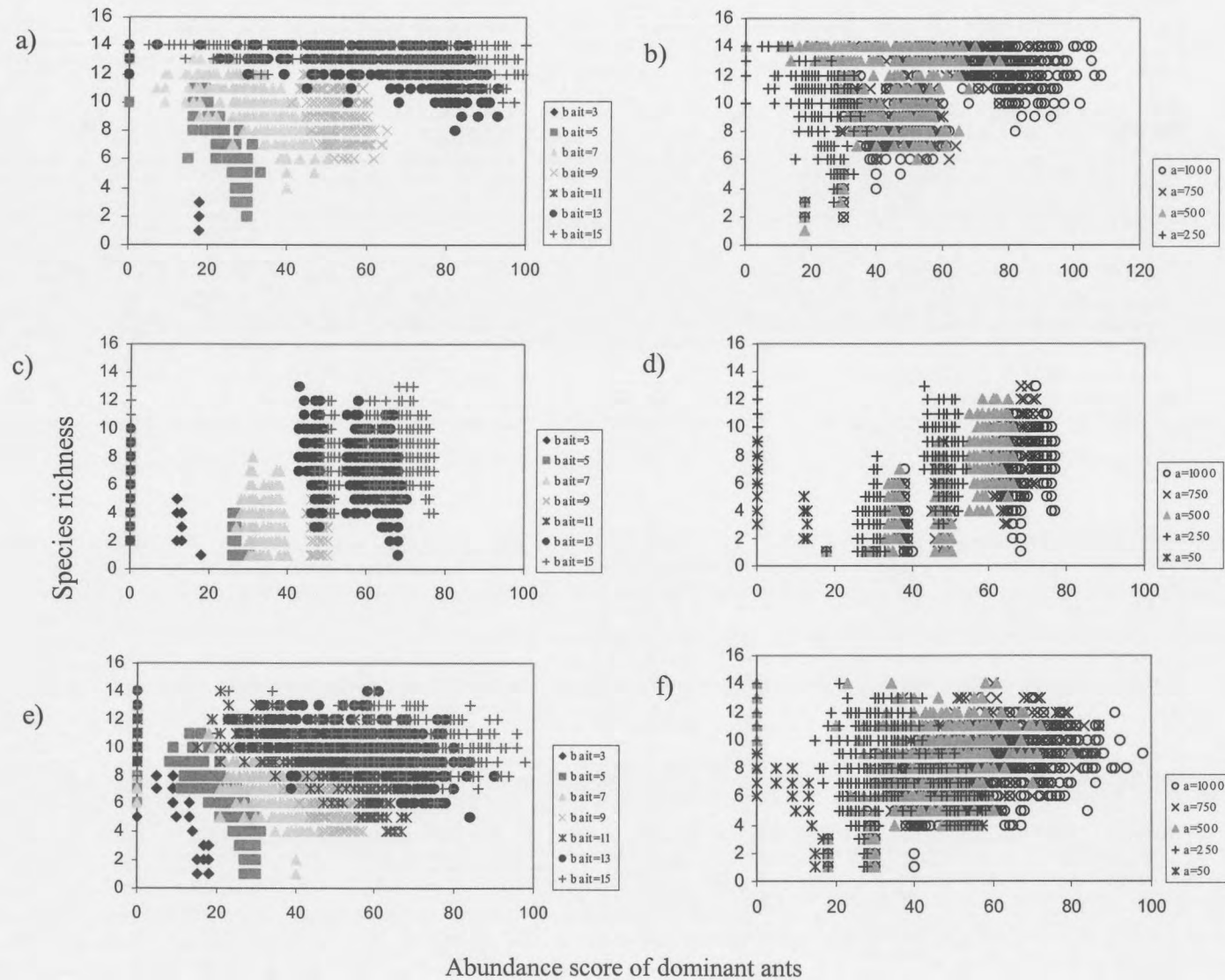


Figure 8. Relationship between species richness and abundance score of dominant ants for three species abundance frequency distributions using a competitive model which simulates the effect of changing the number of baits that are occupied, and patchiness within baits. For each frequency distribution the same data are presented first according to number of baits occupied (variable a) (Figs a, c, e), and second, according to starting abundance, a , (with variable number of baits occupied) (Figs b, d, f). Even distribution = a and b; skewed distribution = c and d; realistic distribution = e and f. Number of baits occupied ranged from 3 – 15 baits. Starting values for a ranged from 50-1000. Each data point represents the result of 100 iterations of the model.

Using a skewed distribution, dominance did not exceed 80, and it was not possible to have high species richness and relatively low dominance (Fig. 8c). Using a realistic distribution (Fig. 8e) data points are mostly concentrated in the central area of the graph, but with some at low dominance and low species richness, and others at high dominance and high species richness. Five percent of these data points have dominance scores of >90. This is because on occasion several species/ baiting run met the monopolisation criteria; increasing the monopolisation threshold would reduce the number of baiting sessions with dominance scores of >90 (see Sensitivity Analyses below). As with *Competition1* and *Competition2*, to have high dominance a high abundance of ants was necessary, combined with a large number of occupied baits (Fig. 8b, d and f).

Because the very top right hand corner of Figures 8c and 8e could not be filled using a realistic or skewed distribution, in order to determine the conditions that are necessary to fill this space, the model was re-run with slightly relaxed competition. The model simulated reduced competition by altering the rule restricting the number of species/ bait from four, to five species. Although both an even (Fig. 9a) and a realistic distribution (Fig. 9c) enable both maximum dominance and species richness, the data points based on the even abundance frequency distribution do not represent true dominance because most or all species are dominant, which is highly unlikely in reality. With a skewed distribution, although species richness could be high, dominance values were never greater than 80 (Fig. 9b).

Competition 4

If the maximum number of species at a bait is held at four, for all abundance frequency distributions, the effect of lowering the co-occurrence abundance threshold for monopolisation is lowered species richness (>10 individuals of a species/ bait, instead of >20) (Fig. 10). With an even distribution species richness decreases, as does dominance, and the range of dominance values is narrower (Fig. 10a). A skewed distribution results in lowered species richness, but no change in dominance level (Fig. 10b). Finally, with a realistic distribution the effect of increased competition is that species richness decreases, there are fewer dominance values above 80, and the range of dominance values are reduced (Fig. 10c).

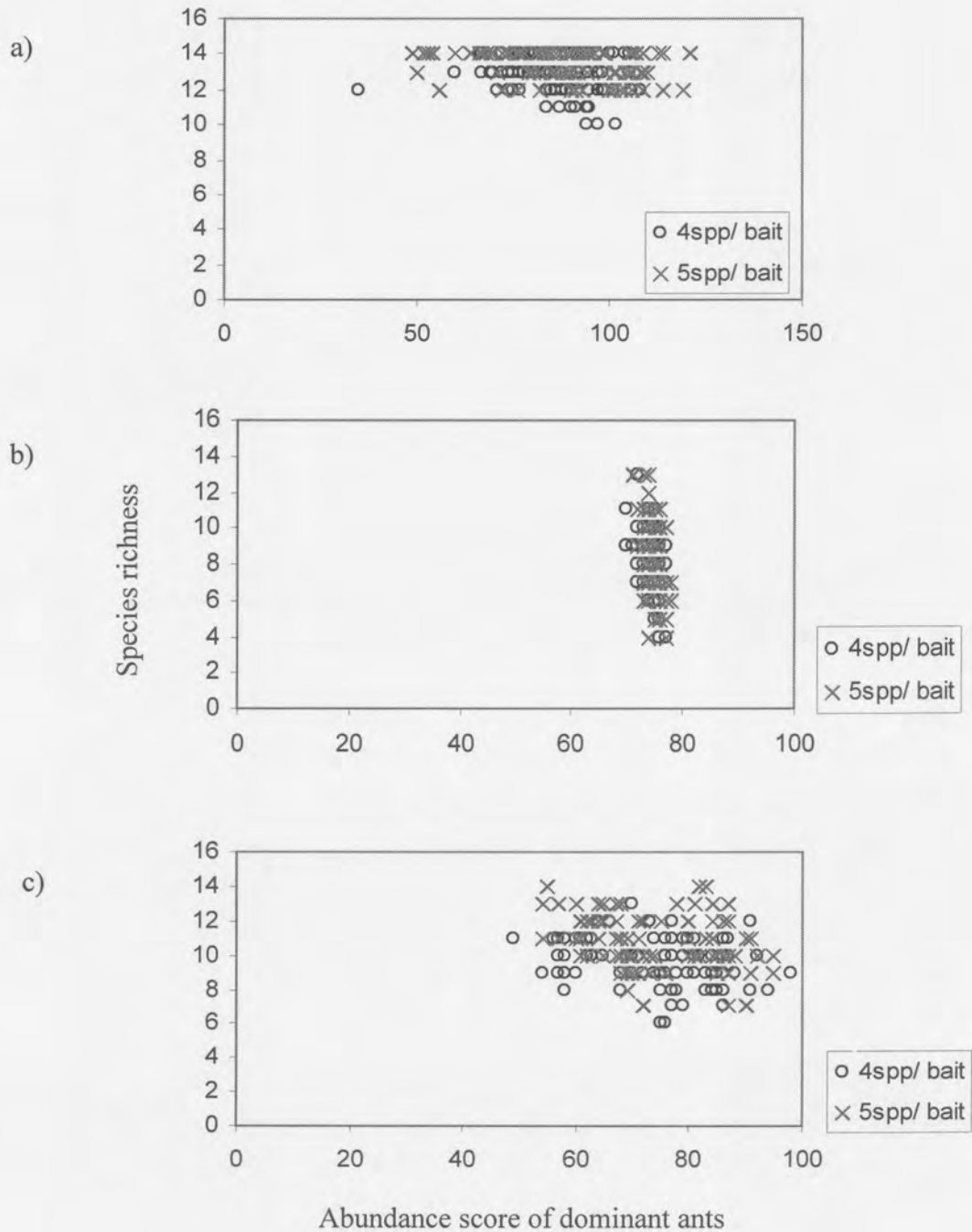


Figure 9. Relationship between species richness and abundance score of dominant ants for three species abundance frequency distributions based on a competitive model with 15 baits occupied, but with relaxed competition enabling 5 species to co-occur at a bait instead of 4 species: (a) even distribution, (b) skewed distribution, (c) realistic distribution. Each data point represents the result of 100 iterations of the model, and for all distributions $\alpha = 1000$.

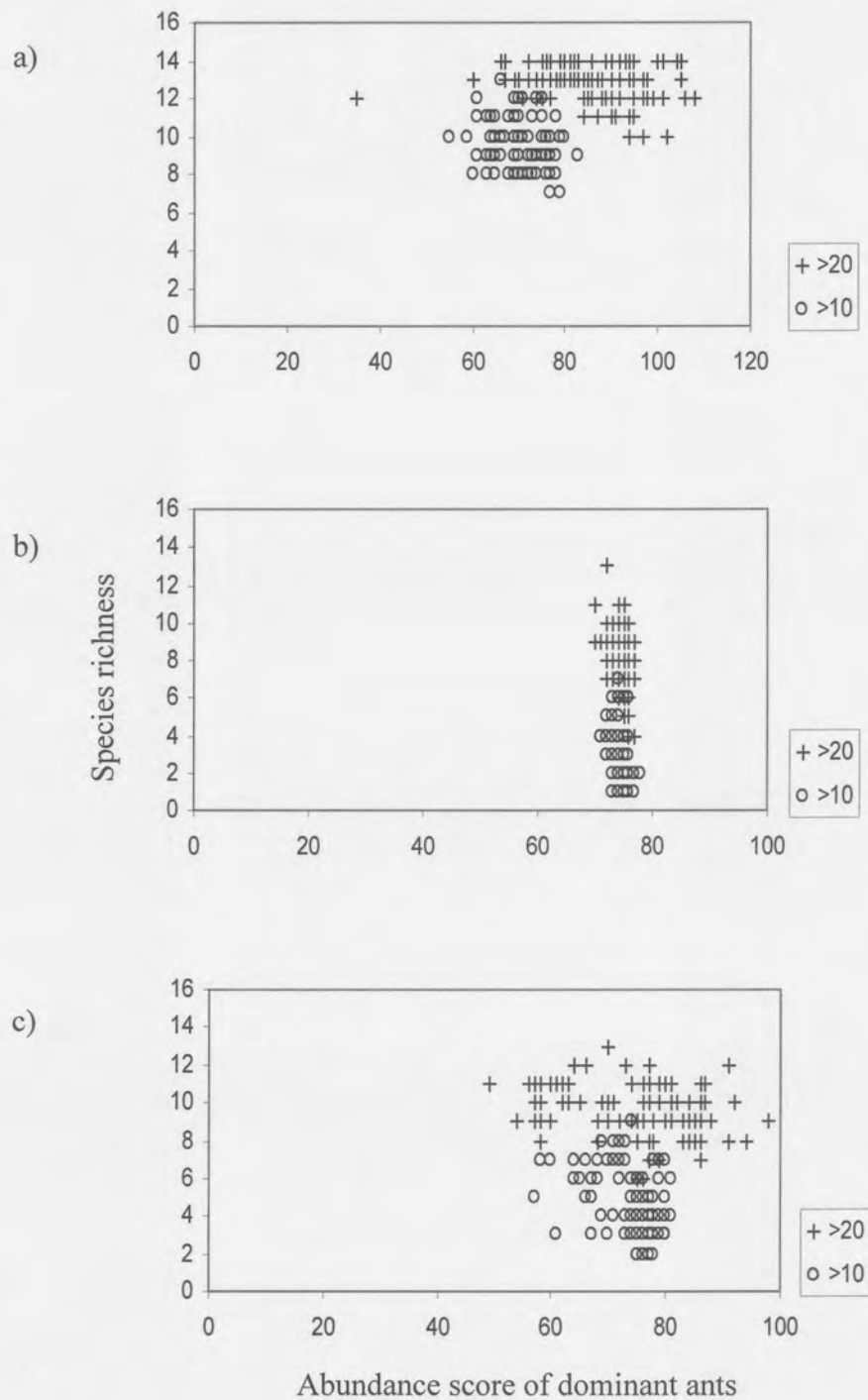


Figure 10. Relationship between species richness and abundance score of dominant ants for three species abundance frequency distributions using a competitive model which alters the threshold for the abundance at which species cannot co-occur from >20 to >10 individuals: a.) even distribution, b.) skewed distribution. c.) realistic distribution. Each data point represents the result of 100 iterations of the model, and for all distributions $a = 1000$.

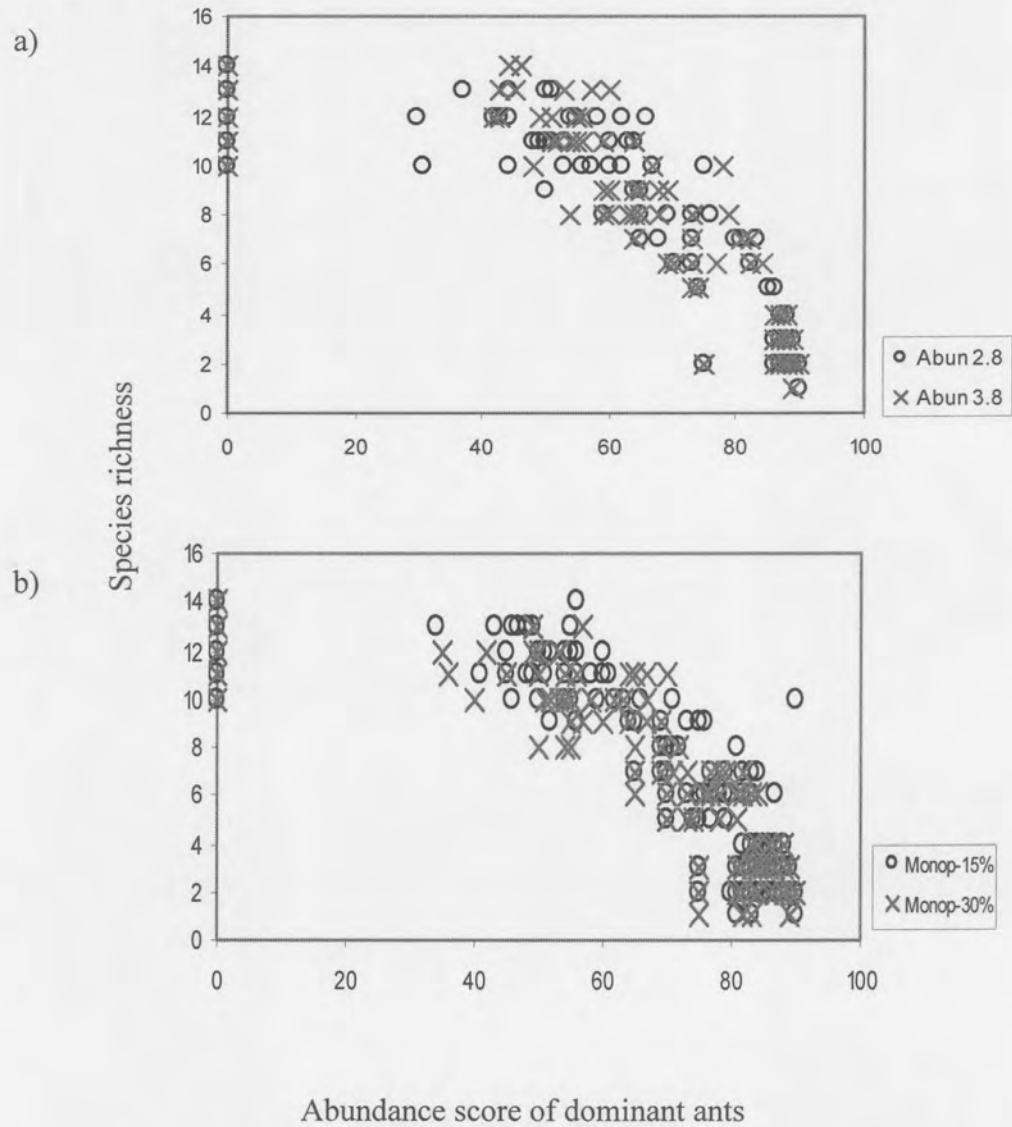


Figure 11. Sensitivity analyses showing the effect of changing dominance criteria thresholds using a competitive model with 15 baits occupied, a realistic abundance frequency distribution, and $a = 1000$: a) mean abundance score thresholds of 2.8 and 3.8, and b) monopolisation percentage threshold of 15 and 30%.

Sensitivity analyses

There was a small effect of altering dominance criteria values, particularly with mean abundance score (Fig. 11a). Decreasing the monopolisation level, increased species richness and dominance very slightly, while increasing percentage monopolisation had the opposite effect (Fig. 11b).

Discussion

Field baiting data for South Africa produced a unimodal relationship between dominance and species richness, albeit with considerable variation in baiting sessions lying between the upper and lower bounds of this relationship. Nonetheless, the unimodal pattern was consistent across all three habitats in the KNP, despite their rather different characteristics and ant assemblages (Gertenbach 1983; C.L. Parr & S.L. Chown, unpublished data). Even more remarkably, the unimodal pattern was also consistent among the three continents on which similar baiting trials were undertaken (Fig. 2). Indeed, the fact that it was possible to plot results from baiting trials in South Africa, North America, and Australia on the same graph serves to emphasise how similar the pattern is among these very different biotas. Therefore, the unimodal relationship between dominance and species richness at baits appears to be general.

Similarity in assemblage structure across continents that have been unconnected for about 140 Ma (see Paleomap project, www.scotese.com/earth.htm) to the extent found here, is unusual. Clearly this similarity cannot be attributed to convergence because the ancestral state of the assemblages is not known (see Schluter 1986). However, the similarity of the ant assemblages is striking. Many previous investigations have concluded that apparently similar (or convergent) natural assemblages do not correspond to the extent that was assumed prior to rigorous quantitative analysis (see Niemi 1985; Wilson et al. 2000). For example, Wiens (1991) found that bird assemblages of Australian and North American desert shrublands, did not exhibit close convergence for a range of behavioural and ecological characteristics despite great similarity in vegetation structure. Therefore, the apparent similarity did not hold up to further exploration, and differences between the assemblages were more pronounced than similarities. Prior to our study, this also seemed to be the case for ants. Previous global comparisons failed to reveal any similarities in assemblage structure that could be attributable

to convergent evolution (e.g. Morton & Davidson 1988; Medel 1995). These authors investigated convergence in harvester ants using several assemblage characters (including abundance at baits, body size, foraging distance and species richness), but overall close convergence was lacking. By contrast, our study investigated a rather different assemblage level characteristic. That is, rather than examining specific traits, we investigated the relationship between richness and dominance patterns across each of the assemblages.

Nonetheless, the cross-continental similarity in assemblage structure immediately begs the question of whether the outcomes of the baiting trials are constrained to take a unimodal shape owing to the form of abundance frequency distributions? If this is the case, then the similarity is of little interest because it provides no evidence of general mechanisms producing the underlying structure, beyond those responsible for producing skewed abundance frequency distributions in any assemblage (see Tokeshi 1993, Cotgreave & Harvey 1994; Gaston & Blackburn 2000; Hubbell 2001; Magurran & Henderson 2003). However, if this is not the case, then one or more additional mechanisms might well be responsible for the pattern. In particular, the main contenders for this role are interspecific competition at high dominance levels and environmental stress where dominance is low. Andersen (1992, 1997a) came out strongly in favour of these two mechanisms, and they have since been widely accepted in the literature (e.g. Retana & Cerdá 2000; Albrecht & Gotelli 2001). Our models have allowed us to make the first exploration of alternative explanations for the unimodal distribution.

The ascending part of the relationship

Our models revealed that it was only possible to have high species richness and low dominance (the upper portion of Area A on Fig. 1) with an even abundance frequency distribution (Figs. 6-8). Since this distribution is biologically unlikely (see examples of abundance frequency distributions in Tokeshi 1999, and Gaston & Blackburn 2000), in reality it is next to impossible to fill this area of species richness-dominance space. Therefore, it appears that the ascending part of the unimodal relationship is, in part, constrained to take this form. In other words, it is not simply stress that results in low richness and dominance (as is often assumed, see Andersen 1995, 1997a; Morrison 1996; Bestelmeyer 1997), but also the way in which resources are apportioned between species so leading to a skewed abundance

frequency distribution (see Tokeshi (1993,1999) and Sugihara et al. (2003) for discussion of the relationship between abundance frequency distributions and niche apportionment).

However, the models also suggested that stress might have some role in producing a positive relationship between richness and dominance at low dominance values. In those models (both null and competitive) where ant abundance was held low and ants constrained to just a few baits there was a strong, positive relationship between dominance and richness at low dominance levels, especially in the case of the realistic and skewed abundance frequency distributions. Thus, any factor that results in low abundances and patchy distributions could also produce the ascending portion of the unimodal curve, without assuming an unrealistic abundance frequency distribution. Environmental stresses, such as limited food availability, lack of nesting sites, and extreme temperatures (see Andersen 1995, 2000; Cerdá et al. 1998; Bestelmeyer 2000), reduce ant abundance (see Grime 1989; Drobnet et al. 1998) and consequently bait occupancy, and could therefore result in the positive relationship between dominance and richness. In sum, area A in Figure 1 is probably unoccupied as a consequence of both the form abundance frequency distributions are constrained to take, and the effects of stress.

The descending part of the relationship

Without competitive interactions (all Null models), both dominance and species richness were very high (Figs. 4 and 5). When competition was introduced into the model, high dominance and high species richness (Area B, Fig.1) were possible with an even abundance frequency distribution and very high ant abundances (Figs. 7 and 8). However, under these conditions, there were a high number of species at the baits of which all or the majority, were dominants, and had high abundances, a situation which is not realistic. Under natural circumstances there is seldom more than one species dominant at a bait after 60 minutes (see Bestelmeyer 2000; C.L. Parr & A.N. Andersen, unpublished data), and where there is more than one species dominant across a number of baits in a given area at one time, the number of species co-existing at a bait is low (e.g. <3) (C.L. Parr & A.N. Andersen, unpublished data). Thus, it might initially be imagined that an absence of baits with high richness and dominance is also a consequence of the shape of abundance frequency distributions.

However, our models indicated that it is also possible to have high dominance and high richness in a competitive situation with a realistic abundance frequency distribution, high ant abundance, many baits occupied, and a weighted, rather than uniform, occupancy frequency distribution (Fig. 8e and f). The high level of bait occupancy and high abundance coupled with at least some measure of aggregation meant that although dominant ants controlled some of the baits, at least several other baits could support a variety of non-dominant species (and also occasionally dominant species at low abundances). That this was the case is clearly shown by the relaxed competition model, which tended to result in even higher richness at high dominance levels (Fig. 9c), and the intensified competition model, in which the reduction in the number of ants which could co-occur at a bait strongly depressed species richness (Fig. 10c). Indeed, these outcomes also suggest that the mechanism underlying the presence of both high dominance and richness is similar to the aggregation model of coexistence proposed by Atkinson and Shorrocks (1981, 1984). In this model, developed originally for species on patchy, ephemeral resources, and since supported in many taxa (Ives 1991; Giller & Doube 1994; Kouki & Hanski 1995; Inouye 1999; Krijger & Sevenster 2001; Woodcock et al. 2002), higher levels of intraspecific competition relative to interspecific competition, enable inferior competitors to co-exist. Thus, high species richness can be maintained (see Wertheim et al. 2000). In other words, the upper right hand portion of the “dominance-richness space” can be filled given a scenario that might be considered realistic for a variety of organisms.

If this space can be filled under a biologically realistic scenario the question remains as to why the combination of high richness and dominance is so uncommon for ant assemblages in Africa, North America and Australia. One reason might be that interspecific competition is much more pronounced than intraspecific competition in ants, so making coexistence via an aggregation model of the kind proposed by Atkinson and Shorrocks (1981, 1984) unlikely. Indeed, this does seem to be the case. Usually, ants from the same colony do not compete against each other, but rather recruit additional nestmates to food resources (Hölldobler & Wilson 1990; Tsutsui et al. 2000). Moreover, in our models in which interspecific competition was increased (Fig. 10), or where competition was pronounced in the absence of low levels of aggregation (Fig. 7), high dominance was never accompanied by high richness. Therefore, it is clear that interspecific competition of the form envisaged by

Anderson (1992, 1997a), and accepted by several other workers, can produce the descending part of the dominance-richness relationship. Interspecific competition does indeed seem to be the hallmark of ant ecology (Hölldobler & Wilson 1990), at least at baits.

The area between the bounds

Variation in the central area of the unimodal relationship, between the upper and lower bounds (Area C, Fig.1), is clearly a consequence of patchiness at baits. The introduction of patchiness into the models (via reduced occupancy of baits) resulted in a variety of outcomes especially at intermediate dominance levels (Figs. 7 and 8), producing the variation so typical of the empirical relationships (Fig. 2a-c). Whilst Gotelli and Ellison (2002) argue that patchiness reflects non-limiting resources, our data and models suggest that the converse might be true, that limited resources may result in low abundances of ants and few baits occupied (in the KNP the greatest number of empty baits occurred in the Mopane area, which also has lower abundances of ants than Satara or Pretoriuskop, unpublished pitfall data, C.L. Parr & S.L. Chown). However, the cause of the patchiness is unlikely to affect the fact that it is patchiness that results in a spread of points between the upper and lower bounds. Admittedly our models suggest that patchiness results from low abundance and low occupancy, but we cannot distinguish whether low occupancy is a consequence of a surfeit of resources or an absence of ants. Nonetheless, these models do draw attention to the importance of patchiness in the occupancy of baits as a mechanism generating the scatter of points in dominance-richness relationships. Like many other systems, patchiness is clearly an important component influencing ant assemblages. Previously there has been little discussion of either the scatter or the mechanism underlying it. Rather the focus has been on the unimodal, upper bound (e.g. Morrison 1996; Andersen 1997a). Our models suggest that the full relationship should be investigated.

Assemblage level patterns: linking local and regional processes

A positive, curvilinear relationship was found between Net Primary Productivity (NPP) and species richness (pitfall data), which supports findings from several other studies covering a variety of animal and plant taxa (e.g. Currie 1991, amphibians, reptiles, birds and mammals; O'Brien 1998, woody plants; Kerr & Packer 1999, beetles; Kaspari et al. 2000, ants; Van Rensburg et al. 2002, birds) (Fig. 12).

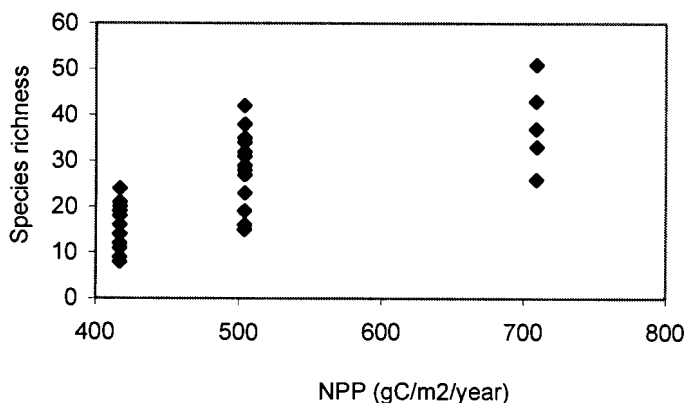


Figure 12. Species richness at the plot scale (20 pitfalls/ plot combined) shows a positive relationship with net primary productivity (NPP). Estimated NPP values for the different habitats are as follows: Mopane = 417, Satara = 504, Pretoriuskop = 709 gC/ m²/ year (data from Schulze 1997).

It is, however, noticeable from the curve that within each site there is considerable variation in species richness. In other words, although regional richness is set by the availability of energy (NPP), local richness is influenced by local level interactions. This is illustrated in Figure 3, which shows that at the plot level, where the abundance of dominant ants is high, species richness is depressed, thus producing the unimodal form of the relationship. Local scale processes such as competition can thus affect species richness at the assemblage level, as well as the bait level, and can contribute to the variation in richness at each site. The translation of interference competition at baits into the control of resources at

the assemblage level and the depression of species richness by dominants, demonstrates that temporal patterns of diversity and dominance at baits are therefore not necessarily merely an artefact of the experimental design, but in fact can reflect broader patterns of foraging activity, and the importance of competition in structuring ant assemblages at a local scale (see Morrison 1996). These findings support the contention that to fully understand variation in biodiversity, both regional and local scale processes require consideration (Ricklefs 1987).

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Chapter 4

The size grain hypothesis: a phylogenetic and field test

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Introduction

The size-grain hypothesis (Kaspari & Weiser 1999) makes the prediction that, because the earth's surface is more rugose for smaller organisms than for larger ones, as organisms decrease in size the benefits of long legs for efficient movement will begin to be outweighed by the costs. Thus, small ants should have proportionally smaller legs than larger ants, with a scaling exponent of $b > 0.33$ for leg length to body mass (or $b > 1.0$ on linear scales, e.g. leg length to head length). One of the implications of the size-grain hypothesis is that ants which forage in planar environments should generally be larger than those which forage in more complex environments, and *vice versa*.

Although both Kaspari and Weiser (1999) and Espadaler and Gómez (2001) found that empirically derived scaling relationships for ants supported the size-grain hypothesis, their tests did not take phylogenetic relatedness into account. Phylogenetic non-independence is not only likely to affect the significance of the scaling relationships (see Harvey & Pagel 1991) but may also have a significant effect on the form of these relationships (e.g. Nee et al. 1991). In addition, only a single field-based test of the size-grain hypothesis has been undertaken (Yanoviak & Kaspari 2000). While these authors did not undertake an explicit test of the scaling components of the size-grain hypothesis, their data did suggest that the body size frequency distributions of the two ant assemblages examined (litter and canopy) differed. Based on this difference, Yanoviak and Kaspari (2000) argued that the effects of environmental rugosity on locomotion might be responsible for habitat-associated differences in these ant assemblages, although they could not discount the possibility that sampling artefacts were also responsible for this pattern. In other words, to date, only a single assessment has been made of the extent to which differences in the rugosity of the environment experienced by ants has an effect on their assemblage structure; one that did not include an explicit test of the scaling predictions of the size-grain hypothesis.

Therefore, in the work reported here, tests of the allometric predictions of the size-grain hypothesis, including those using phylogenetic independent contrasts, were undertaken. In addition, the effects of experimentally manipulated environmental rugosity on both the allometric relationships and ant body size frequency distributions were also examined.

Materials and methods

Ant specimens were collected from three control and three annually burned plots, in each of two savanna vegetation types, *Colophospermum mopane* J.Kirk woodland (Mopane sites) and *Acacia nigrescens* Oliv. savanna (Satara sites), in the Kruger National Park, South Africa (23°33'S, 31°26'E and 24°26'S, 31°46'E, respectively). The Satara and Mopane areas are \approx 100 km apart, and each of the experimental plots was approximately 7 ha. The control plots have remained unburned since 1945 (Trollope et al. 1998). In consequence, they are densely vegetated with moribund grass and an obvious litter layer. By contrast, the annually burned plots are more open, with reduced ground cover and fewer trees (see below). This work forms part of a longer, on-going study (1999-2003) that has as its main aim an understanding of the effects of fire frequency and timing on epigaeic ant assemblages (see also Parr & Chown 2001). For the larger study, the similarity of the ant communities (sampled using pitfall traps, see below) in the Satara and Mopane areas was examined using cluster analysis of the species abundance data based on group averaging and Bray-Curtis similarity measures (PRIMER v. 5.0; Clarke & Gorley 2001). Abundance data were fourth-root transformed prior to analysis to reduce the weight of common species. Analysis of similarity (ANOSIM), which tests for significant differences between assemblages (Clarke & Warwick 1994), was then used to test whether the assemblages in the Mopane and Satara areas were significantly different, and whether this was true also for the assemblages in the annual and control burn plots in both areas.

Epigaeic ants were sampled using a total of 20 pitfall traps per plot, arranged in a grid (5 x 4) with 10 m spacing between each pitfall trap. Each trap contained a 50% propylene glycol solution. The pitfalls were left to settle for 5 days to reduce the 'digging-in' effect (Greenlade 1973). Collecting grids on each plot were at least 50 m from the plot edge to prevent ants from outside the plot from falling into the traps. The traps at Satara were opened from 25 to 30 November 2000 (5 days), and those at Mopane from 27 November to 2 December 2000 (6 days). Samples were washed with water, sorted, and stored in 80% alcohol. For each pitfall trap, the ants were identified and counted. Voucher specimens are lodged at the South African Museum, Cape Town.

Bare ground in each site was assessed to provide a measure of the surface rugosity likely to be encountered by ants. The percentage of exposed bare ground and percentage

vegetation cover on each plot were estimated using 1 m² quadrats placed next to each of the 20 pitfall traps in each plot. Bare ground can play an important role in the structuring of ant communities (Crist & Wiens 1994; Bestelmeyer & Wiens 1996) and acts as an indirect measure of vegetation cover. The size-grain hypothesis (Kaspari & Weiser 1999) emphasises that ants move primarily through their environment, rather than over and around it. Thus, ants with shorter legs are able to move better between the horizontal and vertical obstacles of litter and leaves, while species foraging in planar environments move over the ground surface and should therefore have longer legs. Bare ground was used as a measure of surface planarity in each plot. In this savanna system, the fine-textured clay soils are often compacted and develop a clay skin that has a smoother surface than loose, coarse soils (Areola 1996).

Up to 10 specimens for 86 species collected were selected for measurement (see Table 1 for taxonomic summary). In dimorphic species, only minors were used. For each ant, five standard linear measurements were taken using an ocular micrometer mounted on a dissecting microscope accurate to 0.01 mm: maximum head width, not counting eyes, maximum head length, hind tibia length, and hind femur length. Total hind leg length was estimated from hind tibia length + hind femur length. Head length was used in all analyses as an indication of total body size because of the strong correlation between head length and body mass (Kaspari & Weiser 1999; Espadaler & Gómez 2001). For each body size measurement, a standardised measure of size range [$pWR = \log_{10} (M_{\max} / M_{\min})$] was calculated for each species. pWR indicates the orders of magnitude spanned (Prothero 1986) (Table 2).

Allometries were investigated using least squares linear regression analyses of the \log_{10} -transformed mean values (for each species) to estimate b in the scaling equation $y = aM^b$. To test the null hypothesis of isometry, a t-test was used to determine whether the slopes of the regression lines were significantly different from 1 (linear measure vs head length). Phylogenetic independent contrast analyses were subsequently used to investigate the extent to which the relationships are influenced by phylogenetic non-independence. A current *best tree* was compiled from the literature (subfamilies: Grimaldi & Agosti 2000; tribes and genera: Bolton 1994), and entered into the PDAP software (Garland et al. 1999). Phylogenetic independent contrasts were calculated for head length, head width, femur length, and total leg length. Because information on branch lengths was lacking, branch lengths were assigned

using Pagel's (1992) and Grafen's (1989) methods, and by assuming that all branches had equal lengths (all segments equal to one).

Ordinary least squares regressions were then used to investigate relationships between the standardised contrasts of femur length and total leg length as dependent variables, and head length and head width as independent variables. T-tests were used to determine whether the slopes of these relationships were isometric ($b = 1.0$). F-tests were then used to determine whether there were significant differences between the slopes of the original ordinary least squares regressions and those based on the independent contrasts (Sokal & Rohlf 1995).

To determine whether the regression slopes for total leg length against head length differed between the control and the annual burn plot, an ANCOVA (test for parallelism; STATISTICA 5.5) was used. This was done separately for the Mopane and Satara areas. Because no differences were found between the analyses using the original data and those based on the independent contrasts, the former data were used. Body size frequency distributions for ants (based both on numbers of species in a given size class and on numbers of individuals in a size class) were constructed using head length and total leg length measurements for both plot types in the Mopane and Satara area savannas. The resulting body size frequency distributions were compared using a Kolmogorov-Smirnov two-sample test.

Results

The analyses of similarity revealed that the Mopane and Satara areas had significantly different ant communities ($R = 0.357$, $p = 0.001$). Likewise, ant communities differed between the annual and control plots at both Satara ($R = 0.487$, $p < 0.01$, data from full sampling period 2000-2002) and Mopane ($R = 0.328$, $p < 0.02$, data from 2000-2002). The proportion of bare ground on the annual and control plots for each area (Satara and Mopane) differed significantly (Table 3), showing that the surface environment for foraging ants on the annual plots was much more planar than on the control plots. Species accumulation curves for Mopane and Satara increase only slowly, and thus although no asymptote was reached, sampling was relatively complete and therefore unlikely to bias the results (Fig. 1).

Table 1. Taxonomic summary of the ants collected in the Mopane and Satara areas of the Kruger National Park, South Africa.

	Aenictinae	Cerapachyinae	Dolichoderinae	Dorylinae	Formicinae	Myrmicinae	Ponerinae
Number of species	3	1	3	1	13	50	17
Tribes	Aenictini	Cerapachyini	Dolichoderini	Dorylini	Camponotini Plagiolepidini	Dacetoniini Crematogastini Formicoxenini Meranoplini Myrmicariini Pheidolini Pheidologetonini Soleopsideini Tetramoriini	Ectatommini Ponerini
Genera	<i>Aenictus</i>	<i>Cerapachys</i>	<i>Tapinoma</i> <i>Technomyrmex</i>	<i>Dorylus</i>	<i>Anoplolepis</i> <i>Camponotus</i> <i>Lepisiota</i> <i>Plagiolepis</i> <i>Polyrhachis</i>	<i>Cardiocondyla</i> <i>Crematogaster</i> <i>Decamorium</i> <i>Meranoplus</i> <i>Messor</i> <i>Monomorium</i> <i>Myrmecaria</i> <i>Ocymyrmex</i> <i>Oligomyrmex</i> <i>Pheidole</i> <i>Solenopsis</i> <i>Strumigenys</i> <i>Tetramorium</i>	<i>Anochetus</i> <i>Hypoponera</i> <i>Leptogenys</i> <i>Odontomachus</i> <i>Pachycondyla</i> <i>Plectroctena</i> <i>Prionopelta</i>

Table 2. Summary of the size range (pWR) for each body measurement for all subfamilies.

$$pWR = \log_{10}(M_{\max}/M_{\min})$$

Subfamily	Head width	Head length	Tibia length	Femur length	Total leg length
All ants	1.14	1.14	1.40	1.32	1.34
Aenictinae	0.43	0.30	0.51	0.55	0.51
Cerapachyinae	0.05	0.02	0.07	0.07	0.07
Dolichoderinae	0.16	0.18	0.21	0.20	0.19
Dorylinae	0.39	0.35	0.47	0.42	0.44
Formicinae	0.79	0.82	1.22	1.19	1.20
Myrmicinae	0.86	0.77	1.17	1.16	1.15
Ponerinae	1.14	1.03	1.07	1.09	1.07

All linear measurements showed an allometric relationship. The null hypothesis for isometry was rejected for all but one of the relationships (head width vs head length, $b = 1.012$, $p > 0.1$), and it was clear that larger ants had proportionately longer legs (head length vs femur length, $b = 1.234$; head width vs head length, $b = 1.196$; head length vs leg length, $b = 1.250$) (Table 4). There were no significant differences between the ordinary least squares regression and the phylogenetic independent contrast slopes [using equal branch lengths, or those calculated using Pagel's (1992) or Grafen's (1989) methods], for any of the allometric relationships (F-test, $p > 0.1$, data not shown).

The ANCOVA for the regressions slopes for total leg length against head length revealed no significant difference between the allometric relationship on the annual and control plots, for either Satara or Mopane. For both head length and total leg length measures, there was no significant difference in body size frequency distributions, based on species, for the two plot types (Mopane: $D = 0.088$ and 0.158 ; Satara: $D = 0.095$ and 0.084 for head length and total leg length respectively, $p > 0.1$) (Fig. 2: head length). There were, however, significant differences in the abundance frequency distributions for head length and total leg length size categories, in both vegetation types (Mopane: $D = 0.373$ and 0.06 ; Satara: $D = 0.346$ and 0.309 for head length and total leg length respectively, $p < 0.05$) (Fig. 3: head length).

Table 3. Summary statistics of the measure of bare ground (m²) around individual pitfall traps for each of the sites in the Satara and Mopane areas. One-way ANOVAs for both areas showed that control plots had significantly smaller areas of bare ground than did annual plots.

Site	Treatment	Mean	Minimum	Maximum	SE
Satara					
1	Annual	0.55 ^A	0.35	0.65	0.02
2	Annual	0.60 ^A	0.40	0.75	0.03
3	Annual	0.54 ^A	0.20	0.70	0.02
1	Control	0.08 ^B	0	0.20	0.01
2	Control	0.02 ^B	0	0.15	0.01
3	Control	0.06 ^B	0	0.20	0.01
ANOVA: $F_{(1,4)} = 396.8.1$, $p < 0.001$. Different superscripts (A, B) denote significant differences.					
Mopane					
1	Annual	0.37 ^A	0.10	0.65	0.04
2	Annual	0.53 ^A	0.30	0.65	0.02
3	Annual	0.48 ^A	0	0.70	0.03
1	Control	0.19 ^B	0	0.80	0.05
2	Control	0.06 ^B	0	0.25	0.02
3	Control	0.11 ^B	0	0.60	0.03
ANOVA: $F_{(1,4)} = 31.53$, $p < 0.01$. Different superscripts (A, B) denote significant differences.					

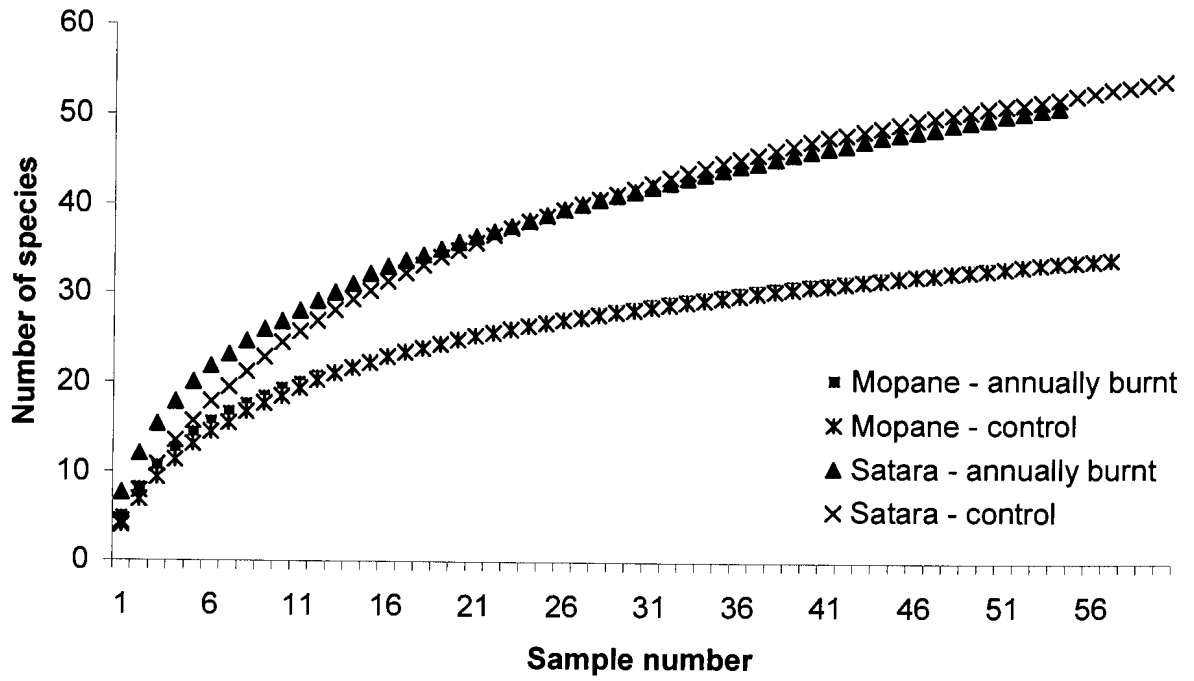


Figure 1. Species accumulation curves for Mopane and Satara (annually burned and control plots) indicating completeness of sampling.

Table 4. Least-squares regressions of three linear measures against head length and one linear measure against head width for all ant species, with regression analysis based on the raw data and on the phylogenetic independent contrasts using different arbitrary branch lengths. All data were \log_{10} transformed. Significance of deviation from isometry ($b = 1.0$) (tested using a t-test) is denoted by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Phylogenetic branch length	Independent variable	Dependent variable	t_s	r^2	b		SE of b	d.f.
No phylogenetic correction	Head length	Head width	0.533	0.961	1.012	NS	0.022	84
		Leg length	4.936	0.878	1.250	***	0.051	83
		Femur length	5.066	0.894	1.234	***	0.046	84
	Head width	Leg length	3.513	0.845	1.196	***	0.056	83
Equal branch lengths	Head length	Head width	1.123	0.961	1.027	NS	0.024	31
		Leg length	4.765	0.874	1.242	***	0.051	31
		Femur length	3.473	0.868	1.180	**	0.052	31
	Head width	Leg length	2.834	0.835	1.156	**	0.055	31
Pagel's (1992) method	Head length	Head width	1.284	0.961	1.033	NS	0.026	31
		Leg length	5.431	0.874	1.269	***	0.050	31
		Femur length	2.519	0.868	1.142	*†	0.056	31
	Head width	Leg length	3.127	0.835	1.170	**	0.054	31
Grafen's (1989) method	Head length	Head width	1.899	0.961	1.048	NS	0.025	31
		Leg length	5.541	0.874	1.265	***	0.048	31
		Femur length	4.905	0.868	1.238	***	0.048	31
	Head width	Leg length	3.517	0.835	1.169	**	0.048	31

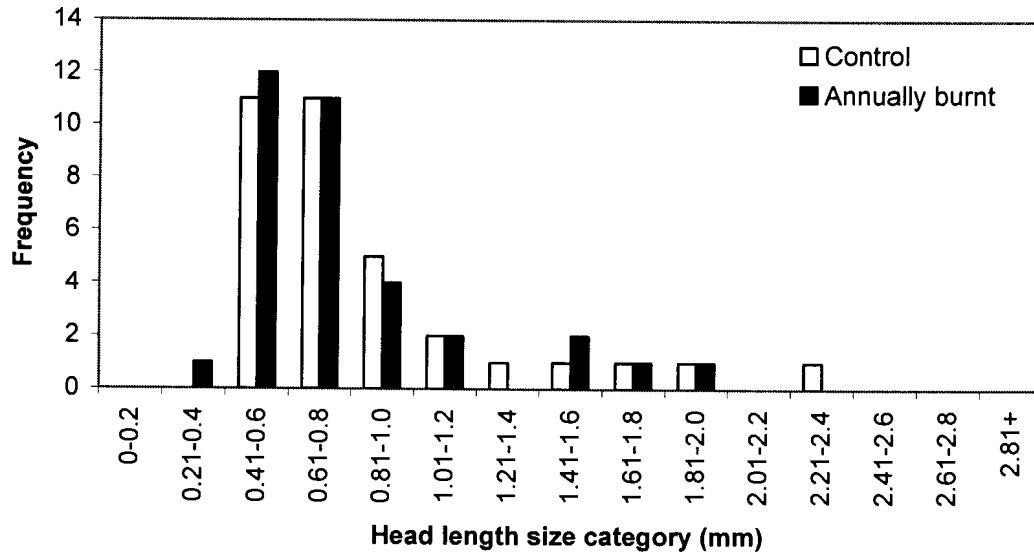
Significance of deviations from isometry following tablewide Bonferroni corrections at the $p = 0.05$ level were considered significant for all tests, except at †.

Discussion

Previous tests of the size-grain hypothesis have been based on ant specimens from five subfamilies from the New World (Kaspari & Weiser 1999), and from ants in the subfamily Formicinae (Espadaler & Gómez 2001). These studies found that leg size increases disproportionately to body mass ($b > 0.33$), with larger ants being relatively longer legged, and in small ants leg length is smaller relative to head size. The results of this allometric investigation, based on a data set of ants from Southern Africa, provide additional support for the size-grain hypothesis, and confirm that larger ants have a proportionately larger leg length, irrespective of whether the raw data are used or the regressions are based on phylogenetically independent contrasts. Thus, like Kaspari and Weiser (1999) and Espadaler and Gómez (2001), this study provides support for the size-grain hypothesis, at least on morphological grounds.

There has only been one previous field-test of the size-grain hypothesis, which compared ant body sizes in tropical forest canopy and surface litter (Yanoviak & Kaspari 2000). Some support for the size-grain hypothesis was found: the more planar environment (tree canopy) had ants of an intermediate size, whereas in the more rugose environment (litter layer), there was a bimodal distribution of ants, with small ants apparently moving through interstices and larger ants moving over the rugose environment. In the present study, instead of comparing ants from different foraging environments (litter and canopy), the emphasis was on ground foraging ants that were collected from plots with differing surface rugosity. The differing surface rugosity was clear in both the Satara and Mopane sites. In the annually burnt plots, the extent of the bare ground (i.e. no vegetation, no litter, and a generally compacted surface) was significantly larger (Table 3) than that of the unburnt, control plots. These latter plots have built up a considerable litter layer and have dense vegetation (see also Enslin et al. 2000; Parr & Chown 2001). Fire influences ants primarily through the modification of habitat structure and complexity (Greenslade & Greenslade 1977; Andersen & Yen 1985; Greenslade 1997). Regular annual burning thus prevents the build-up of a litter layer and suppresses vegetation height, and it is these changes in habitat structure with fire that are reflected in changes in ant community composition (Andersen 1983).

a)



b)

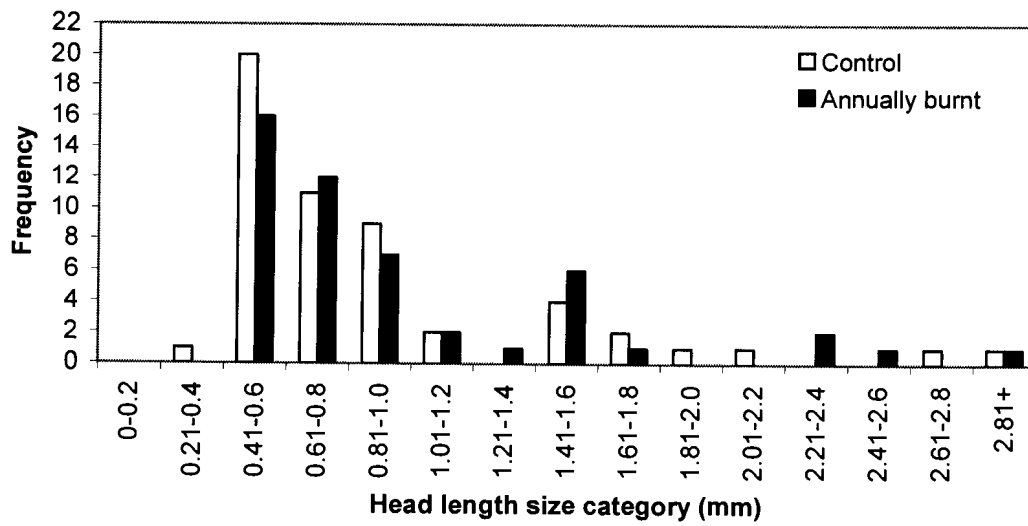
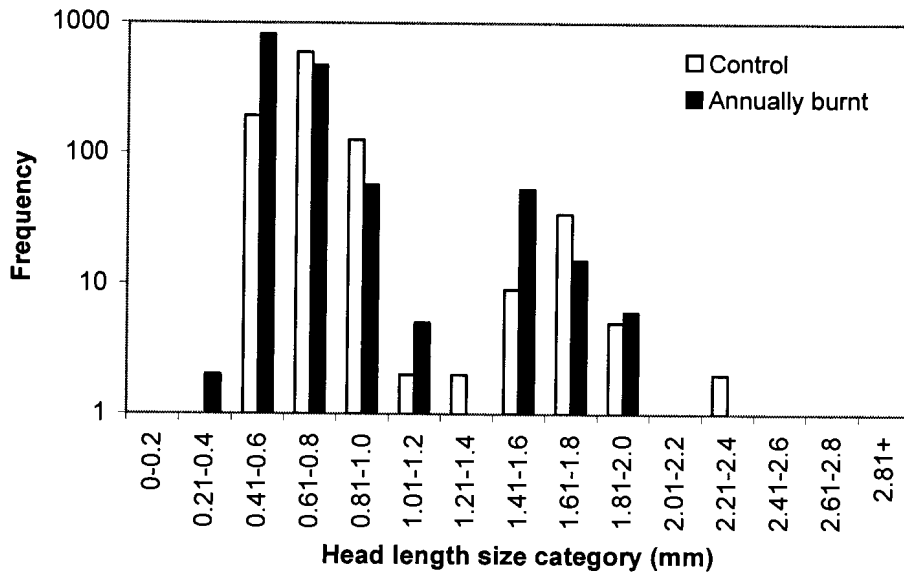


Figure 2. Species frequency distributions for head length size: (a) *Mopane* woodland and (b) *Acacia* savanna.

a)



b)

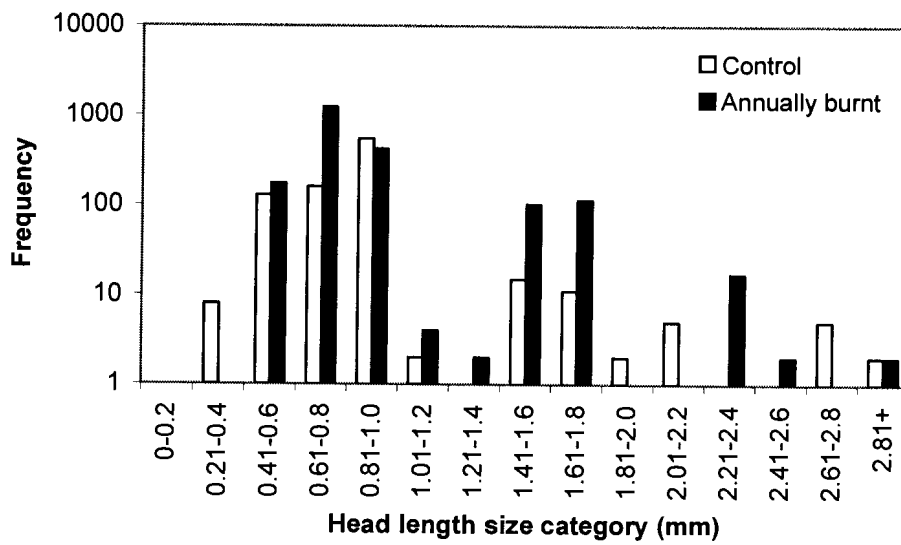


Figure 3. Abundance frequency distributions for head length size (log scale): (a) *Mopane* woodland and (b) *Acacia* savanna.

Despite these clear differences in habitat rugosity, which clearly meet the criteria for significant differences in terms of the size-grain hypothesis (Kaspari & Weiser 1999: 531), there was little support for differences in the ant assemblages in the direction predicted by the size-grain hypothesis. Not only were the allometric relationships consistent across the experimentally manipulated plots but, contrary to the predictions of the size-grain hypothesis, smaller body size classes were no more speciose on the control (rugose) plots than on the annually burnt (planar) plots. Moreover, small ants were more abundant on the annual burn plots than on the control plots. While the size-grain hypothesis is predicated on the basis of differences in species within assemblages, if there is an energetic advantage to long legs in planar environments, it might be expected that these benefits would be realised both by larger individuals and by larger species. No evidence in favour of this idea was found.

Like the study undertaken by Yanoviak and Kaspari (2000), results presented here might be a consequence of sampling bias associated with the methods used. However this is not likely because the pitfall trapping technique used has been shown to be highly efficient for sampling the full epigaeic assemblage in savanna habitats (Parr & Chown 2001). Furthermore, in this instance the size-grain hypothesis has been applied to epigaeic ants experiencing different environmental textures. Had the test been extended to ants that utilise the sparse canopy layer, or dwell below ground, a different result might have been found, owing to differences in the three-dimensional environment that they experience (see Yanoviak & Kaspari 2000); however, this sampling was restricted to the relatively well-defined epigaeic guild of ants for which the size-grain hypothesis makes clear predictions (Kaspari & Weiser 1999: 530) that were not supported in this field-based test.

In sum, although allometric considerations appear to support the size-grain hypothesis, at least two independent tests have found little support for it in the field; other explanations must be sought for the allometric relationships. The most likely candidates appear to be a combination of the requirements for and costs of load carriage and unloaded movement under a variety of environmental conditions related to both rugosity and the thermal landscape (see Feener et al. 1988; Cerdá & Retana 1997; Morehead & Feener 1998). Perhaps most promising among these is the idea that balance is critical for ants to maintain laden speed, and long legs are particularly advantageous in this regard (Nielsen et al. 1982; Burd 2000). In consequence, an allometric increase in leg length with size is not unexpected.

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Chapter 5

The response of Southern African savanna ants to long-term fire regimes

Risokoti ri diele dlopfu
The ants can kill the elephant

- *Shagaan traditional*

Introduction

Although the relative importance of processes structuring local communities is widely debated (see Cornell & Lawton 1992; Lawton 1999; Srivastava 1999; Gaston 2000), it is accepted that both local processes, such as competition, predation and parasitism (see Gaston 2000; Godfray & Lawton 2001), and regional factors, which include the size of regional species pools and evolutionary history (Ricklefs & Schluter 1993; Caley & Schluter 1997; Karlson & Cornell 1998; Gaston 2000; Gering & Crist 2002), contribute significantly to local species richness. Thus, an improved understanding of variation in biodiversity is only possible by determining the relative contributions of local and regional processes to local assemblage structure (Ricklefs 1987; Lawton 1999; Gaston & Blackburn 2002)

As might be expected, both regional and local processes have been shown to make significant contributions to local ant species richness and community composition. Kaspari et al. (2000, 2001) demonstrated that species richness is initially determined by net primary productivity (NPP). That is, NPP sets an upper limit to the species richness of a region. Local processes, such as competition (Savolainen & Vepsäläinen 1988; Andersen 1992; Cerdá et al. 1997), parasitism (LeBrun & Feener 2002) and disturbance (Perfecto & Snelling 1995; Hoffmann et al. 2000; Watt et al. 2002), subsequently interact with regional processes to reduce local species richness below the potential maximum set by NPP. Hence they play an important role in determining ant assemblage structure.

While competition is often considered a key mechanism structuring local ant assemblages (Savolainen & Vepsäläinen 1988; Andersen 1992; Cerdá et al. 1997; see also Chapter 3), the relative importance of other local processes, such as disturbance, is not as well understood. In part, this is because the variety of disturbance types that have been shown to affect ant assemblages is large. These include natural disturbances such as mound building by mammals (Schooley et al. 2000), flooding (Meason et al. 2002), and fire (Swengel 2001), as well as anthropogenic disturbances such as agriculture (Roth et al. 1994; Perfecto & Snelling

1995), mining (Majer 1985; Hoffmann et al. 2000), forest logging (Belshaw & Bolton 1993), invasive species introductions (Vanderwoude et al. 2000; Morrison 2002), and habitat fragmentation (Carvalho & Vasconcelos 1999; Perfecto & Vandermeer 2002).

In Southern African savannas, fire is regarded as a major disturbance. Fire modifies broad patterns in the abundance and distribution of both vertebrates and plants, which are set predominantly by rainfall and edaphic factors (see Andrews & O'Brien 2000; O'Brien et al. 2000; Van Rensburg et al. 2002), and thus plays a crucial role in determining the structure and functioning of these systems (Scholes & Walker 1993; Scholes & Archer 1997; Van Langevelde et al. 2003). While the effects of fire on vegetation are reasonably well documented in Southern African savannas (e.g. Tainton & Mentis 1984; Bond 1997; Trollope et al. 1998a), for animals, and invertebrates in particular, there are few studies detailing the effects of burning (see Trollope 1984; Parr & Chown in press for discussion). Invertebrate studies, focusing on only a handful of taxa (termites, Ferrar 1982, Gandar 1982; beetles and grasshoppers, Gandar 1982; ants, Parr et al. 2002) have produced mixed results. For example, arboreal beetles both increased and decreased in abundance in response to fire (Gandar 1982), and termite abundance increased in fire-protected plots (Ferrar 1982). Given that for Southern Africa there is no other information available on the effects of fire on savanna invertebrates (see also Scholtz & Chown 1993), it is clear that the importance of fire in structuring assemblages of this large and ecologically important savanna group remains unknown.

The lack of understanding of fire effects is particularly concerning given that fire is widely used as a management tool in many of the region's protected areas, where the primary aim is the conservation of biodiversity as a whole (Mentis et al. 1990; Brown et al 1991; Stander et al. 1993; Van Wilgen et al. 1998; Brockett et al. 2001; Parr & Chown in press). Both within reserves, and in extensive livestock farming areas outside them, fire is used for a variety of purposes including the improvement of grazing quality, preventing bush encroachment, and reducing fire risk to infrastructure (Trollope 1982; Edwards 1984; Hough 1993). Managers of protected areas alter aspects of the fire regime (e.g. intensity, frequency, season of burn) by deciding when, where, and how fires should be lit. If the effects of alterations to the fire regime on a variety of taxa are not well understood, then the aims of conserving biodiversity as a whole clearly cannot be met. Fire regimes that promote one taxon might have the converse effect on another (Keith et al. 2002). Equally, there may be little or

no effect of fires on one group relative to those on another. Whatever the case, it is incumbent on managers of protected areas to understand the impacts of fires not only on vegetation and large vertebrates, but also on other taxa, especially if their overriding objective is the conservation of biodiversity (Parr & Brockett 1999).

Unfortunately, many fire studies in Southern Africa (like others elsewhere) tend to be short-term and small scale, while in practice fire policies in protected areas tend to be applied to larger areas for longer periods. Moreover, many fire studies use only a limited range of fire regimes to test community responses (where often the range of fire regimes bears no resemblance to naturally occurring fires), or focus on responses to single fires (for discussion see Parr & Brockett 1999; Parr & Chown in press; Williams et al. in prep). Because the ecological effects of a single fire or the cumulative effects resulting from the imposition of a fire regime (where a consistent sequence of several fires has been applied to an area) may be quite different (Bradstock et al. 1996; Blanche et al. 2001; Moretti et al. 2002), it is important that fire studies make a careful distinction between the two. For studies investigating fire regime effects, long-term fire studies are particularly valuable because if a fire regime has been applied to an area for only a relatively short period of time, it may not be long enough for ecological responses to be detected (see Andersen et al. 1998). The experimental limitations thus often compromise the robustness of the findings of many of these studies (see also Orgeas & Andersen 2001). Moreover, if the studies themselves and the fire regime applied to an area differ considerably, then the utility of the experimental results for management purposes is questionable.

Given that there is a need to provide conservation managers with reliable information on the effects of burning on invertebrates, and that this information should be based on careful experimental design, this study makes use of a long-term fire experiment to investigate the responses of an ant assemblage to a long-term burning regime. The experiment, initiated in 1954 in the Kruger National Park, South Africa, one of the largest protected areas in the sub-region, was originally established to test the effect of different seasons and frequencies of burn on vegetation (Brynard 1964). The experimental treatments were established in four major vegetation types across the park (Trollope et al. 1998b), and within each vegetation type different fire treatment plots (different season and frequency combinations) were replicated four times. These treatments are still currently maintained. Although the fire

experiment was designed with the predominant focus on fire regime effects, in this study the effects of individual fires are also considered.

Specifically, the aims of the current study were to 1) determine what effects season and frequency of burn, and post-fire fuel age (time-since-fire) have on ant species richness and relative abundance, 2) compare the response of ant assemblages to fire in the different vegetation types, and 3) to assess whether any changes in ant assemblage structure can be linked to differences in vegetation structure and habitat composition.

Study area

The study was conducted in the Kruger National Park (KNP), South Africa in three savanna habitats, Mopane woodland (Mopane area), *Acacia* savanna (Satara area) and *Terminalia* woodland (Pretoriuskop area). Ant sampling was carried out on experimental burn plots that form part of a long-term burning experiment initiated in 1954 (see Trollope et al. 1998b). Although there are four replicates within each vegetation type, because the fourth replicate differed in soil type from the other three, it was considered unrepresentative of them (Venter 1999). Therefore, this study only focused on three replicates. Replicates were situated 10 to 20 km apart. Replicates in the Mopane area are Tsende (23°41'S 31°31'E), Mooiplaas (23°34'S 31°27'E) and Dzombo (23°26'S 31°22'E), while in the Satara area they are N'wanetsi (24°26'S 31°51'E), Marheya (24°32'S 31°46'E) and Satara (24°24'S 31°45'E). At Pretoriuskop, the replicates are Kambeni (25°15'S 31°26'E), Numbi (25°13'S 31°20'E) and Shambeni (25°12'S 31°23'E). Each replicate is divided into twelve to fourteen plots laid out in a strip. Each of these plots measures approximately 380 m x 180 m (7 ha) and represents a different burning regime (season and frequency combination) (Trollope et al. 1998b). Fire-break roads separate the plots in each replicate. In the Mopane and Satara areas, sampling was carried out on the following burn plot treatments: August annual, August biennial, August triennial, April biennial, April triennial, and control, which has remained unburnt since 1954. The exception to this was one of the Satara control replicates, which accidentally burnt in April 2001. August burns represent late winter burns at the end of the dry season, while April burns represent autumn burns at the end of the wet season (see Rutherford & Westfall 1986 for a discussion of seasonality in South Africa's biomes).

Additional sampling was also carried out adjacent to each replicate in the general landscape to assess the effect of the general burning regime that had been applied by KNP management: these were referred to as 'variable' plots. Fire records for Mopane and Satara areas (unpublished, KNP Scientific Services, Skukuza) indicate that variable plots were last burnt at least 4 years prior to sampling, and had burnt very infrequently (i.e. twice in last 40 years). Two variable plots (adjacent to the Dzombo and Satara replicates) were older than 20 years. The variable plot for the N'wanetsi replicate burnt in 2001. In the Pretoriuskop area, because of sampling constraints, ants were sampled on two burn plot treatments only: control (unburnt) and August annual plots.

The Satara plots are situated in a mixed Knobthorn (*Acacia nigrescens*, Oliv.) and Marula (*Sclerocarya birrea*, (A. Rich) Hochst.) savanna in the Sweet Lowveld Bushveld (Low and Rebelo 1996). In addition to these trees, Sicklebush (*Dichrostachys cinerea*, (L.) Wight & Arn.), Sandpaper bush (*Ehretia obtusifolia*, Hochst. ex A.DC.) and Jackal Berry (*Diospyros mespiliformis*, Hochst. ex DC.) are also common. The mean annual rainfall in this area is approximately 550 mm, and the altitude ranges from 240 to 320 m (Gertenbach 1983). The Mopane plots are situated in the Mopane shrubveld, a Mopane (*Colophospermum mopane*, J. Kirk ex J.Léonard)-dominated habitat with very few other woody species (Low and Rebelo 1996). The altitude of the Mopane area ranges from 300 to 340 m, and the mean annual rainfall ranges from 450 to 500 mm (Gertenbach 1983). Satara and Mopane areas share basalt derived clay soils (Gertenbach 1983). Dominant grass species in both areas include *Bothriocloa radicans* (Lehm.) A.Camus, and unpalatable *Urocloma mosambicensis* (Hack) Dandy. Annual grasses include *Eragrostis* and *Aristida* spp. The vegetation of the Pretoriuskop area is described by Low and Rebelo (1996) as Sour Lowveld Bushveld. This is an open tree savanna dominated primarily by Silver Clusterleaf (*Terminalia sericea*, Burch. ex DC.), but also with Bushwillow (*Combretum collinum*, Fresen.) and Sicklebush. Grasses in this area are tall, with common species being *Hyperthelia dissoluta* (Nees ex Steud) W.D. Clayton, *Hyparrhenia hirta* (L.) Stapf, and *Heteropogon contortus* (L.) Beauv. ex Roem. & Schult. Soils are sandy and granitic-derived. The mean annual rainfall of 700 mm is substantially higher than that at Satara or Mopane, and altitude ranges from 560-640 m (Gertenbach 1983).

Methods

Ant sampling

Epigaeic ants were collected by pitfall trapping during the two sampling periods of November - December 2000, and January - February 2002 (hereafter referred to as sampling periods 2000 and 2002). In the Pretoriuskop area, sampling was carried out in January and February 2002 only. In the summer rainfall region of South Africa, ants are most active and abundant at this time (e.g. Swart et al. 1999; Lindsey & Skinner 2001). Collections could not be made in November and December 2001 because heavy rains prevented sampling. Pitfall trapping was determined to be the optimum sampling method based on a pilot study comparing winkler and pitfall sampling (see Parr & Chown 2001).

On each plot, 20 pitfall traps (62 mm diameter) were laid out in a grid (5 × 4) with 10 m spacing between traps. All grids were situated at least 50 m from the plot edge to reduce the possibility of ants from adjacent areas being collected in the traps, and to reduce edge effects (vegetation is typically taller and denser along the plot edges probably due to increased runoff and lower intensity of the fires at the plot edge where fire are initiated, Brockett pers comm.). Pitfall traps contained 50 ml of a 50 % solution of propylene glycol, which has been shown to neither significantly attract nor repel ants (Adis 1979). The pitfalls were left to settle to reduce the 'digging-in' effect (Greenslade 1973), and then all traps were opened for a period of five days. A pilot study indicated that this period of time was sufficient for reasonably complete sampling, and it precludes the collection of excessive numbers of ants. There was no rain during the periods that the pitfall traps were open, and the weather during both sampling periods was hot and humid. Pitfall samples that had been destroyed (dug-up by animals) were excluded from the analyses.

Samples were washed in the laboratory, and sorted for ants. Whenever possible ants were identified to species, otherwise they were assigned to morphospecies. Voucher specimens of each species of ant collected are held at the Iziko South African Museum.

Vegetation sampling

To assess the overall effect of fire regime on vegetation, vegetation foliage height profiles (for sampling period 2002), were determined based on the methods discussed by Rotenberry and Wiens (1980) and Bestelmeyer and Wiens (1996). Foliage height profiles provide an indication of the relative vertical complexity of vegetation. Vegetation height was measured at four points located 90° apart on a 1.5 m radius centered on each pitfall trap. At each point, a 1.5 m long pole was placed vertically, and the number of times vegetation came into contact with the pole in each height class (1 = 0-0.25 m, 2 = 0.26-0.50 m, 3 = 0.51-1.00 m, 4 = 1.00-1.50 m) was recorded.

Ground cover was estimated on each plot by placing a 1 m² quadrat next to each pitfall, and estimating the percentage cover of grass, bare ground, litter and dead grass, and forbs.

Analyses: Ant assemblages

To assess the completeness of sampling, species accumulation curves (observed) were plotted for each plot (see Colwell & Coddington 1994). For pitfall samples from 2000 and 2002 combined (maximum of 40 per plot), species accumulation curves for the observed number of species in the pooled samples (SOBS) were computed using EstimateS (Version 5, Colwell 1997). The program randomised sample order 100 times, and averaged randomisations to produce smooth species accumulation curves. In addition, the non-parametric incidence-based coverage estimator (ICE) provided in EstimateS was used to improve the estimate of species richness per plot. ICE has been found to be a promising, and reliable estimator of species richness (see Chazdon et al. 1998; Fisher 1999; Longino et al. 2002) because it stabilises fairly well, and provides an estimate that is independent of sample size. ICE is based on the number of species found in 10 or fewer sampling units (Lee & Chao 1994). Whilst estimators are valuable tools, Longino et al. (2002) stress that they should not be viewed uncritically, and should be considered as yielding minimum estimates of species richness.

Total species richness and abundance were compared between and within habitat types for both sampling periods using Analysis of Variance (ANOVA), and for each habitat type species richness and abundance were also compared between sampling periods. ANOVAs were used to determine if there were any significant differences in species richness and

abundance between replicates and burn plot treatments for each sampling period separately, and combined. This was done for Mopane and Satara areas separately. Variable plots were classified as unburnt if they had burnt infrequently and their post-fire fuel age was greater than the burnt plots in the experiment (time since fire ranged from 4-30 years). The N'wanetsi variable plot was classified as recently burnt since it had burnt prior to sampling in 2002. Because the use of ANOVA requires that data are normally distributed, where necessary data were log transformed (abundance data). For data that could not easily be transformed, non-parametric tests, Mann-Whitney U and Kruskal-Wallis ANOVA, were applied to the data. Sequential Bonferroni corrections were applied to adjust the statistical significance for multiple tests (see Rice 1989).

Multivariate community analyses were undertaken using PRIMER v.5.0 (Clarke & Gorley 2001) to assess overall changes in ant assemblage composition. Cluster analyses using group averaging and Bray-Curtis similarity measures were used to determine whether ant assemblage structure varied between years, and within- and between- habitats. Data were fourth-root transformed prior to analyses to reduce the weight of common species. Analyses of similarity (ANOSIM) were used to establish if there were significant differences in the ant assemblages on plots that differed in burn season (August, April, control and variable), frequency (annual, biennial, triennial, control and variable) and age (i.e. time since fire). The ANOSIM procedure of PRIMER is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke & Warwick 2001). ANOSIM produces a global R-statistic, which is an absolute measure of distance between groups. An R-value approaching one indicates strongly distinct assemblages, whereas an R-value close to zero indicates that the assemblages are barely separable. These R-values were used to compare ant assemblages between habitat types, and burn plot treatments within and between sampling periods.

R-values may occasionally be very low indicating that assemblages are barely separable, but these values may also be significantly different from zero. This reflects a high number of replicates or samples, and the fact that R is inconsequentially small is of greater importance (see Clarke & Warwick 2001). The converse may also be found, where R-values may be very high (indicating that assemblages are almost completely different) but these

values are not significant. This situation occurs when the sample size is small, and in such instances the R-value is of greater importance (see Clarke & Gorley 2001).

The relationships between habitat types and burn plot treatments for both sampling periods combined were displayed using non-metric multi-dimensional scaling (MDS) ordinations. Although the experiment was designed originally to test season and frequency aspects of the fire regime, the effect of individual fires cannot be ignored since different post-fire-fuel ages may result in successional effects (see York 1994). For age analyses, plots were classified as follows: young = 4-5 months since fire, intermediate = 8-16 months since fire, old = 20-28 months since fire, and unburnt = control and variable.

The effects of frequency, season and age were initially assessed using a series of pair-wise ANOSIM tests. First, the age of the plots was varied (young, intermediate and old), while controlling for season and frequency. Ant assemblage composition did not differ with age for these pair-wise tests. Additional pair-wise ANOSIM tests were necessary to determine whether it was possible to combine all frequencies or both seasons when doing subsequent analyses. Thus, frequency of burn was controlled for, while season was altered (pair-wise tests: August biennial vs. April biennial, and August triennial vs. April triennial), and season of burn was controlled for while frequency of burn was altered (pair-wise tests: August biennial vs. August triennial, August annual vs. August biennial, August annual vs. August triennial, and April biennial vs. August triennial). There were no significant differences in ant composition between any of the burn treatment pairs, therefore, for all further analyses both seasons were combined when testing for frequency, and frequencies were combined when testing for effects of season.

Finally, ant species characteristic of the three habitat types (Mopane, Satara and Pretoriuskop), and of burnt and unburnt plots in each area were identified using the Indicator Value method (Dufrêne & Legendre 1997, <http://mrw.wallonie.be/dgrne/sibw/outils/indval/home.html>). This method assesses the degree to which a species fulfils the criteria of specificity (uniqueness to a particular habitat or site) and fidelity (frequency of occurrence). A high indicator value (IndVal, expressed as %) indicates that a species has high specificity and fidelity, and the species can be considered characteristic of a particular habitat or site. This method can derive indicators for hierarchical and non-hierarchical site classifications, and is robust to differences in the numbers of sites

between site groups (McGeoch & Chown 1998). Indicator values for each species were calculated based on a species abundance matrix, and Dufrêne and Legendre's (1997) random reallocation procedure of sites among site groups was used to test for the significance of IndVal measures for each species. Species with significant IndVals >70 % were considered as species characteristic of the site or habitat in question (subjective benchmark, see Van Rensburg et al. 1999; McGeoch et al. 2002).

Analyses: Vegetation

Differences in vegetation structure (vertical complexity) were assessed for each area, by comparing the mean number of hits/ plot in each foliage height category using ANOVA. Vegetation structure was compared between replicates within an area, and between different burn plot treatments.

Percentage cover for each habitat cover component was summed across all quadrats on each burn plot treatment for each replicate. Kruskal-Wallis tests were used to determine whether total habitat cover differed significantly between burn plot treatments. The BIOENV procedure in PRIMER was used to examine the relationship between habitat cover on the plots, and the ant assemblages (Clarke & Gorley 2001). A single, among-site species similarity matrix was constructed using Bray-Curtis similarity measures, while several similarity matrices are constructed for each of the possible combinations of the specified habitat cover variables also using Bray-Curtis similarity measures because measurement scale for all variables was percentage cover. Spearman's Rank correlation coefficients (ρ) were then calculated for the species matrix and each of the possible habitat matrices. The variable or set of variables that have the highest ρ value are those that best explain the species data (Clarke & Gorley 2001). Unfortunately this ρ value does not come with an associated significance value.

In addition, ANOSIM analyses were carried out for Mopane and Satara areas to determine the effect of plot age (single fire effect) on habitat cover composition. The effect of season and frequency of burn (i.e. for fire regime) on habitat cover could not be investigated (as was done for ant assemblages) because ANOSIM tests revealed that there were significant differences in vegetation cover between burn treatments of different ages. Vegetation analyses did not include Pretoriuskop because data were only available for one sampling period.

Results

Ant assemblage composition

A total of 54 736 ants was collected, with 11 184, 40 736, and 2 816 individuals collected in the Mopane, Satara and Pretoriuskop areas, respectively. A total of 160 ant species comprising 37 genera was recorded in pitfall traps for all areas combined (Table 1). The richest genera were *Tetramorium* (29 species), followed by *Monomorium* (26 species), *Camponotus* (17 species), and *Pheidole* (13 species). *Pheidole* species were the most abundant ants in all habitats. At Mopane, *Pheidole* sp. 3 represented 18.4% of all ants, and together all *Pheidole* species represented 45 % of all ants. At Satara, *Pheidole* sp. 2 accounted for 34.1 % of all ants, and together all *Pheidole* species represented 56.6 % of all ants. At Pretoriuskop, although the most abundant species was *Crematogaster* sp. 5 (17.9 % of all ants), *Pheidole* species still accounted for nearly a third of all ants caught (31.5 %).

Sampling completeness

Species accumulation curves for the observed number of species in the pooled samples (SOBS) indicate that sampling was fairly complete, and that the majority of ant species on each plot were sampled (Fig. 1a-i). The species accumulation curves for some plots are still increasing slightly (e.g. Dzombo April triennial plot, Marheya control plot). This is probably because additional species that are being recorded are rare hypogaieic or arboreal species (e.g. *Hypoponera* spp.) but are unlikely to be critical to the overall analysis and findings.

Species richness, relative abundance, and fire effects

There was a significant difference in species richness across the three habitats (ANOVA, $F_{(2,45)} = 34.69$, $p < 0.0001$). Mean species richness/plot was greatest at Pretoriuskop (mean 39.0 species/ plot, SE = 3.38), intermediate at Satara (28.19 species/ plot, SE = 1.78), and lowest at Mopane (mean 15.67 species/ plot, SE = 0.97). There was no significant difference in mean species richness between sampling periods (2000 and 2002) for Satara, although in Mopane, mean species richness was higher in 2000 (ANOVA, $F_{(1,40)} = 11.04$; mean species richness/ plot and SE = 20.09 ± 0.87 and 15.67 ± 0.97 for 2000 and 2002 sampling periods respectively).

Table 1. Species richness and abundance for each area in KNP per sampling period, and for both sampling periods combined. n = total number of pitfall traps summed across all plot types, and sampling years.

	Mopane n = 791	Satara n = 815	Pretoriuskop n = 120
<i>Species richness</i>			
2000	81	95	-
2002	69	111	89
2000 & 2002	98	121	-
<i>Abundance</i>			
2000	8306	16 169	-
2002	2878	24 567	2816
2000&2002	11 184	40 736	-

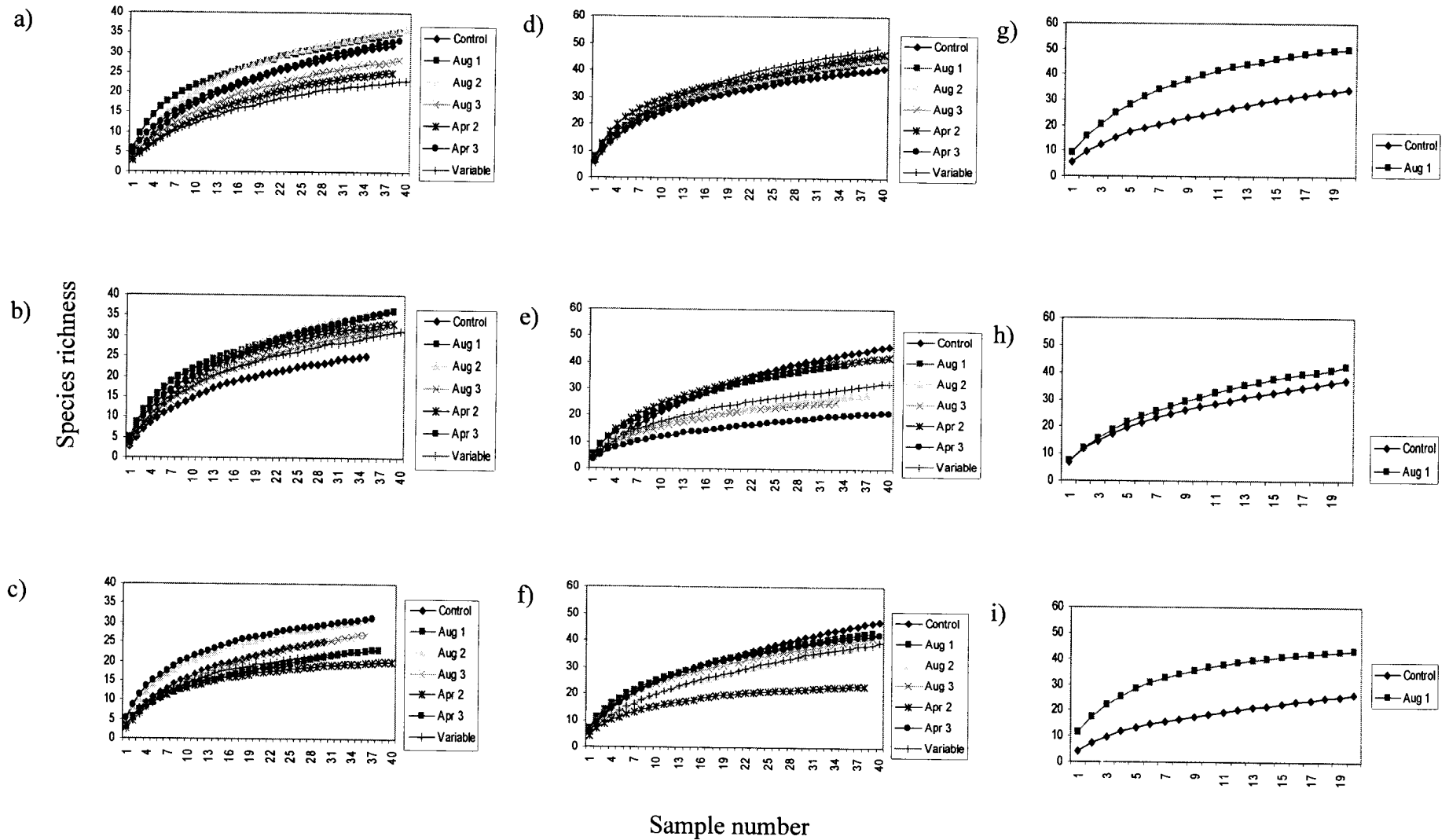


Figure 1. Species accumulation curves for burn plots on each replicate in Mopane, Satara and Pretoriuskop areas indicating completeness of sampling, a-c) Mopane: Dzombo, Mooiplaas and Tsende replicates, d-f) Satara: N’wanetsi, Marheya and Satara replicates, g-i) Pretoriuskop: Numbi, Shabeni and Kambeni replicates.

At Mopane and Satara when all burn plot treatments were compared, there was no significant difference in mean species richness between burn plot treatments for either sampling period or when both sampling periods were combined. At Pretoriuskop, mean species richness was marginally significantly higher on annual than on control plots (Mann-Whitney U test, $p = 0.049$, d.f. = 2).

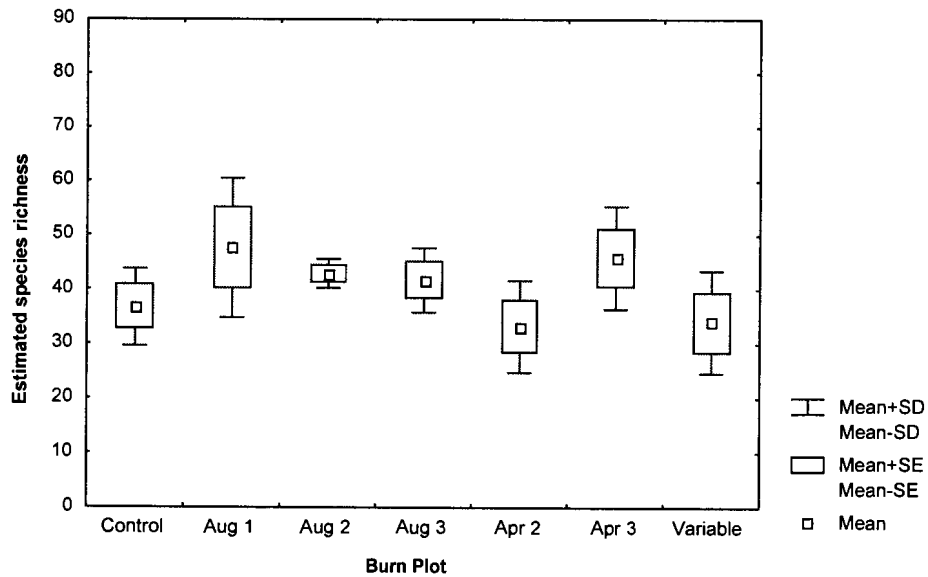
There was also no significant difference in the estimated total number of species using ICE between burn plot treatments in both the Mopane and Satara areas (ANOVA, $F_{(6,14)} = 1.34$, $p = 0.30$ and $F_{(6,14)} = 1.14$, $p = 0.39$ for Mopane and Satara respectively) (Fig. 2).

The effect of single fires on species richness was also assessed for Mopane and Satara areas. No clear trends could be detected in terms of responses to individual fires when species richness/ plot for each sampling year was plotted for each replicate (Fig. 3a-f). For example, at Mopane, the August biennial burn prior to the second sampling period resulted in species richness increasing at Dzombo, showing little change at Mooiplaas, and declining at Tsende (Fig. 3a-c). At Satara, the April biennial burn before the second sampling period resulted in both an increase (N'wanetsi replicate) and decrease (Marheya and Satara replicates) in species richness (Fig. 3d-f). Single fire events did not result in consistent predictable trends, and local site differences (i.e. differences between replicates) appeared to be more important in determining species richness.

There was a significant difference in ant abundance across the three habitats (ANOVA, $F_{(2,45)} = 40.01$, $p < 0.0001$). Mean abundance (log) was greatest at Satara (mean abundance = 2.92, SE = 0.07), intermediate at Pretoriuskop (mean abundance = 2.60, SE = 0.09), and lowest at Mopane (mean abundance = 2.04, SE = 0.07).

There was no significant difference in abundance (log) between burn plot treatments for both Mopane and Satara. This was consistent for both sampling periods: 2000 ($F_{(6,14)} = 2.00$, $p = 0.13$ and $F_{(6,14)} = 1.75$, $p = 0.18$ for Mopane and Satara, respectively), and 2002 ($F_{(6,14)} = 1.62$, $p = 0.21$ and $F_{(6,14)} = 1.96$, $p = 0.14$ for Mopane and Satara, respectively).

a)



b)

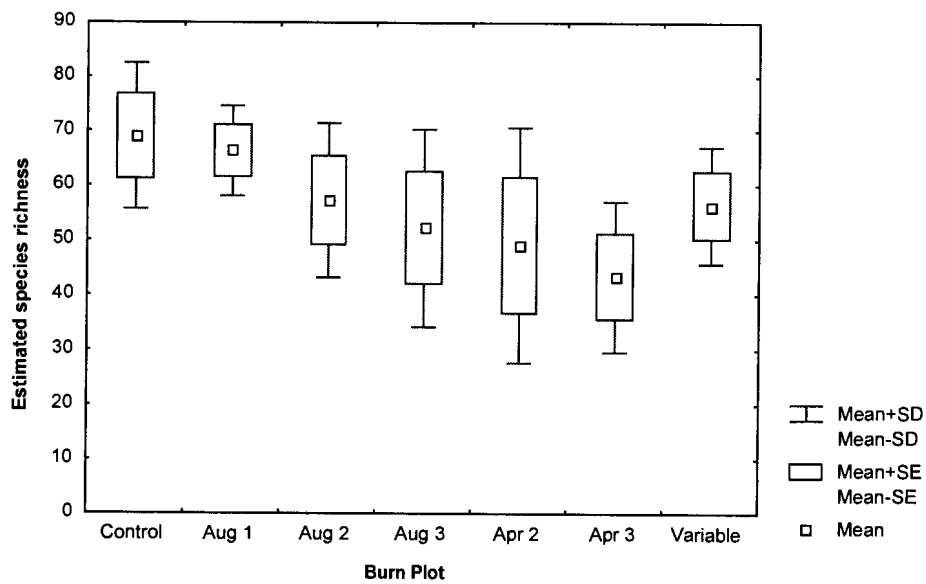


Figure 2. Estimated species richness (ICE) for (a) Mopane and (b) Satara, for each burn plot treatment. Aug 1 = August annual burn, Aug 2 = August biennial burn, Aug 3 = August triennial burn, Apr 2 = April biennial burn, Apr 3 = April triennial burn.

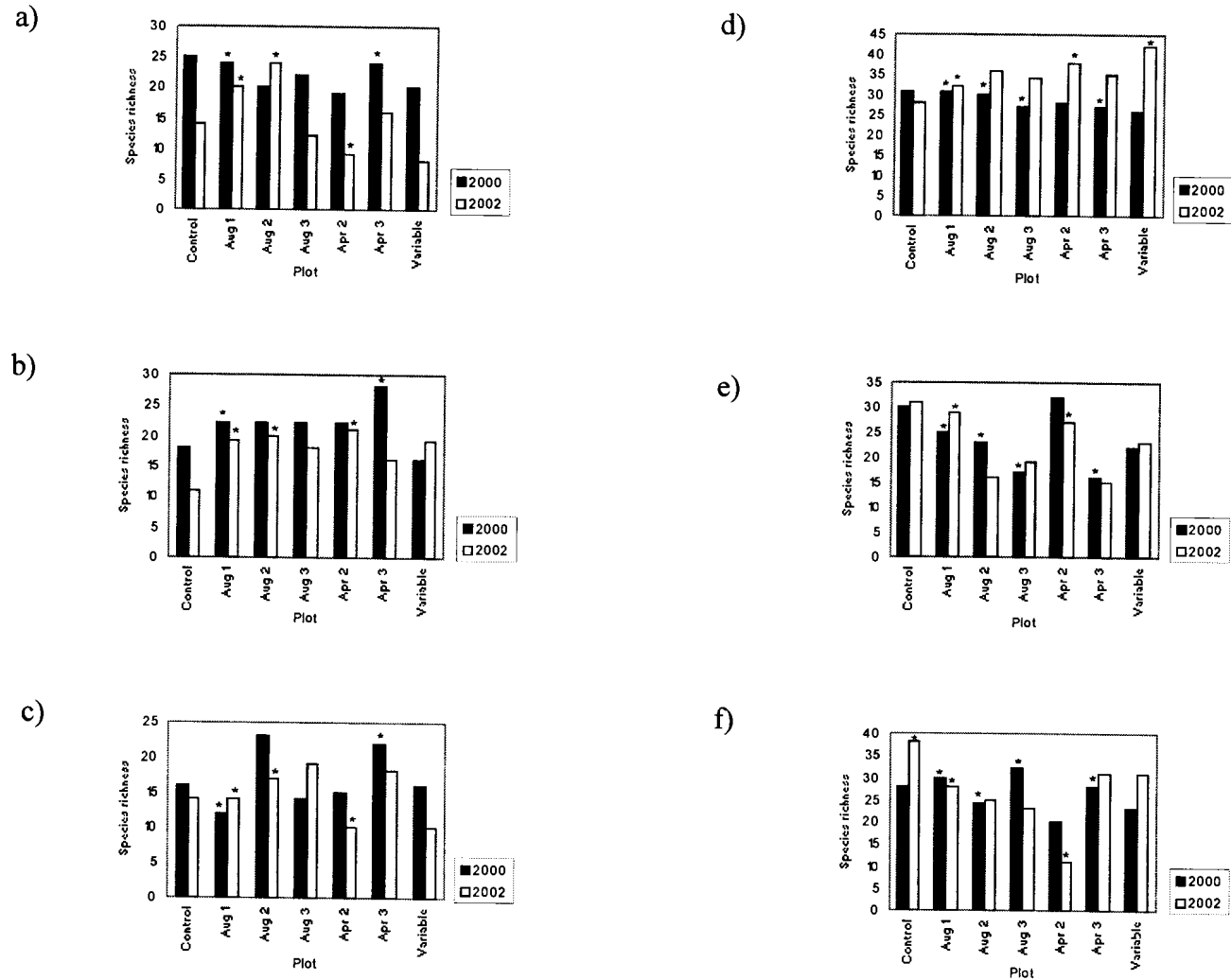


Figure 3. Species richness for burn plots on each replicate for sampling periods 2000, and 2002, a-c) Mopane: Dzombo, Mooiplaas and Tsende replicates, d-f) Satara: N'wanetsi, Marheya and Satara replicates. * indicates plots that burnt in the year prior to the sampling period. Overall for each replicate there is little difference in species richness patterns between sampling periods, which indicates that individual fires do not have a large and consistent effect of species richness.

Community compositional changes

Within each habitat, ant assemblages were barely separable between sampling periods ($R = 0.178$, $p = 0.001$ and $R = 0.085$, $p = 0.005$ for Mopane and Satara, respectively). Thus, for all subsequent analyses for each area, data for 2000 and 2002 were combined. There were significant differences between the ant assemblages occupying the different habitat types (Global $R = 0.448$, $P < 0.001$, Fig. 4).

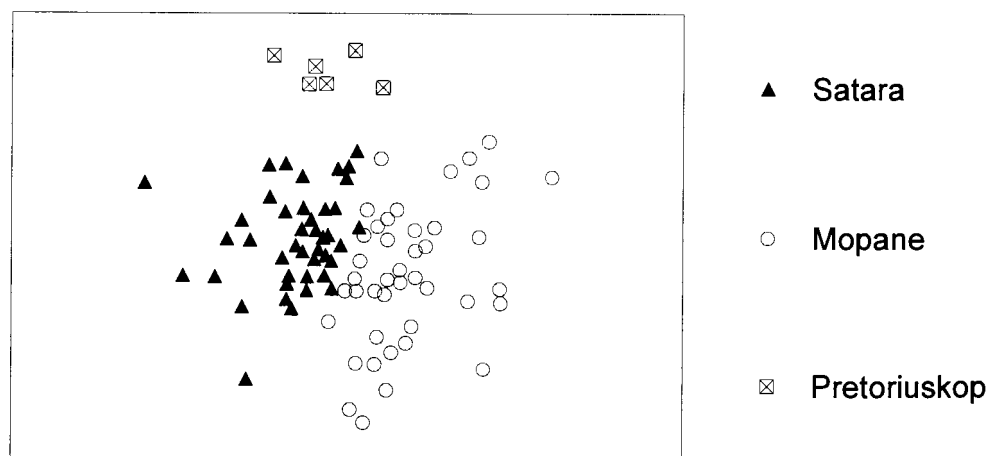


Figure 4. Non-metric MDS ordination of abundance of ant species in three different savanna habitats in KNP (stress = 0.23). Satara vs. Mopane, $R = 0.349$, $p = 0.001$; Mopane vs. Pretoriuskop, $R = 0.788$, $p = 0.001$; Satara vs. Pretoriuskop, $R = 0.831$, $p = 0.001$.

Mopane

A two-way crossed ANOSIM revealed that there was a significant difference in ant community composition between replicates with the Tsende replicate being significantly different from the Dzombo replicate ($R = 0.538$, $p = 0.001$), and from the Mooiplaas replicate ($R = 0.344$, $p = 0.001$). To remove the effect of landscape from our analyses, data for the Tsende replicate were therefore excluded for all other analyses.

All ANOSIM tests revealed that there was no effect of fire frequency on ant assemblage composition, and only a small effect of season of fire, with ant assemblages on August plots being significantly different from those on control and variable plots (see Table 2). In terms of age, or time since fire, control plots, which are never burnt, were significantly different from young and intermediate-aged plots (irrespective of season or frequency). Although young plots were significantly different to old plots the R-value was low indicating substantial overlap between assemblages (Table 2).

Satara

Ant assemblages did not differ significantly between the three replicates. Cluster analyses revealed that ant assemblage composition on the Satara replicate control plot (both sampling periods) was more similar to annually burnt plots than to control plots on the other replicates. Thus, because the Satara replicate control plots differed so much from control plots on the other replicates, and because an unburnt control plot was necessary for baseline comparison, the Satara replicate control plots were excluded from further analyses.

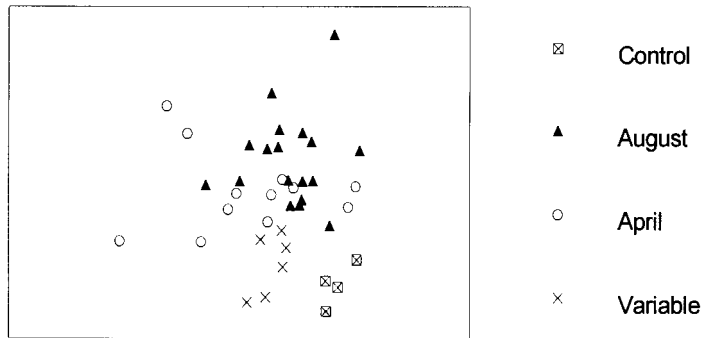
Pair-wise ANOSIM tests on experimental burn plots revealed that differences in ant assemblage composition lay between burnt and unburnt plots, rather than between burning treatments (Table 2). Ant assemblages on variable plots differed significantly from those on control plots, August plots, and on plots burnt annually and triennially. Significant differences in assemblage composition were found with season and frequency of burn, and plot age (post-fire fuel age) (Table 2, Fig. 5a-c), although differences occurred between unburnt (control and variable plots), and burnt plots, not between August and April burns. Differences in ant assemblage composition were much more pronounced between August and control plots than between April and control plots (higher R value, and lower significance level). Ant assemblages on plots with annual and triennial burn frequencies were more dissimilar to

Table 2. Analysis of similarity for ant assemblages between plots types for Mopane and Satara areas (data for 2000 and 2002 sampling periods combined). The R statistic is a measure of the similarity of assemblages, and reflects the degree of separation of assemblages: the closer the value to 1, the greater the difference in assemblage composition (Clarke & Warwick 2001). *P* is significant at the α -level of 0.05 using sequential Bonferroni tests for each fire parameter (Rice 1989). Significance level is denoted by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Age: Y = 4-5 months since fire, I = 8-16 months since fire, O = 20-28 months since fire, U = unburnt.

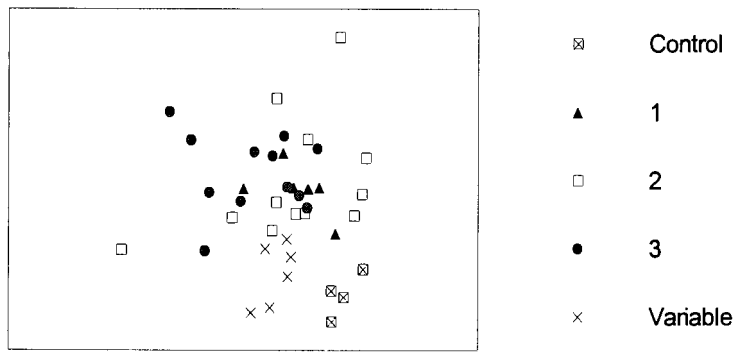
<i>Area</i>	Mopane		Satara	
	R	p	R	p
<i>Fire parameter</i>				
Season				
Control vs August	0.444	NS	0.654	**
Control vs April	-0.009	NS	0.383	NS
August vs April	0.180	NS	0.102	NS
August vs variable ^a	0.472	NS	0.357	**
April vs variable ^a	0.053	NS	0.121	NS
Frequency				
Control vs annual	0.219	NS	0.909	**
Control vs biennial	0.143	NS	0.317	NS
Control vs triennial	0.085	NS	0.709	***
Annual vs biennial	-0.125	NS	-0.180	NS
Annual vs triennial	-0.057	NS	0.115	NS
Biennial vs triennial	0.098	NS	0.060	NS
Annual vs variable ^a	0.250	NS	0.533	**
Biennial vs variable ^a	0.171	NS	0.098	NS
Triennial vs variable ^a	0.138	NS	0.440	**
Age				
U vs Y	0.458	**	0.589	***
U vs I	0.274	NS	0.569	**
U vs O	-0.167	NS	0.417	**
Y vs I	0.098	NS	0.101	*
Y vs O	0.250	***	0.103	*
I vs O	0.035	NS	0.192	**
Control vs variable ^a	-0.250	NS	0.726	**

^a Variable plots vary in age (time-since-fire) from 4 years to >20 years old, thus although these plots have burnt at some time, then are generally older than the experimental burnt plots, and several are much closer in age to control plots.

a)



b)



c)

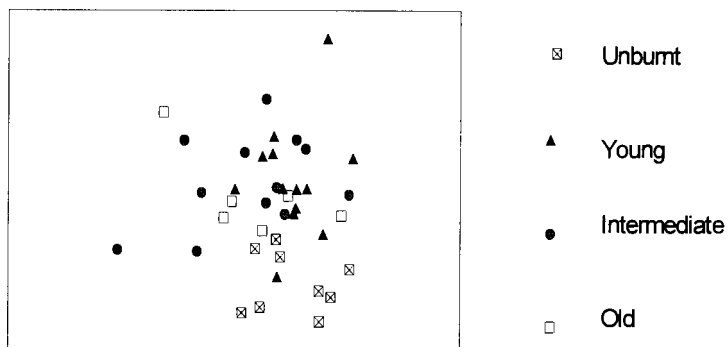


Figure 5. Non-metric MDS ordination of abundance of ant species in Satara, KNP based on: (a) season of burn, (b) frequency of burn, (c) age (stress = 0.21). Frequencies: 1 = annually burnt, 2 = biennially burnt, and 3 = triennially burnt. Age: young = 4-5 months since fire, intermediate = 8-16 months since fire, old = 20-28 months since fire, unburnt = control and variable plots >4 years old. For ANOSIM results see Table 2.

control and variable plots than assemblages on plots with biennial burn frequencies (Table 2, Fig. 6b).

There was no significant difference in assemblage composition between burnt plots of different ages (i.e. between young, intermediate and old plots, not including unburnt plots). Of the burnt plots, young and intermediate aged plots were most different from unburnt plots ($R = 0.589$, $p = 0.001$ and $R = 0.568$, $p = <0.01$ for young vs. control and intermediate vs. control respectively).

Pretoriuskop

Although the ant assemblages on control and August annually burnt plots differed considerably (ANOSIM, $R = 0.630$, $p = 0.1$), the small number of replicates ($n = 3$) meant the difference was not significant (see Clarke & Gorley 2001).

Fire regime effect on individual species

Given that the responses of ant assemblages to fire lay between burnt and unburnt plots only, and not between burning treatments, IndVal analyses were carried out to identify characteristic species, first, with control and August annually burnt plots only (based on hierarchical clustering), and second, using non-hierarchical clustering with plots classified according to area and plot type (control and burnt plots) prior to analysis (see McGeoch & Chown 1998). This second IndVal analysis, using all burn plots classified either as burnt or control plots, allows the robustness and applicability of potential indicators identified from the first analysis to be confirmed.

Using abundance data from all plots, IndVal analyses revealed that there were three species that could be considered as generalists and characteristic of all three areas (*Tetramorium frigidum* Arnold, *Monomorium albopilosum* Emery, and *Tetramorium setigerum* Mayr). These indicator values were not significant because significance at the level of the hierarchy cannot be determined due to the nature of the permutation procedure used to calculate significance (Duf rene & Legendre 1997). Potentially reliable indicators for habitat type could only be found for Satara and Pretoriuskop areas (Table 3). There were no species that could be regarded as indicators of plot type (annually burnt, burnt or control) in the Mopane area. At Satara, there were only three species characteristic of control plots (when

Table 3. Percentage indicator values (IndVal >70 %) of ant species for each area and burn plot type (hierarchical clustering: annually burnt and control plots, and non-hierarchically clustered: burnt plots and control plots). * = maximum indicator values.

Classification	Satara	% IndVal	Pretoriuskop	% IndVal
<i>Areas</i>	<i>Pheidole</i> sp. 2	87.3*	<i>Pheidole</i> sp. X	94.3
	<i>Monomorium zulu</i>	82.5*	<i>Crematogaster</i> sp. 2	82.9*
			<i>Monomorium</i> sp. 7	81.5*
			<i>Lepisiota</i> sp. 8	80.0
			<i>Pyramica</i> sp. 1	79.6*
			<i>Tetramorium</i> sp. 2	78.0*
			<i>Oligomyrmex</i> sp. 2	71.7*
<i>Annual & control plots</i>				
Annual	-	-	<i>Monomorium notulum</i>	100.0*
			<i>Lepisiota</i> sp. 6	98.7*
			<i>Monomorium</i> sp. 2	86.6*
			<i>Tapinoma</i> sp. 1	76.8
			<i>Pheidole</i> sp. X	70.1*
Control	<i>Tetramorium sepositum</i>	100.0*	<i>Plagiolepis</i> sp. 4	100.0*
	<i>Pheidole</i> sp. 7	97.4*	<i>Lepisiota</i> sp. 1	82.0*
	<i>Tetramorium gladstonei</i>	93.8*		
<i>Burnt & control plots</i>				
Burnt	-	-	<i>Monomorium notulum</i>	98.0*
			<i>Lepisiota</i> sp. 6	96.7*
			<i>Lepisiota</i> sp. 8	85.9*
			<i>Monomorium</i> sp. 2	80.4*
			<i>Pheidole</i> sp. X	80.0*
			<i>Tapinoma</i> sp. 1	79.4*
			<i>Crematogaster</i> sp. 2	70.0
Control	-	-	<i>Solenopsis</i> sp. 1	82.1

annually burnt and control plots only were used), and no species characteristic of either burnt or unburnt areas when all burn plot types were used. Satara had fewer characteristic species with high abundance and high site fidelity than Pretoriuskop.

For Pretoriuskop, all five of the species that were identified as indicators of annually burnt plots, were also identified as indicators of burnt plots when plots were classified as either burnt or control plots i.e. with a coarser classification (Table 3). This serves to confirm the robustness of species such as *Monomorium notulum* Forel or *Lepisiota* sp.6 as indicators of burnt areas. In addition, almost all species identified as indicators for Pretoriuskop (area and plot type) reached their maximum level.

Vegetation vertical complexity and fire effects

In both Mopane and Satara areas, replicates did not differ significantly in the vertical complexity of vegetation, but for each area when all burn plot treatments were compared there were several significant differences in the vertical complexity of vegetation between plots (see Table 4). At Mopane there was no significant difference in vegetation complexity between burn plot treatments for the two lowest height strata (i.e. up to 50 cm). However, for the upper two foliage height classes (51-100 cm and 101-150 cm stratum) there was a significant difference between control plots and all other burn plot treatments (Table 4). Vegetation on the control plots was denser and taller.

At Satara, for each height stratum there was a significant difference in vegetation complexity between burn plot treatments (Table 4). Foliage height profiles for the two lowest strata indicated that annually burnt plots had a lower height and density of vegetation compared to all other plot treatments, while differences in structural complexity for the upper strata indicated the presence of taller vegetation (grasses and shrubs) on control and variable plots. Differences in vertical complexity at Pretoriuskop were most pronounced for the upper strata, with much greater density of vegetation on control plots.

Table 4. One-way ANOVA tests results for differences in vegetation structural complexity between burn plot treatments for each height class (sampling period 2002). Significance level is denoted by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Mopane		Satara	
	F _(6,14)	p	F _(6,13)	p
<i>Height (m)</i>				
0-0.25	2.20	NS	3.82 ^A	*
0.26-0.50	2.07	NS	7.29 ^A	***
0.51-1.0	5.83 ^B	**	7.12 ^B	**
1.0-1.50	13.03 ^B	***	15.76 ^B	***

^A denotes significant difference between annually burnt plots and other plot types.

^B denotes significant difference between control plots and other plot types.

Habitat cover and fire effects

BIOENV analysis revealed that at Mopane the overall pattern in ant assemblage composition was best explained by grass cover ($\rho = 0.214$). At Satara, the habitat cover variables that best explained overall pattern in ant assemblages were bare ground and litter ($\rho = 0.203$), and bare ground ($\rho = 0.272$) for sampling periods 2000 and 2002, respectively.

There was a significant difference in habitat cover overall between sampling periods at Satara ($R = 0.583$, $p = 0.001$), but not at Mopane. Thus, for subsequent ANOSIM analyses, the two sampling periods for Satara were analysed separately. The difference in cover between sampling periods at Satara indicates that the effect of individual fires on habitat cover is greater at Satara than at Mopane.

In both areas there was a significant effect of plot age (effect of single fires) on habitat cover with young plots (i.e. most recently burnt) differing significantly from unburnt plots (Table 5). The effect of plot age on habitat cover was more pronounced at Satara than at Mopane; not only were the R-values higher at Satara, but also there were differences in

Table 5. ANOSIM results for effect of post-fire-fuel age on habitat cover for Mopane and Satara. The R statistic is a measure of the similarity, and reflects the degree of separation of assemblages: the closer the value to 1, the greater the difference in assemblage composition (Clarke & Warwick 2001). *P* is significant at the α -level of 0.05 using sequential Bonferroni tests for each column (Rice 1989). Significance level is denoted by * $p < 0.05$, ** $p < 0.01$. Age: Y = 4-5 months since fire, I = 8-16 months since fire, O = 20-28 months since fire, U = unburnt.

<i>Area</i>	Mopane		Satara			
	R	p	2000		2002	
	R	p	R	p	R	p
Age						
U vs Y	0.429	*	0.958	**	0.982	NS
U vs I	0.175	NS	0.667	NS	0.486	*
U vs O	-0.102	NS	-0.012	NS	-0.073	NS
Y vs I	0.127	NS	-0.020	NS	-0.026	NS
Y vs O	0.260	**	0.789	**	0.524	**
I vs O	0.027	NS	0.333	NS	-0.019	NS

habitat cover between intermediate aged and unburnt plots, and young and old plots which were not apparent at Mopane. The response of ant assemblages to plot age was similar to that found for habitat cover: not only were R-values higher at Satara than Mopane, but also ant assemblages at Satara responded to a wider range of age combinations. The vegetation analyses also illustrated that fire has a greater effect on vegetation than on ant assemblages because for the habitat cover analyses, R-values were often higher (indicating a stronger effect), and there were also differences between burnt plots rather than just between burnt and unburnt plots (Tables 2 & 5).

The immediate effect of burning is the consumption and removal of vegetation by fire, which increases the amount of bare ground. In both Mopane and Satara there was a significant difference in bare ground cover between burn treatment plots in both sampling periods: Kruskal-Wallis, $H = 15.73$, $p = 0.015$ and $H = 13.70$, $p = 0.018$ for Mopane and Satara in 2000 respectively, and Kruskal-Wallis, $H = 14.78$, $p = 0.02$ and $H = 10.46$, $p = 0.005$ for

Mopane and Satara in 2002 respectively. Control plots had very little bare ground, but tended to have higher litter loads: Kruskal-Wallis, $H = 16.71$, $p = 0.01$ and $H = 7.93$, $p = 0.02$ for Mopane and Satara 2002 sampling respectively.

Discussion

Ant assemblages and response to fire

Ant species richness and abundance differed significantly between the three areas in KNP. These differences between areas correspond to broad underlying differences in habitat type (*Mopane savanna*, *Acacia savanna*, *Terminalia savanna*) and soil type (clay and sand). Net primary productivity (NPP) has been closely correlated with rainfall in Southern Africa (see O'Brien et al. 1998; Van Rensburg et al. 2002). It therefore seems reasonable to assume that differences in rainfall between the three areas also correspond to differences in NPP. This idea is also supported by differences in vegetation between the three areas. It appears that differences in ant species richness may be linked to variation in NPP: ant richness was lowest in Mopane which has the lowest rainfall (and presumably NPP), intermediate at Satara, and highest at Pretoriuskop where rainfall (and presumably NPP) is highest (see Gertenbach 1983; see also Chapter 3). These findings thus concur with Kaspari et al. (2000) who found that regional richness of ants is correlated with NPP.

However, within each area when all burn plot treatments were compared, fire had no effect on either mean species richness or mean abundance. This contrasts with other studies carried out across a range of habitat types, which have found that ant species richness is generally lower in areas that remained unburnt for long periods (see Donnelly & Giliomee 1985; Andersen 1991, York 1994), and higher in areas that have recently burnt (Andersen & Yen 1985). Furthermore, contrary to a number of other studies, including several conducted in savanna systems, ant species richness in this savanna system did not decline with time since fire (see Donnelly & Giliomee 1985; Andersen 1991; York 1994; Parr et al. 2002; Hoffmann 2003). Although some studies have documented an increase in the abundance of ants following a fire (Andersen 1991; York 1999) and others have recorded a decrease (Andersen & Yen 1985), in this system no consistent trends were found.

Despite the absence of a significant effect of burning on mean ant species richness and abundance between burn plot treatments, there were clear differences in ant assemblage

structure, in keeping with many other studies across a wide range of habitats (e.g. tropical savanna woodland, Andersen 1991; Vanderwoude et al. 1997; York 1999, low-latitude steppe, Farji-Brener et al. 2002, desert grassland, Zimmer & Parmenter 1998). Despite these broad overall differences between treatments, across all areas the only pronounced response that could be detected was between burnt and unburnt plots, and not between different burning treatments. The ant assemblages in KNP thus exhibited a high degree of resistance to burning (i.e. remaining largely unchanged or unaltered following a disturbance, see Pimm 1984) at least for the burning regimes used in this study. Indeed, ant assemblages at Mopane exhibited quite remarkable resistance to burning; even after >40 years of annual burning, ant assemblages on this plot did not differ significantly from the fire exclusion plot. By contrast, at Satara, ant assemblages displayed a wider range of responses to fire than those in Mopane.

The identification of indicator species also reflects how the ant assemblages in the three areas of KNP differed in their response and resistance to burning. No reliable indicators of habitat could be identified for the Mopane area despite clear differences in ant assemblages with area and habitat type. For Satara and Mopane the number of species that could be identified as displaying significant responses to fire (i.e. indicators) was very low (three species out of a possible 121 species in Satara, and out of a possible 98 species in Mopane, no species were identified). The larger number of potential indicators at Pretoriuskop suggests that fire has a greater effect on ant assemblages in this habitat than Satara or Mopane. These findings are in keeping with those from other savanna systems where ant assemblages were also found to be highly resistant to fire, with relatively few species exhibiting clear and significant responses to fire (Parr et al. 2002; Hoffmann 2003).

In addition to high resistance, ant assemblages also displayed little change between sampling periods (i.e. with single fires): trends in species richness for each replicate were quite consistent across sampling periods, particularly at Satara, despite the number and identity of plots that burnt varying between sampling periods (Fig. 3). In fact, patterns in species richness appeared to be determined more by the replicate site than burn plot treatment, with patterns in species richness varying substantially between replicates within the same area (Fig. 3). A variety of factors (e.g. historical context, invasion sequence and environmental variability) have been shown to cause assemblages to differ between replicates (for discussion see Drake 1991; Lockwood et al. 1997; Jenkins & Buikema 1998; Fukami 2001). It is likely

that the effect of individual fires on ant species richness would have been more pronounced at the beginning of the experimental burn plot trial when all plots would have had a similar fire history, than much later after the repeated application of many fires when ant assemblages may have diverged (see Fukami 2001). The application of the same long-term treatment to replicates therefore does not guarantee the same deterministic path (see Drake 1991; Fastie 1995; Chambers & Samways 1998).

The ant assemblages investigated in this study were also highly resilient to fire (i.e. they quickly return to their pre-fire state; see Pimm 1984). This was particularly evident at Mopane where, although there was a significant difference between young and unburnt plots, there was no significant difference between intermediate aged and unburnt plots. Thus only eight months after a fire, the assemblage has returned to its pre-fire state.

Vegetation and ants: fire regime and single-fire effects

The results from the Satara area confirmed the importance of bare ground and litter cover as factors responsible for overall structuring of ant assemblages (see also Andersen 1991; Crist & Wiens 1994; Bestelmeyer & Wiens 1996). Reduced litter cover on burnt plots is likely to result in the loss of cryptic species from these areas (see Robertson 1999; York 2000). For example, in KNP, dacetine ants such as *Strumigenys*, *Pyramica* and *Calyptomymex* spp. that forage and nest within and beneath leaf litter, would be particularly vulnerable to fire. In most savanna systems, however, fire has little direct impact on epigeic ants since many ant species nest in the soil, and they are therefore largely protected from fire (see Andersen & Yen 1985). More importantly for ants, the effects of fire are primarily considered to be indirect through changes in vegetation structure and habitat composition (Lévieux 1983; Andersen & Yen 1985; Greenslade 1997; Chambers & Samways 1998).

The application of repeated fires to an area alters vegetation structure and composition (see Trapnell 1959; Trollope 1984; Trollope & Tainton 1986). The effects of fire on vegetation structure were more pronounced at Satara than at Mopane (Table 4). At Mopane, low biomass accumulation at ground level due to low rainfall is likely to account for the lack of difference in vegetation complexity between plot burn treatments for the two lower height strata. Long-term application of fires at Mopane and Satara caused differences in vegetation structure (for the two upper height strata) between control and burnt plots (Table 4). The high

resistance of Mopane ants to burning, and the responses of ant assemblages to burning at Satara can thus also be interpreted as a response to changes in habitat structure as well as habitat cover. Differences in ant assemblage composition between burnt and unburnt plots are likely to be related to changes associated with habitat structure such as different microhabitat, food resource availability, and biotic interactions (Greenslade & Greenslade 1977; Lynch et al. 1988; York 1999).

It was clear from this study that in Mopane and Satara, the effects of individual fires were much more pronounced on vegetation cover than on ant assemblages: while habitat cover differed almost completely between unburnt and young, the difference in ant assemblages was less pronounced (i.e. lower R-values) (Tables 2 and 5). Furthermore, the effect of fire on both vegetation and ant assemblages was less marked at Mopane than at Satara (e.g. lower R values at Mopane than Satara for both habitat cover and ants on young and unburnt plots). In Mopane, lower biomass accumulation, means there is a smaller change in habitat cover post-fire than at Satara (see also Farji-Brener et al. 2002). Thus the lack of response of Mopane ants to burning can be interpreted as a result of a limited difference in habitat cover and vegetation structural complexity at ground level (see Table 4 & 5). At Satara, where rainfall (and thus biomass accumulation) is higher, the change in habitat cover following a fire is greater. It thus takes longer for habitat cover variables to return to pre-fire levels, hence differences in vegetation cover and ant assemblages are evident for longer (e.g. between intermediate and unburnt plots, as well as between young and unburnt plots). These vegetation differences thus also explain the higher resilience of ant assemblages at Mopane than Satara.

Why such resistance?

Although other studies have also found that ant assemblages can be relatively resistant to fire (see Friend & Williams 1996; Siemann et al. 1997; Andersen & Müller 2000; Parr et al. 2002; Hoffmann 2003), the ant assemblages in this savanna system exhibited a remarkable degree of both resistance and resilience to burning. The degree of response of ant assemblages is likely to be related to two main contributory factors: mean annual rainfall and changes in vegetation structure with burning, and the assemblage's history of association with fire.

It is likely that the greatest effects of burning on ant assemblages will be in areas with the greatest change in vegetation structure following a fire, or series of fires. Typically the greatest long-term change in vegetation structure occurs in wooded or forested habitat with high rainfall. Thus, in high rainfall areas (such as tropical savannas or sclerophyllous forests in Australia) ant assemblages exhibit strong responses to burning because fires generally have a large impact on habitat structure due to high biomass accumulation (see Andersen 1991; York 1994, 2000; Vanderwoude et al. 1997). Conversely, in lower rainfall areas (such as semi-arid savannas and grasslands) where biomass loads are generally lower, fire typically has less effect on vegetation structure, and thus the effect on ant assemblages is reduced (see Siemann et al. 1997; Farji-Brener et al. 2002; Parr et al. 2002; Hoffmann 2003). Although in KNP the Mopane area is wooded, the combination of low rainfall (450 mm/ year, Gertenbach 1983) and the fact that *M. colophospermum* is rarely killed by fire (it rather coppices) means that the vegetation in this area remains wooded, although tree height may vary. Thus, the lack of response of ant assemblages to fire in this area might be because vegetation changes with fire are too subtle to affect the ants. By contrast, in Pretoriuskop, high rainfall (700 mm/ year, Gertenbach 1983) and the relatively wooded habitat result in very pronounced differences between burnt and unburnt plots, and thus very different habitats for ants.

Finally, where taxa have had a long association with fire, they are likely to display greater resistance and resilience to burning (Andersen & Müller 2000; Orgeas & Andersen 2001). It has been suggested, for example, that grass-layer arthropods in the savannas of Ivory Coast may be particularly responsive to the effects of burning because the savannas are only relatively recently derived from forests due to anthropogenic clearing, and thus the assemblages are less adapted to fire (Gillon 1983). In southern and eastern African savannas, the biota has had a long history of frequent, extensive fires (i.e. human ignited fires, and not just lightning fires), with the controlled use of fire dating back about 1.0 – 1.5 million years ago (Gowlett et al. 1981; Brain & Sillen 1988) and more extensive use estimated at 250 000 years ago (see Pennisi 1999). By contrast, in Australia where ant assemblages have been shown to exhibit a greater response to burning, extensive frequent use of fires by humans is much more recent dating from about 50 000 – 40 000 years ago (see Kershaw 1986).

Conservation implications

In this savanna system, fire has a relatively small and indirect effect on ant assemblages. The response of ants to fire was less affected by the subtleties of when and how often an area burnt, than the simple distinction of whether an area burnt or not. Although there are some effects of individual fires, these do not persist for long (less than a year). A possible exception to this overall trend is in higher rainfall areas where fire can play a greater role, and more detailed investigation in these areas is required.

Nonetheless, it seems clear that for the central and northern areas of the Kruger National Park, and indeed for similar savanna areas in southern Africa (see also Parr et al. 2002), at least for ants the type of fire is not crucial in structuring assemblages. Rather the effects have to do with the presence or absence of fire, and even then ant assemblages appear to be remarkably resistant and resilient to fire. This finding contrasts strongly with the idea that fire is an important disturbance in savanna systems (Scholes & Walker 1993; Van Langevelde et al. 2003).

This resistance of southern African savanna ant assemblages to burning has considerable implications for savanna conservation and fire management in protected areas. Indeed it means that managers can afford to be fairly flexible in their approach to burning. The extent to which the responses of other invertebrates to fire reflect those of ants is not known, but based on findings from elsewhere (see Andersen & Müller 2000; Orgeas & Andersen 2001) it seems likely that a large number will also be highly resistant to burning. Conservation managers can thus focus conservation and research efforts on taxa or area (e.g. botanically important areas) of particular concern. Because there may be other taxa with different burning requirements (Keith et al. 2002), adaptive management principles should be adopted to deal with this uncertainty.

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Chapter 6

Burning issues for conservation: a critique of faunal fire research

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He was moving through a new order of creation, of which few men had ever dreamed. Beyond the reaches of the sea and land and air and space lay the realms of fire which he alone had been privileged to glimpse. It was too much to expect that he would also understand.

- Arthur C. Clarke

Introduction

Fire is a major disturbance force in many biomes across the world including forests (Johnson 1992), grasslands (Tainton & Mentis 1984), savannas (Walker 1987) and Mediterranean systems (Keeley 1986). As a multi-scale process, fire plays a key role in determining the structure, functioning and dynamics of these systems (Cowling 1987; Scholes & Walker 1993; Scholes & Archer 1997). It is therefore important to be able to predict and understand community responses to fire, especially when managing for biodiversity. Historically most fire studies have concentrated on the effects of fire on vegetation (Pyne 1997; for examples see Phillips 1919; Trapnell 1959; Daubenmire 1968; Stronach & McNaughton 1989), although many conservation organisations now have as their primary goal the conservation of biodiversity as a whole. Therefore, it is essential that information on the effects of fire on groups other than plants is available for management purposes. However, the effects of fire management on biodiversity as a whole, or even on smaller, less charismatic vertebrate taxa, have rarely been comprehensively addressed, except perhaps in an indirect fashion by assuming that vegetation heterogeneity can frequently be used as a surrogate measure of biodiversity (or at least species richness) (Bradstock et al. 1995; Brockett et al. 2001). Despite the fact that fire management for biodiversity conservation is constrained by inadequate knowledge (Bradstock et al. 1995), fire continues to be used as a management tool in many protected areas (e.g. see Stander et al. 1993; Russell-Smith 1995; Biggs & Potgieter 1999). Therefore, there is clearly a need for information on the effects of fire management policies on all aspects of diversity, or at the very least on the effects of fire at the species, population and community levels for a broad range of taxa.

In this paper we use examples of fire studies in the Southern African sub-region to provide an overview of the published information on the effects of fire on fauna. Fire is used in the sub-region as a rangeland management tool both in agriculture and in conservation (Edwards 1984; Mentis & Bailey 1990; Brockett et al. 2001). In the latter case, fire was

applied from the early 1950s based on a controlled pastoral model of burning, which altered the suitability of landscapes and pastures, primarily for large herbivores (Pyne 1997). However, rather than purely reviewing the effects of fire on fauna, we offer an assessment of the way studies have been conducted and document the foci of fire ecology research in the region. This approach was adopted because a first reading of the literature indicated that although considerable work had been done in the field, much of it requires substantial interpretation to determine what the effects of fire have been. Currently, most faunal responses to fire are understood in only very general terms. For large grazing mammals, fire acts as a generalist herbivore (Bond 1997), removing dead vegetation, and initiating a flush of new growth. This is particularly valuable in winter and spring when food quality and quantity are limiting. It appears that small mammal responses are characterised by recolonisation succession post-fire (see Rowe-Rowe 1995), while for certain bird species fire has a marked influence on feeding and breeding strategies (e.g. Dean 1987). Invertebrate studies are so few that making broad generalisations is problematic.

It is thus crucial that fire research be sufficiently well documented to extend understanding and to enable informed decisions for biodiversity conservation to be made. Therefore, rather than reviewing the outcome of the work, we assess approaches adopted in these investigations, provide information on the spatial and temporal extents of the work, list the taxa that have been most regularly studied, and highlight the extent to which the effects of the many different parameters that characterize fire have been investigated. By critically evaluating fire studies in Southern Africa, we highlight key information that is largely absent, and suggest ways in which the experimental design of fire studies both in Southern Africa, and elsewhere in the world, can be improved to maximize the return from the often large investment that is made in this work (e.g. see Trollope et al. 1998), and in turn, to maximize the utility of future studies to conservation managers.

Because fire ecology research in Southern Africa, like in many other fire-prone biomes, has often been conducted under the auspices of statutory organizations, results have frequently been presented in 'in-house' reports (e.g. unpublished CSIR reports). In consequence, the issue of 'grey literature' must be addressed, especially because much of the information contained in these reports would be overlooked in a review that focused purely on

published literature. For instance in *'Ecological Effects Of Fire In Southern Africa'* (de V. Booyesen & Tainton 1984) the majority (57%) of the references relating to the effects of fire on fauna were either from the grey literature, or were personal communications or observations. Of the remaining published citations, 41% of these were from journals that are not listed by the Institute for Scientific Information (ISI). For studies on vegetation in the same book, grey literature and personal communication-based citations accounted for 47.5% of all references. While there may be much useful information tied up in such publications and observations, the incentives to make this information more broadly available are often lacking. In consequence, reports generally only have a limited circulation, and are often not held for extensive periods in libraries, even of the institutions for which the reports were written (CLP, unpublished information), making access problematic. Furthermore, it is extremely difficult to assess the reliability of the information (even though it often becomes adopted as accepted wisdom), because of an absence of careful reporting of methods and results. Thus, for these reasons we have chosen not to consider grey literature. In the future, however, the accessibility allowed by the World Wide Web might help to reduce the difficulties associated with the grey literature.

Rather, we have based our assessments on the 57 published studies that constitute the literature on the effects of fire on fauna for the Southern Africa sub-region, published between 1965 and 2002 (Table 1 - studies published prior to 1965 are primarily observational reports, and were excluded on these grounds). These 57 studies include several that focus on a variety of taxa and methods. Therefore, the number of investigations of particular taxa or approaches varies between 57 and 77.

Hierarchical scope and biome coverage

Most fire studies in Southern Africa have concerned large and small mammals and birds, while few studies have examined the effects of fire on invertebrates (Fig. 1). Only a single study has focussed specifically on the effects of fire on reptiles (tortoises; Wright 1988), and none have reported influences on amphibians. Much of the work on large mammals has been

Table 1. Published literature used in this study.

Taxa	Order/species	Source
Birds	Drongos, hornbills and rollers	Paintin (1965)
	Coursera	Kemp & Maclean (1973)
	Dusky lark	Dean (1974)
	Dickinson's Kestrel	Hanmer (1978)
	Greywing and Redwing Francolins	Mentis & Bigalke (1979)
	Greywing and Redwing Francolins	Mentis & Rowe-Rowe (1979)
	Various	Crope <i>et al.</i> (1981)
	Greywing and Redwing Francolins	Mentis & Bigalke (1981)
	Hornbills	Gandar (1982)
	Bald ibis	Manry (1982)
	Bald ibis	Manry (1984)
	Bald ibis	Manry (1985)
	Kestrel, buzzard and kite	Barnard (1987)
	Various	Dean (1987)
	Various	Dean (1989)
	Various	Fraser (1989)
	Various	Fraser (1990)
	Helmeted Guineafowl	Malan (1998)
	Greywing and Redwing Francolins	Jansen <i>et al.</i> (1999)
Oxpeckers	Robertson & Jarvis (2000)	
Invertebrates	Isoptera	Ferrari (1982)
	Orthoptera, Coleoptera & Isoptera	Gandar (1982)
	Hymenoptera	Donnelly & Giliomee (1985)
	Hymenoptera	Fraser (1990)
	Orthoptera	Chambers & Samways (1998)
	Metastigmata	Zieger <i>et al.</i> (1998)
Large mammals	Hymenoptera	Parr <i>et al.</i> (2002)
	Blesbok	Du Plessis (1972)
	Blesbok and springbok	Novellie (1978)
	Various antelope	Oliver <i>et al.</i> (1978)
	Various antelope	Mentis & Rowe-Rowe (1979)
	Various antelope	Rowe-Rowe (1982)
	Various antelope	Rowe-Rowe (1983)
	Elephant	Bell & Jachmann (1984)
	Oribi	Shackleton & Walker (1985)
	Elephant	Lewis (1987)
	Various antelope	Novellie (1990)
	Oribi	Everett <i>et al.</i> (1991)
	Various ungulates	Shackleton (1992)
	Roan antelope	Dörgeleh (1998)
Elephant	Kennedy (2000)	
Various rare antelope	Gureja & Owen-Smith (2002)	
Small mammals	Various rodents	Christian (1977)
	Multimammate mouse	Meester <i>et al.</i> (1979)
	Various	Mentis & Rowe-Rowe (1979)
	Various	Kern (1981)
	Various	Swanepoel (1981)
	Various	Willan & Bigalke (1982)
	Various	Rowe-Rowe & Lowry (1982)
	Various	Breytenbach (1987)
	Various rodents	Bowland & Perrin (1988)
	Various rodents	Fraser (1990)
	Various	Botha & LeMaitre (1992)
	Bush Karoo rat	Kerley & Erasmus (1992)
	Various	Van Hensbergen (1992)
	Various	Bowland & Perrin (1993)
	Various	Rowe-Rowe (1995)
	Various	Els & Kerley (1996)
	Rodent- <i>Lemniscomys rosalia</i>	Monadjem & Perrin (1997)
Rodent- <i>Mastomys natalensis</i>	Monadjem & Perrin (1998)	
Murid rodents	Monadjem (1999)	
Reptiles	Angulate tortoise	Wright (1988)

done at the species level and specifically on antelope (e.g. oribi (*Ourebia ourebia*) (Shackleton & Walker 1985), grey rhebuck (*Pelea capreolus*), mountain reedbuck (*Redunca fulvorufula*), eland (*Taurotragus oryx*) and blesbok (*Damaliscus dorcas phillipsi*) (Rowe-Rowe 1983)), and elephants (*Loxodonta africana*) (Lewis 1987; Kennedy 2000). Perhaps expectedly, given generally low trapping returns, the bulk of the small mammal work has been concerned with assemblage responses to fire (e.g. Bowland & Perrin 1988). Most of the work on birds has been undertaken at the species level, and only on the responses of a few species to fire. Thus, 35% (7/20) of all bird studies focus on two species of francolin (*Francolinus levaillantii* and *F. africanus*) (e.g. Mentis & Bigalke 1979, 1981), and the Southern bald ibis (*Geronticus calvus*) (Manry 1984, 1985). Most other work has examined single species such as two of the coursers (*Rhinoptilus cinctus* and *Cursorius temminckii*) (Kemp & Maclean 1973), the dusky lark (*Pinarocorys nigricans*) (Dean 1974), fork-tailed drongo (*Dicrurus adsimilis*) (Paintin 1965), grey hornbill (*Tockus nasutus*) (Gandar 1982), helmeted guineafowl (*Numida meleagris*) (Malan 1998), oxpeckers (*Buphagus erythrorhynchus* and *B. afrucabus*) (Roberston & Jarvis 2000) and several species of raptor (Dickinson's kestrel (*Falco dickinsoni*) (Hanmer 1978), rock kestrel (*Falco tinnunculus*), jackal buzzard (*Buteo rufofuscus*) and black-shouldered kite (*Elanus caeruleus*) (Barnard 1987)).

Despite the wealth of invertebrates present in fire-driven biomes, and their importance in ecosystem functioning (e.g. Scholtz & Chown 1993; McGeoch 2002), work has been carried out on only a handful of taxa, including beetles (Gandar 1982), termites (Ferrar 1982), ants (Donnelly & Giliomee 1985; Parr et al. 2002), grasshoppers (Gandar 1982; Chambers & Samways 1998) and ticks (Zieger et al. 1998). The paucity of invertebrate studies is in part a consequence of the initial focus of research on the influence of burning practices on vegetation (e.g. Phillips 1919; Trapnell 1959), and later on the large mammals that were of primary conservation interest (e.g. Oliver et al. 1978). However, insufficient taxonomic knowledge of invertebrates (the taxonomic impediment – see Samways 1994) also increases the complexity of such studies, and might thus have deterred potential investigators (indeed some studies have measured responses solely at the family level – see Gandar 1982).

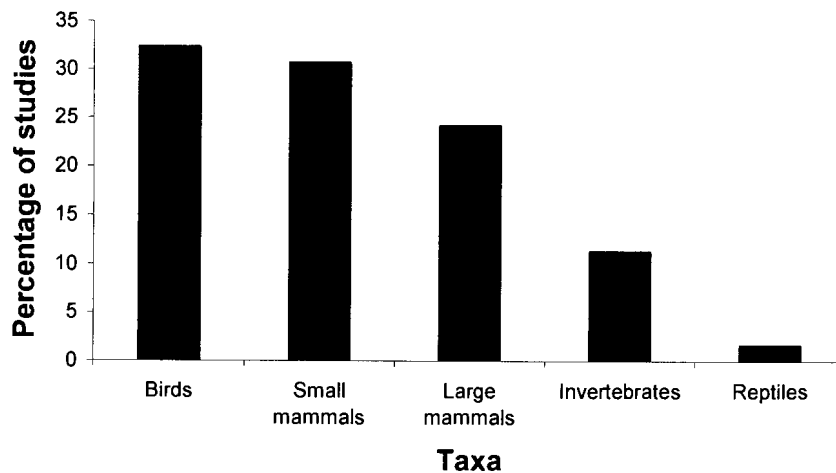


Figure 1. The percentage of published studies on the effects of fire on each of the major taxa in Southern Africa.

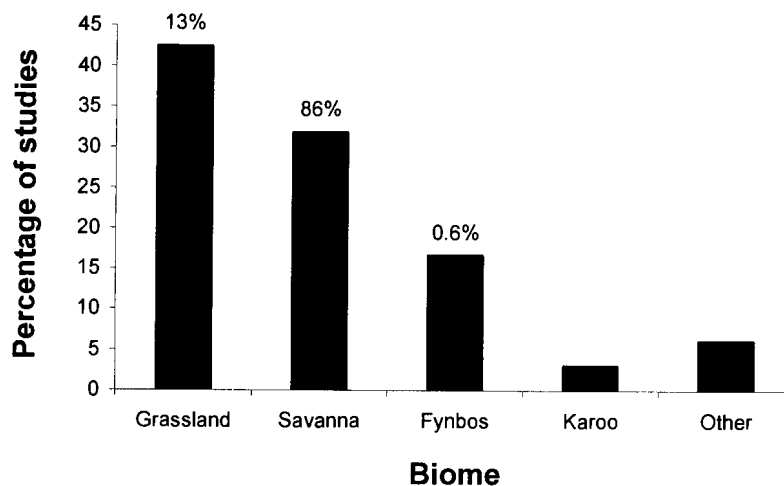


Figure 2. The percentage of studies on the effects of fire on animals in the Southern African biomes. The category ‘Other’ includes studies on agricultural land and studies where the biome is not explicitly mentioned. Relative percentage area of the total area of Southern Africa covered by fire-prone biomes is indicated above the bars, except for ‘Karoo’ which is not typically considered fire-prone, and ‘Other’ which includes studies in grazed land in several biomes.

In terms of the coverage of the subregion's biomes (see Rutherford & Westfall 1986; Low & Rebelo 1996) studies have covered all of the fire-prone biomes with most work being done in the Grassland and Savanna biomes, which, respectively, make up approximately 13% and 86% of fire-prone biomes in the sub-region. There is little information available on the effects of fire on Fynbos animals (Fig. 2). The latter is surprising, despite this biome's small size (0.6% of fire-prone biomes in the sub-region), for several reasons. Fire is considered vital in this biome (Cowling 1992), the Fynbos is the major constituent of the geographically smallest floral kingdom (Low & Rebelo 1996), and there are many species endemic to the biome (see Lombard 1995; Picker & Samways 1996; Willis et al. 1996).

Experimental design

As in all conservation management, it is crucial that the management objectives are clearly articulated at the outset. The stated objectives, such as the state of diversity required, determine the research approach that should be adopted to ascertain how the management goals could be met, and, to some extent, how the research should be implemented. The effects of fire on fauna can be assessed in several distinct ways. These range from the use of remote sensing to develop fire histories combined with local sampling to estimate the effects of change (e.g. Russell-Smith et al. 1998, 2002), use of once-off large-scale events, modelling (e.g. McCarthy & Lindenmayer 1999), Bayesian inference, and manipulations based on careful experimental design. In combination these approaches represent a powerful suite of tools to address the effects of fire on fauna.

If an experimental approach is adopted, sound design is essential for decisive tests of competing hypotheses (Hairston 1989; Underwood 1997). This includes explicit consideration of the key components of experimental design, i.e. controls, replication, randomisation, and interspersed (Hurlbert 1984), to avoid problems of scale, variability, replication and control that commonly plague biological experiments. In general, the care with which each experiment is designed (and executed) provides a measure of the reliability of its conclusions (Underwood 1997; Raffaelli & Moller 2000). Thus, poorly designed experiments are unlikely to produce the results necessary for critical testing of hypotheses.

The fire studies examined here were classified as (1) observational reports, (2) reports of inferred effects, and (3) experimental tests of effects. Many early studies on fauna, especially those on birds (e.g. fork-tailed drongo, Paintin 1965; Dickinson's kestrel, Hanmer 1978), were observational reports mostly of feeding habits during a fire. These kinds of observational studies can be usefully applied to generate further hypotheses for investigation, and consequently, if carefully documented, are valuable. In this context, several studies have also inferred the effect of fire, although in many cases no evidence to support the inferences was provided. For example, Robertson and Jarvis (2000) suggest that oxpeckers may be declining as a result of increased area and frequency of burning which reduces the abundance of their food source (ticks), but neither the change in tick abundance nor fire regime was directly examined.

Studies explicitly testing the effects of fire can be grouped into those carried out in a general landscape of burning, and explicit tests with an experimental set-up where fire is applied to plots. Few of the burning experiments undertaken to date have been specifically set up as fire experiments, with 87% (55/63) of studies taking place in a landscape of general burning. These are field experiments where control is only exercised over one or two variables, and often the manipulation of variables is not specifically for the purpose of the experiment. For example, the primary aim of burning may be for firebreaks to protect property, and not explicitly for a fire experiment (for an example see Manry 1985). Of the field experiment studies, 16.4% (9/55) were conducted opportunistically on accidentally burnt areas, while a third (19/55) of studies failed to state clearly if the fire was planned or not. Only 9% (6/63) of all the fire studies we examined were explicitly experimentally designed (e.g. Chambers & Samways 1998). Of these, only half ($n = 3$) were long-term experiments (ranging from 26 to 40 years). Clearly, this general lack of adequate control over the experimental design is likely to introduce much uncertainty in the data (Hairston 1989), and thus cast doubt on any mechanistic conclusions of the effects of fire on fauna based on these experiments. At best, much of the published literature on fire in Southern Africa should therefore be considered a series of observational reports which might suggest mechanisms, but which seldom test them.

Scale

Fire as a multi-scale process has consequences on biodiversity over a range of scales. Thus, for experiments in fire ecology to produce meaningful results, the most appropriate scale for the questions posed should be chosen. However, despite the obvious importance of scale in ecology (see Wiens 1989; Levin 1992), many investigators failed to report the extent of the area burnt or sampling area, and it is often difficult to ascertain the grain or resolution of their work (i.e. sampling unit size). Most studies (68%, 43/63) did not provide any information about the size of the area burnt, nor whether data were collected from the whole area or a portion of it. Information on the extent of the study area is critical because the results of studies undertaken over small areas differ considerably from those undertaken over larger areas owing to area-related differences in fire characteristics (e.g. intensity, Gill et al. 1990) and ecological responses (e.g. changes in density and species richness, Turner et al. 1997). The incorrect scaling of fire experiments can also produce misleading results. Frequently, replicated fire experiments are undertaken at too small a scale, which limits the applicability of results. For example, in the botanical study by Le Maitre (1988) in which the regeneration of Proteaceae after fire was investigated in Cederberg Mountains, South Africa, seedling predation by small mammals was dramatically enhanced owing to movement of animals into the small plots (<1ha), from the surrounding area, making comparisons with the more common, large burns impossible. Large-scale experiments enable the study of fire effects on landscape level patterning, and provide a different view of ecosystem structuring and functioning to smaller scale studies. These experiments are, however, usually undertaken in a natural landscape, and are regularly beset by problems such as inadequate replication.

Spatial Replication

When all studies were considered, most authors provided little information on replication and whether the sampling was repeated in different years. Although sampling in a number of studies was replicated (28%) (this ranged from 2 to 54 replicates, mean = 6.8, SD = 12.0, 18/63), a substantial number were either partially replicated (e.g. sampling in only one habitat type was replicated, while other habitat types were not replicated), or not replicated at all (40%, 25/63). Furthermore, in a surprising 32% (20/63) of the studies it was not clear what

was done, nor whether there was any replication. Pseudoreplication was also a feature of many studies where several sampling grids, or several traps were often set on an area burnt by one fire (e.g. Botha & Le Maitre 1992). The issue of replication in such instances is further complicated because frequently no information is given as to the fire size and the spacing of 'replicates'. In many cases, the understanding of studies could be improved enormously simply by providing unambiguous reporting and a complete description of methods. Sound replication remains a fundamental requirement of much scientific work (for an ecological perspective see Hurlbert 1984; Hairston 1989), and, where possible, a prerequisite for experimental ecology (Carpenter 1990). Thus, the absence of replication, especially in small-scale experimental studies, is concerning.

When replication is not possible: the alternatives

Although classical experimental design and statistics stress the importance of replication, there are instances where replication, especially in fire ecology, is not always possible. Infrequent, extreme disturbances, such as fires, can have an important influence on ecosystem dynamics (Lertzman & Fall 1998), and as such cannot be excluded from research solely on the basis of replication problems. Large-scale experiments can prove almost impossible to replicate, usually owing to a lack of funding, logistic constraints, and/or the heterogeneity of ecosystems (Carpenter 1990), and the extreme nature of the fire events. In instances such as these, where replication is not possible (e.g. the South African Cape Peninsula fires of 2000), the lack of replication can be overcome with alternative approaches. For example, investigations could be based on 'natural experiments' where the fire history of an area is documented using remote sensing and areas with different fire histories compared using local sampling. Other approaches include the use of detailed observation, inference, and modelling, and the use of non-classical approaches to statistical analyses, to differentiate between alternative hypotheses (Carpenter 1990; Hilborn & Mangel 1997; Innes 1998). Using alternatives such as observation and inference to evaluate results from non-replicated experiments may be particularly useful for management situations when immediate action may be required before statistical significance can be obtained (Hilborn & Mangel 1997).

Bayesian methods might also prove to be useful for analyses of single, non-replicated events, observational studies, incomplete data sets, and other problems that conventional statistical analysis cannot adequately address (Reckhow 1990; Hilborn & Mangel 1997; Anderson 1998). Bayesian analysis assesses the probability of a hypothesis being true based on previous experience (prior probability). New information (data from a new experiment) is then considered in the light of the prior probability, and the degree of confidence in the hypothesis modified. This process can be repeated indefinitely so that the degree of confidence in any hypothesis is a function of the current balance between what was known before, and new knowledge from additional data. This method thus allows the estimation of how much confidence should be placed in each hypothesis under consideration. Bayesian analysis differs from classical statistics because it is based on prior probability estimates (quantitative statements of previous experience), and it allows intermediate degrees of probability to be assigned to hypotheses, rather than traditional all-or-nothing inferences ('reject/accept the hypothesis') (Anderson 1998). A Bayesian model averaging approach was used by Platt et al. (2002) to determine whether prior fire regimes were linked to the survival of pine trees in Florida after a single, large-scale event, Hurricane Andrew. Hilborn and Mangel (1997) also provide several worked examples of Bayesian analysis. Although Bayesian inference has received little attention from ecologists to date, it can offer a viable and flexible solution to many studies that might otherwise never have been conducted, or published.

Temporal replication

Where replication is limited, repeating the experiment may, in some instances, also increase the robustness of results (Raffaelli & Moller 2000), although this is not a solution to poorly designed experiments. Only 36.5% (23/63) of studies we examined were repeated temporally, with a further third of them (21/63) not being repeated at all. Although many studies were repeated in successive months or seasons, such repetition is plagued both by the statistical problem of temporal autocorrelation (Hurlbert 1984) (which can be accounted for), and the biological problem of seasonality. While repetition of a study on the same date over successive years may also be confounded by autocorrelation and inter-annual variability, the

effects of non-independence are likely to be at least somewhat reduced. Furthermore, repetition of a particular experiment under similar conditions, though at a different place and time can be extremely useful for assessing the repeatability of results and thus the robustness of conclusions (Carpenter 1990; see McGeoch 1998, 2000).

Duration

Fire has an impact on fauna through the effects of given fire events, and the cumulative effects resulting from the imposition of a fire regime, where a consistent sequence of several fires has been applied to an area (Bradstock et al. 1995; Blanche et al. 2001). Because the direction and magnitude of response to a disturbance may differ temporally, short-term observations of a system (especially in variable environments like savannas) do not necessarily provide a useful estimation of long-term impacts (see also Yodzis 1988; Raffaelli & Moller 2000). Therefore, the ecological effects of an individual fire may be quite different to those resulting from a fire regime. For example, immediately after a fire, ant abundance has been shown to increase and then decline (Andersen 1988). However, with the application of a particular fire regime, ant abundance may generally remain consistently lower (York 1999). Likewise, a short-term study might indicate that an increase in the abundance of a given species coincides with a fire, while a longer term study might demonstrate that the increase had more to do with rainfall changes than with the fire itself (see Blanche et al. 2001). Moreover, if a fire regime has only been applied for a few years this may not be long enough to detect an ecological response, especially because the new regime has to override the effects of the previous one (Andersen et al. 1998). Changes might also be too subtle to detect in the short-term, and may only be detectable once a threshold has been reached, or the effects might be cumulative (see Orgeas & Andersen 2001). Thus, a short-term experiment might be especially prone to a conclusion of no effect.

Despite the obvious importance of the duration of the experiment, and the clear need to report it, nearly a third of the works we examined failed to specify the duration of the study. Of the remainder, many were short-term, carried out over a period of a year or less (49% of the total). Nearly forty percent (24/63) of studies examined here concerned individual fires, and a third (21/63) were conducted on systems with an applied fire regime. The majority of

studies focusing on fire regime were, however, short-term experiments (only three out of 12 studies are based on long-term experimental fire regimes, with the minimum being 22 years: Kern 1981; Chambers & Samways 1998; Kennedy 2000). This is not surprising however, given that reliable long-term fire records are the exception rather than the norm (see Van Wilgen et al. 2000; Brockett et al. 2001). For the remaining studies it was unclear whether the study was carried out on an individual fire or in an area with a consistent fire regime applied for some time.

Fire parameters

In most studies, the effect of burning was quantified in terms of both faunal species relative and absolute abundance, species richness, and to a lesser extent, density (usually per ha or km²). The fire parameters that were used to test these faunal responses were varied (Fig. 3). Many studies (30%, 23/77) investigated the presence of a burn by comparing the effect of burnt and unburnt areas (adjacent areas) on various taxa. Time-since-fire (or post-fire fuel age) was also well studied (31% of studies, 24/77), as was season (17% of studies, see Dean 1974; Gandar 1982; Rowe-Rowe 1982 for justification of the importance of investigating seasonal effects). Few faunal studies focused on the frequency of burning (only 9% of studies, 7/77), and none investigated the effects of fire intensity. In studies on the responses of vegetation to fire these parameters are frequently thought to be significant and are therefore examined (e.g. Trollope & Tainton 1986; Bond & Van Wilgen 1996).

Burn patch size, fire shape (e.g. linear or rounded) and burn heterogeneity or patchiness may contribute to the maintenance of diversity (Bradstock et al. 1995; Parr & Brockett 1999). The shape, size and patchiness of a fire are important because they could affect animal movements (during and after a fire) and the potential to survive on unburnt islands or refugia, and hence re-colonisation possibilities (Collett et al. 1993; Bradstock et al. 1995). A study by McCarthy and Lindenmayer (1999) illustrates the importance of disturbance regimes such as fire in influencing metapopulation dynamics. Core and edge effects, and the influence of fire on metapopulation dynamics (such as spatial synchrony) could be tested by integrating information about survival after a fire with data on dispersal,

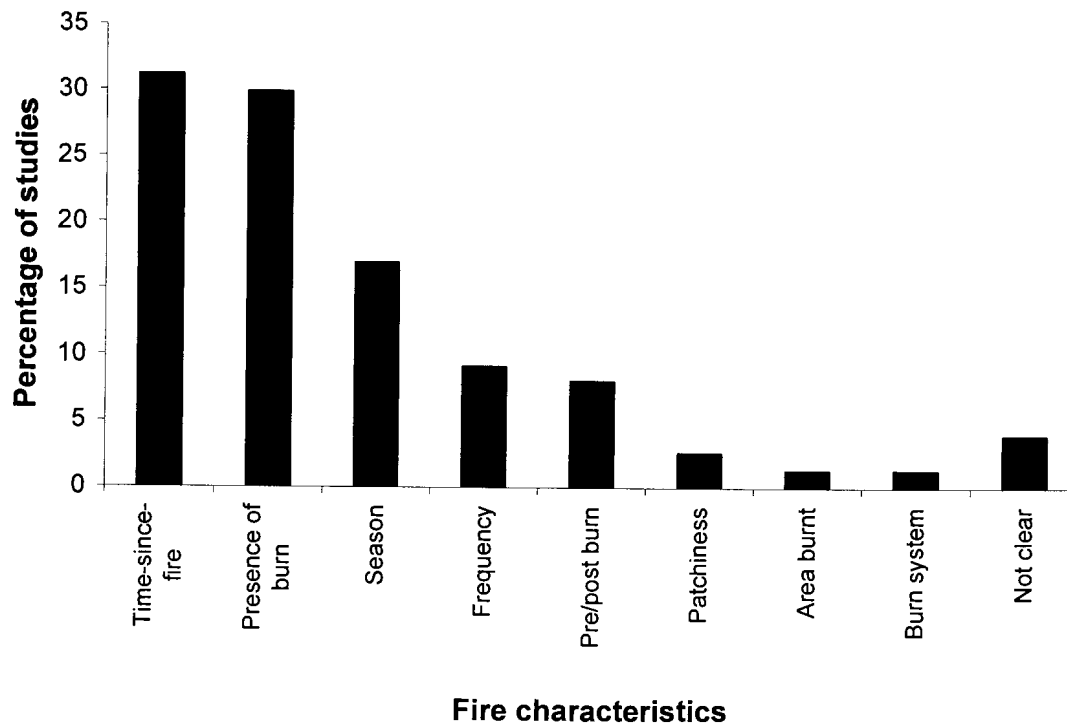


Figure 3. The percentage of studies that have investigated the effects of each of the different fire characteristics on animals. *Time-since-fire*: time since the last fire; *Presence of burn*: studies comparing burnt/unburnt areas; *Pre/post burn*: study on the same area but pre-fire treatment and post-fire treatment; *Patchiness*: completeness of burn indicated by number and size of unburnt patches; *Burn system*: refers to the method e.g. rotational block burning, mosaics.

and thus provide information on the dynamics of the system and the effects of fire mosaics (Bradstock et al. 1995). However few of the studies examined here have explicitly investigated these fire characteristics (studies on patchiness by Mentis and Bigalke (1981) and, Bowland and Perrin (1988) are the exception). Clearly, this is an area for future research.

Moreover, there were no recorded studies investigating the effects of ignition method (e.g. point or line) or type of fire (e.g. crown or surface). Ignition methods may play a role in affecting fauna because line-ignited fires are likely to cover a wider area and be more intense (often two fronts can draw each other with the consequence that intensity increases) than point ignited fires, and thus it could be expected that they would have a greater impact on fauna. Time of day of fire is another important fire characteristic because it will influence the extent of activity of the species at the time of the fire, and might thus affect the survival of animals (see Gandar 1982). These aspects of the fire regime are important from a biodiversity conservation perspective, but are rarely investigated, and certainly have only been explored in a perfunctory manner in the Southern African subregion.

Potential solutions

In this analysis we have deliberately avoided synthesizing the results of the research conducted on the effects of fire on the Southern African fauna. Our main reason for doing so is that our initial analysis of the available data, presented here, suggested that the information available is insufficient for either discursive review or meta-analysis. Both of these synthetic methods require at the very least that the information be based on reliable, replicated experimental, or observational work that is careful in reporting the details of the study. In the latter, meta-analysis case, reliable information on means of experimental and control groups, variances, and sample sizes are required, and if this cannot be inferred from the original work, the study cannot be used (Gurevitch et al. 1992). Unfortunately, work on the effects of fire on the Southern African fauna that is sufficiently well documented for either kind of synthetic analysis is rare. Therefore, we must conclude that, despite several careful studies (e.g. Bell & Jachmann 1984; Chambers & Samways 1998), there is some considerable way to go before a coherent view of the effects of fire on the fauna of the Savanna, Grassland or Fynbos biomes can be developed.

While this conclusion might not be palatable to conservation agencies responsible for the maintenance of biodiversity, both within and outside protected areas, we are of the opinion that the limitations of existing studies must be highlighted for several reasons. Foremost amongst these is that the effects of fire on biodiversity are poorly known. This situation is concerning because currently many of the decisions being taken regarding fire in protected area management are based on poor understanding, and there is ongoing debate about the effects of fire on fauna. Decisions based on poor, or inappropriate information, could have a detrimental impact on fauna, and could compromise biodiversity conservation in protected and other areas. Acknowledging that the available data are not sufficiently extensive should ensure that management decisions are taken with greater appreciation for the lack of appropriate knowledge. Furthermore, it should ensure that future experimental work adopts a more rigorous approach based on sound and carefully considered design. In this respect, fire ecologists in Southern Africa could learn a great deal from their colleagues investigating the effects of habitat fragmentation in the subregion (see Van Jaarsveld et al. 1998, and see also Margules 1993 for work in Australia) and the effects of fire elsewhere (e.g. Andersen et al. 1998). The former studies have been particularly careful in ensuring that areas are compatible and that sound baseline data are available in advance of any experimental treatment. Furthermore, in these experiments great care has been taken to ensure that the replication is appropriate for the questions that are being posed. While such an approach might not always be practicable in fire ecology, it sets the benchmark for fire experiments undertaken at a similar scale. The importance of good fire records and baseline data for fire research, serves to highlight the need for conservation organisations and other relevant authorities to establish and maintain reliable and up-to-date databases; something which to date, has received little attention. Combined with multidisciplinary studies (see Andersen et al. 1998), such historical data can generate considerable insight into the effects of fire on fauna.

Although this paper has focused exclusively on Southern African fire studies, it is likely that many of the experimental design problems mentioned here also apply to studies elsewhere, particularly if in other regions understanding of the effects of fire on fauna is as poorly developed as it is here. To remedy this situation, careful planning of the research work, incorporating consideration of the factors we have discussed, is required (see Fig. 4). While

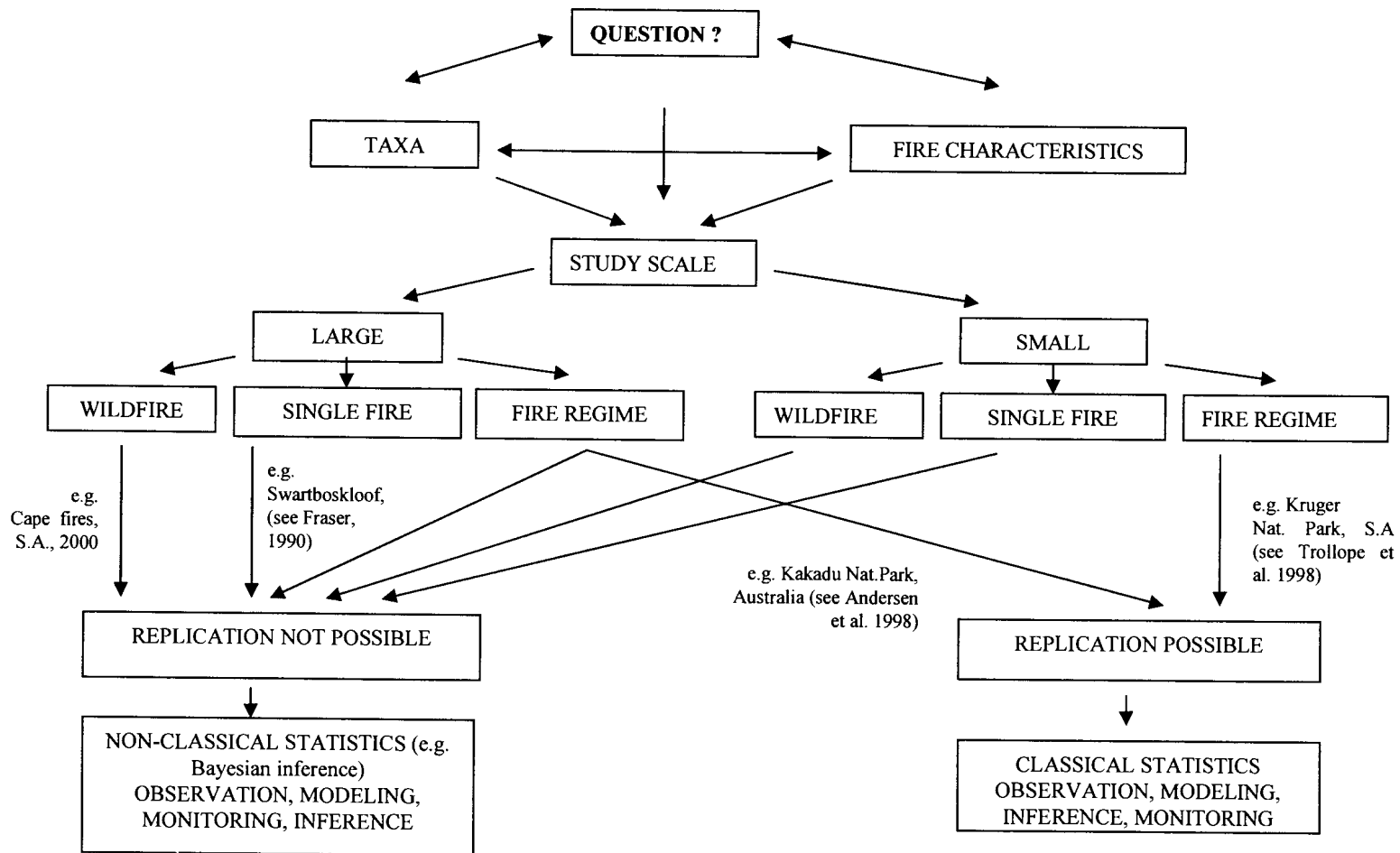


Figure 4. Flowchart illustrating the salient factors to consider in fire experiment design and analysis. ‘Wildfires’ are considered to be those that are unplanned or accidental, ‘single fire’ refers to an individual fire that has been planned and purposefully ignited, and ‘fire regime’ refers to consistent sequence of fires.

future experimental work on the effects of fire on faunal diversity should ideally be based on more rigorous design and reporting, we recognise that this is not always possible. For such cases we urge the use of alternative methods of analysis, and stress that what are often considered statistical limitations need not constrain the scale of the experiment (Carpenter 1990). In this context, it is clear that there is a need for a more detailed and critical investigation of long-term fire effects, and of once-off, large-scale fires, which are likely to impact quite differently on ecosystems to smaller fires. These studies would elucidate relationships concerning the magnitude and direction of the difference between small and large fires, which at present are unclear.

In sum, although we have highlighted the fragmentary state of fire research in Southern Africa, improving our understanding of the effects of fire on fauna should be viewed as an exciting challenge and opportunity. There is much scope for future work, the results of which will improve the conservation of faunas in the protected areas that constitute an ever-growing proportion of the habitat available to many species.

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Chapter 7: Conclusions and Recommendations

This thesis has addressed pattern and process in relation to ant assemblages in Southern African savannas. In doing so not only was information on ants occurring in the region provided, but also the relative importance of different processes in maintaining ant diversity was investigated.

The ant sampling that was undertaken for this thesis forms the first quantitative, systematic, repeatable and reasonably complete survey of ground-foraging ants in two savanna habitat types (Mopane and Satara areas) of the Kruger National Park (KNP), South Africa. Although a third area, Pretoriuskop, was sampled in a quantitative, repeatable way, the survey was not as extensive as the sampling in the other two areas. Nevertheless, sampling over two years yielded a total of 169 species from 41 genera. This includes additional species from hand-collecting and baiting (*Agraulomyrmex* sp.1, *Camponotus* sp.15, *Cataulacus* sp.1, *Meranoplus nanus* André, *Polyrhachis gagates* Smith, *Leptothorax* sp.1, *Rhoptromyrmex transversinodis* Mayr, *Tetramorium* sp. 18), and an *Apomyrma* queen found in a pitfall trap. This is a substantial improvement on previous records.

Because ant species abundance and richness is likely to be higher in higher rainfall areas and also those areas with sandy soils, additional sampling in the sandveld, high rainfall areas in the North of the park and the granitic-based Mopane veld could be particularly informative. Further sampling in the Pretoriuskop area is likely to be fruitful given that recorded species richness was high relative to the sampling effort (i.e. the number of pitfall traps used). The use of ants as bioindicators appears to have most potential in high rainfall areas such as Pretoriuskop. Although, this study focused primarily on ground-foraging ants, arboreal and litter-dwelling ants are particularly poorly known. Thus, litter and arboreal ants may exhibit different responses to burning, and this requires more attention.

With the conservation of biodiversity as a whole being the primary goal of most conservation organisations, attention is increasingly being paid to inventories and surveys to improve understanding of patterns of insect diversity both inside and outside of formal conservation areas. As a result, sampling methods for monitoring and inventorying need to be as efficient, rapid and as cost-effective as possible (Margules & Austin 1991; Kim 1993; Oliver & Beattie 1996; Fisher 1999). This thesis demonstrated that in open savanna systems,

pitfall sampling is more efficient, productive and consistent than winkler sampling for epigeic ants. These results also serve to emphasise the importance of pilot studies, and the testing of alternative methods: an area of research that is unfortunately often neglected.

In addition to knowing what species occur in an area, for conservation managers, it is also important to understand what structures and maintains this diversity. Competition, traditionally seen as the major local process structuring ant assemblages (Fox et al. 1985; Savolainen & Vepsäläinen 1988; Hölldobler & Wilson 1990; Majer et al. 1994), was also found to be important in this savanna system, although the relative importance of competition varied between habitat types. Importantly, the underlying cause for the scatter and variation in the unimodal dominance-richness relationship (see Andersen 1992, Chapter 3 of this thesis) was found to be patchiness at baits. This emphasises the important role of environmental heterogeneity in modifying the role of competition, and thus ultimately affecting species richness of an area. Other structuring factors acting at a local scale (habitat complexity and fire) had much less influence on ants than competition: no support was found for the size-grain hypothesis (see Kaspari & Weiser 1999), and ant assemblages were very resistant to fire.

This study also demonstrated how regional processes can be modified by local scale processes. Thus, although net primary productivity (NPP) sets limits to species richness for an area (see Kaspari et al. 2000), local factors such as competition can reduce species richness below the maximum set by NPP. The relationship between local and regional processes requires further investigation, however, to determine how these mechanisms interact. Data from KNP suggest that species richness may be less variable at low NPP levels, thus it would be interesting to investigate whether the range of species richness values for a given area varies with NPP, and if so, what is driving this variability and what determines the range of values?

Although this study investigated the effect of burning on ant assemblages, in general for Southern Africa, the responses of animals to fire are very poorly understood. This is mainly because the studies that have been carried out are generally lacking in crucial aspects of experimental design. Therefore there remains a need not only to improve fire research in Southern Africa, but also to extend the scope and coverage of taxa.

With regard to the issues raised in the review of faunal fire studies in Southern Africa, it would be improper if an assessment of the KNP experimental burn plots (EBPs) used in this study was not included. While recognising that there was variability between replicates and a few incidences of accidental burns, overall the KNP EBPs provide a solid basis for savanna fire research. Not only does the experiment incorporate a diverse range of fire regimes across four vegetation types, but also the duration (>40 years) and scale of the experiment is particularly valuable because there are so few large-scale, long-term experiments in Southern Africa. The effects of single fires and fire regime effects can be compared with the EBP set-up, although in order to fully tease out the effect of fire regime from time-since-fire (single fire effects), studies would ideally need to be carried out for several successive years (e.g. 5 years). Although the experiment was originally established to test the effects of burning on vegetation, the experiment has also proved useful for studying a variety of other taxa including small mammals (see Kern 1981) and invertebrates. The experimental plots are sufficiently large enough for selected invertebrate studies and possibly for some reptile studies, but the research potential for very mobile and larger taxa is probably limited.

Conservation implications

Given that fire is used extensively as a management tool in conservation areas where the aim is to conserve biodiversity as a whole (see Braack 1997), it is important for protected area managers to understand the effects and implications of applying different management approaches. Based on the findings from this thesis several recommendations can be made to assist invertebrate conservation in Southern African savannas.

First, because the ant assemblages in this study were both highly resistant and resilient to burning, this means that for large areas of KNP, and for many other savanna areas in Southern Africa, burning can afford to be flexible. Thus, managers can focus attention on other taxa or areas of particular concern. Although it is not clear to what degree ants reflect the responses of other invertebrate groups in this savanna system, results from studies elsewhere suggest that a wide range of other taxa probably show a similar response. For example, a long-term burning experiment in a tropical savanna of Australia found that in addition to ants, a variety of other arthropod taxa, including beetles, wasps and homopterans, also exhibited a high degree of resilience to burning (Andersen & Müller 2000; Orgeas &

Andersen 2001). Invertebrates that probably require closer attention because they may be adversely affected by burning include those that specialise in inhabiting dead wood and litter habitats, such as millipedes or centipedes. Finally, although some species of ants appeared to be specific to unburnt (control) plots, these species may also occur in more wooded or riverine areas in the general landscape. Additional sampling in these areas would thus determine whether it is necessary to maintain large unburnt tracts of land to conserve these species.

Second, this study explored the potential of ants as bioindicators (*sensu* ecological indicators, see McGeoch 1998) by testing the responses of ant assemblages to fire. Although the ant assemblages showed high resistance to fire this does not preclude the use of ants as bioindicators in Southern African savanna systems. Within the Mopane and Satara areas of KNP, the few species that could be identified as indicators of burning emphasised the resistance of these ant assemblages to fire. In Pretoriuskop, there was a greater response of ant to burning, and there appears to be a much greater potential for the development of ants as indicators of burning. However, in conservation areas such as KNP, it is not always necessary for ant species to provide an indication of burn regime since they do not offer any new information: fire history can usually be determined by consulting the relevant fire records. The most important potential use of ants as bioindicators in this system relates to their sensitivity to environmental disturbance, but also, to how representative ants are of other taxa. In Southern African savannas the degree to which ants reflect the responses of other invertebrate groups still requires further investigation. There is also significant scope for studies examining the potential of ants as indicators of other disturbances and stresses in savannas such as the effects of elephant damage, or impacts of alien plant invasions on biodiversity.

Third, while conservation managers can afford to focus fire policy on other taxa of particular interest or concern, because general understanding of the effects of fire on fauna is still fragmentary and incomplete, fire management targets should be based on ranges rather than specific optima. This way there is greater flexibility to deal with uncertainty, and the different requirements that different species have, can be taken into consideration (Keith et al. 2002). Park management in KNP appear to be taking the right approach with the adoption in 1998 of Thresholds of Potential Concern (TPCs) (see Van Wilgen et al. 1998). With TPCs,

fire management goals are framed in terms of a range of fire return periods and seasons, and fire is used as a surrogate measure for assessing the goal of biodiversity conservation. While this approach can provide a useful starting point, the relationship between fire diversity and biodiversity (or at least some elements of biodiversity) needs explicit investigation. In addition to monitoring fire variables and relating these to specified ranges, it would be useful to have concurrent research involving biodiversity monitoring. Without this information it is impossible to understand the effect of fire on individual species, or taxa of specific interest or concern. Given the differential response of ants to fire across the three areas in KNP, it is likely that the responses of other taxa will also vary across the park. Therefore, it may not be useful or informative to apply TPCs in a similar blanket fashion across the park. Thus, given the uncertainty surrounding the biological effects of fire in Southern Africa, an adaptive management approach (see Holling 1978; Walters & Green 1997) should ideally be adopted, with on-going monitoring for specific objectives strongly recommended.

Finally, the EBPs illustrated the important role that savanna heterogeneity can play in influencing ant diversity. Although at the scale of several tens of kilometres vegetation within an area may appear homogenous (particularly in the Mopane area), this study has demonstrated that for organisms such as ants, there is sufficient variability within the landscape to maintain diversity. This inherent heterogeneity and variability in landscapes is unlikely to be easily manipulated by managers of these systems (given that after more than 40 years of burning there were still significant differences between replicates). For research purposes although the differences between the EBP replicates may be seen as problematic, such variation is almost impossible to avoid with such large-scale experiments. Indeed, the importance of landscape variability in structuring assemblages needs to be considered in more depth. This variation needs to be incorporated into design, analysis and interpretation of any research: something which to date has been lacking in large-scale studies such as the EBPs.

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Appendix 1.

Apomyrminae and Aenictogitoninae: Two new subfamilies of ant (Hymenoptera: Formicidae) for Southern Africa

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This note was instigated by the finding of a specimen in the subfamily Apomyrminae in the Kruger National Park, but we take this opportunity of also drawing attention to a museum specimen that is the first record in Southern Africa of the enigmatic subfamily, Aenictogitoninae.

Apomyrminae

This subfamily is monotypic, containing only the species *Apomyrma stygia* Brown, Gotwald & Lévieux. It was initially placed in the tribe Amblyoponini of the Ponerinae by Brown et al. (1970), and later placed by Dlussky & Feiloseeva (1987) in its own tribe, the Apomyrmini. Bolton (1990) transferred this tribe to the Leptanillinae, and Baroni Urbani et al. (1992) raised it to subfamily status: Apomyrminae.

The first colonies of *A. stygia* were collected in the Lamto area of the Ivory Coast in April - June 1968 (Brown et al. 1970). The species is thought to be subterranean because it was found only by digging, and the workers lack eyes. The occurrence of this subfamily in gallery forest and dense, unburned savanna suggested it was a rainforest/ forest margin species. Subsequent studies have reported finding the species in other West African countries: Nigeria, Benin (Bolton 1990), and Ghana (Belshaw & Bolton 1993). A specimen of *Apomyrma* has also been collected from Cameroon, and is either a large specimen of *A. stygia* or a new species (Bolton pers. comm.).

We report here on the first record of *Apomyrma stygia* outside West Africa. An alate queen was collected in the northern Mopane area of Kruger National Park (23°26'S 31°22'E, November 2000) in a pitfall trap by one of us (CLP). Overall, the Kruger specimen is slightly smaller than the dealate queen measured by Brown et al. (1970): total length 2.72 mm, head length 0.52 mm, head width 0.37 mm, scape length 0.24 mm, hind femur length 0.28 mm, Weber's length (from anterior descending face of pronotum to posterior extremity of propodeum) 0.82 mm, petiolar node length 0.24 mm, petiolar node width 0.23 mm, first gastral segment length 0.22 mm, first gastral segment width 0.34 mm, eye length 0.08 mm. The head is relatively narrower than the Ivory Coast specimens, the eyes are relatively smaller, and the postpetiole is larger. We consider the smaller size and these slight differences in relative body measurements to be intraspecific variation. There were no sculptural

differences between the Mopane queen, and the dealate queen as described by Brown et al. (1970).

The Mopane area has a mean annual rainfall of 350-400 mm, and is dominated by the Mopane tree (*Colophospermum mopane*) with few other woody species. The soils in the area are heavy black clay soils. Although the specimen was not found in unburned savanna, as previous colonies in West Africa have been found, the surrounding area is likely to have remained unburned for several years. This specimen of *A. stygia* from Kruger shows that it can be found in dry savanna and is not limited to moist savanna and gallery forest, as found by Brown et al. (1970).

Ants living a subterranean existence are likely to be buffered from extremes of moisture and temperature, enabling them to have wider distributions than most surface dwelling species (Robertson 2000). The extension of the known distribution of *A. stygia* from West Africa down into Southern Africa is therefore not surprising in view of its subterranean habits.

Aenictogitoninae

One of the greatest challenges in African ant collecting is to discover the worker caste of this monogeneric subfamily. All seven species in the genus *Aenictogiton* that have been named, have been described only from males collected in Central Africa, mainly in light traps (Brown 1975).

A male specimen of *Aenictogiton* was discovered by one of us (HGR) in unidentified material in the National Museum of Namibia, and was collected from northern Namibia at 'Ghaub 47, Tsumeb, SE 1917 Bc/Bd [19°23'S 17°45'E], 9-10 Mar. 1979' by S. Louw and M-L. Penrith. Also in the same Namibian collection are two specimens of male *Aenictogiton* from Southern Angola ('Tchivinguire, Huile, SE 1513 Ab. [15°08'S 13°23'E] 14-17 Nov. 1974, H22280'). The subfamily is now known from Zaire, Angola, Zambia, Gabon (Brown 1975), and from Namibia (this study). The subfamily has been considered to be associated with forest and gallery forest areas (Brown 1975) but this new record shows that it can also be found in savanna/woodland.

Conclusion

The discoveries of *A. stygia* and *Aenictogiton* increase the total number of ant subfamilies in Southern Africa (south of the Zambezi and Kunene Rivers) to eleven. These are Aenictinae, Aenictogitoninae, Apomyrminae, Cerapachyinae, Dolichoderinae, Dorylinae, Formicinae, Leptanillinae, Myrmicinae, Ponerinae, and Pseudomyrmecinae.

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Appendix 2.

**Ant Species of the Mopane, Satara and Pretoriuskop areas of
Kruger National Park**

Table 1. Ant species collected with pitfall trapping: 2000 & 2002 sampling periods combined. Data are numbers of ants per species for each plot type. C = control plots, A1 = August annual burn, A2 = August biennial burn, A3 = August triennial burn, Ap2 = April biennial burn, Ap3 = April triennial burn, V = variable plot.

	Mopane							Satara							Pretoriuskop	
	C	A1	A2	A3	Ap 2	Ap 3	V	C	A1	A2	A3	Ap 2	Ap 3	V	C	A1
Aenictinae	32	89	20	0	15	94	3	16	13	0	0	0	0	0	0	0
<i>Aenictus eugenii</i> Emery	2	37	0	63	0	0	92	3	0	7	23	8	9	0	1	99
<i>Aenictus rotundatus</i> Mayr	0	8	0	0	0	0	0	0	0	0	0	2	0	0	0	0
<i>Aenictus</i> sp. 1	0	1	0	2	3	1	0	1	1	1	2	2	6	0	0	0
Cerapachyinae																
<i>Cerapachys</i> sp. 1	0	1	0	2	3	1	0	1	1	1	2	2	6	0	0	0
Dolichoderinae																
<i>Tapinoma</i> sp. 1	0	0	0	0	0	0	0	13	5	33	5	28	24	43	2	70
<i>Tapinoma</i> sp. 2	0	0	0	0	0	0	0	0	4	0	0	2	0	0	5	22
<i>Technomyrmex albipes</i> (F.Smith)	6	6	32	71	15	73	34	18	12	4	8	29	8	17	11	4
<i>Technomyrmex</i> sp. 2	1	0	0	0	1	0	0	3	2	2	1	0	0	1	3	3
<i>Technomyrmex</i> sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	4
Dorylinae																
<i>Dorylus</i> sp. 1	0	0	0	0	1	0	7	1	145	4	0	0	0	11	0	0
Formicinae																
<i>Anoplolepis custodiens</i> (F. Smith)	0	0	0	0	0	0	0	1	7	3988	0	46	0	0	9	48
<i>Anoplolepis</i> sp. 1	0	151	31	19	0	0	0	36	170	251	180	92	95	17	0	14
<i>Anoplolepis</i> sp. 3	0	0	0	2	0	0	1	0	2	0	0	0	0	0	0	9
<i>Camponotus aequitas</i> Santschi	0	0	0	2	0	0	0	0	0	1	0	0	0	1	0	0
<i>Camponotus cinctellus</i> (Gerstäcker)	1	13	5	8	3	6	6	16	31	62	25	45	11	11	6	1
<i>Camponotus crepusculi</i> Arnold	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0
<i>Camponotus debellator</i> Santschi	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1
<i>Camponotus dofleini</i> Forel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2

Table 1. continued

	Mopane							Satara							Pretoriuskop	
	C	A1	A2	A3	Ap 2	Ap 3	V	C	A1	A2	A3	Ap 2	Ap 3	V	C	A1
<i>Camponotus etiolipes</i> Bolton	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
<i>Camponotus mayri</i> Forel	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
<i>Camponotus</i> sp. 1	11	14	14	4	15	16	5	5	0	6	4	6	4	5	2	10
<i>Camponotus</i> sp. 2	0	0	0	1	0	0	0	0	0	3	0	0	1	0	0	0
<i>Camponotus</i> sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
<i>Camponotus</i> sp. 9	0	1	0	0	0	0	1	0	1	2	0	0	0	3	0	0
<i>Camponotus</i> sp. 10	0	5	8	0	0	0	0	0	2	0	0	0	0	0	0	0
<i>Camponotus</i> sp. 11	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
<i>Camponotus</i> sp. 12	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	4
<i>Camponotus</i> sp. 14	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Camponotus</i> sp. 19	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Camponotus</i> sp. 22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Lepisiota</i> sp. 1	1	0	0	0	0	2	1	9	4	5	5	13	5	6	4	0
<i>Lepisiota</i> sp. 2	0	1	18	10	1	7	1	3	4	3	8	9	4	6	14	10
<i>Lepisiota</i> sp. 5	0	0	1	0	0	1	0	0	0	2	0	0	0	0	0	0
<i>Lepisiota</i> sp. 6	0	0	0	0	0	0	0	0	2	1	0	0	0	2	0	52
<i>Lepisiota</i> sp. 7	0	0	0	0	0	0	0	0	0	0	4	0	1	0	0	0
<i>Lepisiota</i> sp. 8	0	0	0	0	0	0	0	4	0	0	0	0	1	0	2	15
<i>Lepisiota</i> sp. 9	0	0	0	0	0	0	0	0	0	1	0	1	3	26	3	18
<i>Lepisiota</i> sp. 12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Lepisiota</i> sp. 13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	26
<i>Paratrechina</i> sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0
<i>Plagiolepis</i> sp. 1	1	6	2	10	4	46	2	15	11	11	26	12	54	16	2	8
<i>Plagiolepis</i> sp. 2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	4
<i>Plagiolepis</i> sp. 3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Plagiolepis</i> sp. 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0

Table 1. continued

	Mopane							Satara							Pretoriuskop	
	C	A1	A2	A3	Ap 2	Ap 3	V	C	A1	A2	A3	Ap 2	Ap 3	V	C	A1
<i>Plagiolepis</i> sp. 5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20
<i>Polyrhachis schistacea</i> (Gerstäcker)	0	0	6	0	1	0	0	7	0	0	1	1	1	1	4	1
Myrmicinae																
<i>Calyptomyrmex</i> sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Cardiocondyla emeryi</i> Forel	0	1	1	0	0	0	0	15	12	16	10	203	1	2	2	18
<i>Crematogaster</i> sp. 1	8	5	14	4	20	13	2	2	1	2	0	0	0	0	0	0
<i>Crematogaster</i> sp. 2	0	0	0	0	0	0	0	0	2	2	1	0	0	11	149	356
<i>Crematogaster</i> sp. 3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Crematogaster</i> sp. 4	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Crematogaster</i> sp. 5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Crematogaster</i> sp. 7	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0
<i>Crematogaster</i> sp. 8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
<i>Decamorium decem</i> Forel	0	0	0	0	0	2	0	2	1	1	0	1	0	1	0	0
<i>Meranoplus glaber</i> Arnold	0	0	0	0	0	0	0	1	1	0	0	0	0	0	9	0
<i>Meranoplus inermis</i> Emery	0	3	12	9	0	1	0	0	0	0	0	0	0	0	0	0
<i>Meranoplus magretti</i> André	6	7	6	14	0	4	5	3	8	1	1	2	1	1	0	1
<i>Messor decipiens</i> Santschi	0	0	1	0	0	1	0	18	177	109	7	102	5	35	0	0
<i>Monomorium albopilosum</i> Emery	121	153	161	201	197	326	341	255	401	150	138	191	183	327	4	61
<i>Monomorium damarensense</i> Forel	23	90	40	39	12	106	25	51	59	25	126	34	162	5	0	0
<i>Monomorium delagoense</i> Forel	0	0	2	0	0	0	0	55	99	10	144	230	189	2649	0	0
<i>Monomorium emeryi</i> Mayr	13	100	85	58	74	72	8	0	31	16	46	10	27	0	0	0
<i>Monomorium exiguum</i> Forel	0	0	0	0	0	0	0	15	4	0	0	0	16	0	0	0
<i>Monomorium hanneli</i> Forel	0	0	0	0	0	0	0	27	0	0	0	0	0	0	20	0
<i>Monomorium junodi</i> Forel	0	0	0	0	0	0	0	105	216	143	25	182	63	5	0	16
<i>Monomorium mictile</i> Forel	0	0	0	0	0	0	0	1	10	0	0	0	0	0	0	12
<i>Monomorium notulum</i> Forel	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	5

Table 1. continued

	Mopane							Satara							Pretoriuskop	
	C	A1	A2	A3	Ap 2	Ap 3	V	C	A1	A2	A3	Ap 2	Ap 3	V	C	A1
<i>Monomorium oscaris</i> Forel	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	14
<i>Monomorium shilohense</i> Forel	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Monomorium vaguum</i> Santschi	0	0	0	0	0	0	0	0	0	2	8	0	0	27	0	0
<i>Monomorium zulu</i> Santschi	0	26	6	8	7	11	6	67	34	66	129	63	130	19	0	0
<i>Monomorium</i> sp. 1	0	3	28	0	0	24	0	0	0	5	0	1	0	2	0	0
<i>Monomorium</i> sp. 2	0	0	0	0	0	18	0	6	2	0	0	109	2	11	2	78
<i>Monomorium</i> sp. 3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Monomorium</i> sp. 4 nr. disertum	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
<i>Monomorium</i> sp. 5	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0
<i>Monomorium</i> sp. 6 nr. havilandi	0	0	0	0	0	0	0	0	0	29	0	0	0	0	0	0
<i>Monomorium</i> sp. 7	6	6	2	2	2	2	3	10	1	1	7	35	8	26	26	44
<i>Monomorium</i> sp. 8	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
<i>Monomorium</i> sp. 9 nr. musicum	0	0	0	2	0	0	0	1	0	0	0	0	0	4	0	0
<i>Monomorium</i> sp. 10 nr. taedium	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
<i>Monomorium</i> sp. 11 nr. subopacum	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0
<i>Monomorium</i> sp. 14	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	14
<i>Monomorium</i> sp. 15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40
<i>Myrmecaria natalensis</i> (F. Smith)	36	16	93	25	259	196	6	29	261	21	43	115	28	106	6	20
<i>Ocymyrmex fortior</i> Santschi	0	150	91	17	51	72	5	154	163	121	77	3	71	8	0	0
<i>Oligomyrmex</i> sp. 1	18	28	8	4	247	3	7	1	7	3	6	12	10	34	4	3
<i>Oligomyrmex</i> sp. 2	0	0	5	0	0	2	0	20	0	3	2	38	1	21	32	49
<i>Oligomyrmex</i> sp. 3	0	0	0	0	0	0	0	2	0	0	0	1	0	1	0	2
<i>Oligomyrmex</i> sp. 4	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0	3
<i>Paedalgus</i> sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Pheidole</i> sp. 1	17	5	211	190	372	299	116	240	349	335	430	240	309	177	0	0
<i>Pheidole</i> sp. 2	541	60	22	259	15	243	61	148	856	1074	2235	5847	2857	884	5	5

Table 1. continued

	Mopane							Satara							Pretoriuskop	
	C	A1	A2	A3	Ap 2	Ap 3	V	C	A1	A2	A3	Ap 2	Ap 3	V	C	A1
<i>Pheidole</i> sp. 3	148	907	159	105	18	658	62	42	144	8	81	40	40	19	21	3
<i>Pheidole</i> sp. 6	6	133	98	44	5	41	42	24	24	35	3	17	5	7	4	56
<i>Pheidole</i> sp. 7	0	0	0	0	0	0	4	1100	132	1418	851	43	0	0	0	0
<i>Pheidole</i> sp. 9	39	16	18	3	4	48	2	2	2	1	5	3	0	2	4	7
<i>Pheidole</i> sp. 10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	93	126
<i>Pheidole</i> sp. 11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	93	0
<i>Pheidole</i> sp. 14	17	3	4	0	0	0	0	0	1	0	0	2823	5	11	1	0
<i>Pheidole</i> sp. X	3	10	2	3	4	1	4	3	25	28	15	14	37	36	0	81
<i>Pheidole</i> sp. Y	0	0	1	0	1	0	0	0	0	0	1	0	7	10	0	0
<i>Pheidole</i> sp. Z	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
<i>Pheidole</i> sp. TBN	1	1	0	0	0	1	3	136	0	0	0	0	20	1	136	251
<i>Pyramica</i> sp. 1	0	0	0	0	0	1	0	3	0	0	2	0	0	1	11	10
<i>Rhoptromyrmex globulinodis</i> Mayr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Solenopsis</i> sp. 1	1	0	0	0	0	0	0	1	0	0	2	2	0	2	7	0
<i>Strumigenys</i> sp. 1 nr. pretoriae	0	0	0	0	1	0	0	3	0	1	0	0	0	2	4	7
<i>Strumigenys</i> sp. 2 nr. arnoldi	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Tetramorium baufra</i> (Bolton)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tetramorium constanciae</i> Arnold	0	0	14	0	0	0	0	0	0	0	0	0	0	0	11	26
<i>Tetramorium erectum</i> Emery	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
<i>Tetramorium ericae</i> Arnold	0	0	1	0	0	0	0	0	2	2	0	0	0	0	0	0
<i>Tetramorium frenchi</i> Forel	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0
<i>Tetramorium furtivum</i> (Arnold)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Tetramorium frigidum</i> Arnold	22	27	26	25	19	44	6	13	59	39	36	28	40	23	6	12
<i>Tetramorium gladstonei</i> Forel	0	8	7	0	0	18	1	120	7	66	78	1	1	0	0	0
<i>Tetramorium hortorum</i> Arnold	0	0	0	0	0	0	0	0	0	0	0	0	25	0	1	0
<i>Tetramorium laevithorax</i> Emery	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0

Table 1. continued

	Mopane							Satara							Pretoriuskop	
	C	A1	A2	A3	Ap 2	Ap 3	V	C	A1	A2	A3	Ap 2	Ap 3	V	C	A1
<i>Tetramorium microps</i> (Mayr)	0	0	0	0	0	0	0	1	2	0	13	1	0	0	0	0
<i>Tetramorium notiale</i> Bolton	2	0	1	1	0	1	4	4	3	10	13	9	9	2	0	1
<i>Tetramorium sepositum</i> Santschi	0	0	2	0	0	0	3	37	0	19	13	0	1	0	0	0
<i>Tetramorium sericeiventre</i> Emery	22	110	47	36	36	68	32	10	195	105	68	155	100	11	0	5
<i>Tetramorium setigerum</i> Mayr	33	15	10	10	18	46	29	6	18	4	13	12	15	30	26	5
<i>Tetramorium setuliferum</i> Emery	1	3	1	2	4	5	0	0	5	32	2	40	17	0	0	16
<i>Tetramorium weitzeckeri</i> Emery	6	1	31	1	5	7	13	0	1	0	1	0	19	1	5	0
<i>Tetramorium</i> sp. 1	0	0	0	0	0	7	2	4	13	4	1	3	6	10	25	11
<i>Tetramorium</i> sp. 2	4	17	12	1	4	10	4	2	25	18	11	26	16	10	29	52
<i>Tetramorium</i> sp. 4	5	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0
<i>Tetramorium</i> sp. 6	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
<i>Tetramorium</i> sp. 7 nr. thoth	0	0	0	0	0	0	2	5	0	0	0	6	0	5	0	0
<i>Tetramorium</i> sp. 8. nr. caldarium	0	0	0	0	0	0	0	0	9	0	0	2	0	0	0	0
<i>Tetramorium</i> sp. 10	0	0	0	0	2	0	0	0	3	0	0	1	0	0	0	0
<i>Tetramorium</i> sp. 11	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
<i>Tetramorium</i> sp. 13	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Tetramorium</i> sp. 17	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Tetramorium</i> sp. 18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0
<i>Tetramorium</i> sp. 20	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Ponerinae																
<i>Anochetus bequaerti</i> Forel	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Anochetus levaillanti</i> Emery	0	3	0	0	0	1	0	0	0	0	0	1	0	0	0	0
<i>Hypoponera</i> sp. 1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hypoponera</i> sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Leptogenys furtiva</i> Arnold	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Leptogenys intermedia</i> Emery	0	0	0	0	0	0	1	10	0	0	0	0	7	0	0	1

Table 1. continued

	Mopane							Satara							Pretoriuskop	
	C	A1	A2	A3	Ap 2	Ap 3	V	C	A1	A2	A3	Ap 2	Ap 3	V	C	A1
<i>Leptogenys schwabi</i> Forel	0	0	0	0	0	0	0	2	1	1	3	0	2	0	0	0
<i>Odontomachus troglodytes</i> Santschi	0	0	0	0	1	13	0	14	0	0	0	0	0	0	4	17
<i>Pachycondyla ambigua</i> André	1	0	0	1	2	0	2	1	1	0	1	0	0	5	0	0
<i>Pachycondyla analis</i> (Latreille)	0	0	4	0	1	1	0	2	11	1	3	137	1	0	0	0
<i>Pachycondyla berthoudi</i> (Forel)	0	0	0	0	0	0	0	0	1	0	0	2	0	1	0	0
<i>Pachycondyla caffraria</i> F.Smith	0	0	0	0	0	0	0	14	0	1	0	1	0	1	2	2
<i>Pachycondyla crassa</i> (Emery)	9	0	2	0	3	0	3	19	8	3	2	3	1	18	0	13
<i>Pachycondyla kruegeri</i> Forel	1	0	0	0	0	0	0	0	6	0	9	0	0	6	0	0
<i>Pachycondyla sennaarensis</i> (Mayr)	0	0	0	0	1	0	0	2	18	0	0	0	0	1	0	0
<i>Pachycondyla sharpi</i> (Forel)	1	6	0	1	1	0	1	1	0	3	2	1	0	3	0	0
<i>Pachycondyla</i> sp. 9	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Platythyrea lamellosa</i> Roger	0	5	6	0	0	39	0	0	0	0	0	0	0	0	0	0
<i>Plectroctena mandibularis</i> Smith	0	0	1	2	0	0	1	2	1	1	0	0	4	0	2	4
<i>Prionopelta aethiopica</i> Arnold	0	0	0	0	0	0	0	5	0	0	0	0	0	4	0	0