THE ROLE OF ANTS IN STRUCTURING INSECT COMMUNITIES ON THE CANOPIES OF *SENEGALIA DREPANOLOBIUM* NEAR LAIKIPIA, KENYA

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Abstract

In the black cotton ecosystem of Laikipia, Kenya, four symbiotic ants coexist at a fine spatial scale on canopies of *Senegalia drepanolobium*. They exhibit different aggressive behaviours and modify their tree canopies differently. These diverse behaviours were expected to affect the associated canopy arthropod communities.

At the Kenya long-term exclosure experiment (KLEE) and its immediate environs at Mpala Research Centre, Laikipia, the insect communities coexisting with each of the four ant species were characterized, and their response to different vertebrate herbivory. Other ant species inhabiting the tree canopies or the ground were surveyed too. Pitfall trapping was used in sampling terrestrial ants, while beating and mist-blowing were used in collecting arboreal insects. Different sampling methods had varying efficacies, revealing the importance of using several methods.

There are at least sixteen ant species in this ecosystem, all occurring on the ground, but only ten species on the trees. Terrestrial ant communities in this ecosystem cannot be used as indicators of grazing pressure for range management. A total of 10,145 individual insects were collected from the tree canopies, comprising of 117 species from seven orders and 25 families, forming a complex community of species interacting at different levels.

Symbiotic ant species had a significant effect on insect community structure and composition. *Crematogaster sjostedti* was associated with a community that was significantly different from the other ant species. There was no significant effect of vertebrate feeding pressure on the canopy insect community, but there was an interaction effect between ant species and treatments. Significant differences between ant species mostly occurred on treatment plots where only cows were allowed to graze. One or more of the ant species may be a keystone species in this ecosystem even though experimental manipulations failed to confirm earlier findings. It was concluded that the one-year period during which experimental manipulations were carried out was not long enough to reflect takeover effects on the insect community.

The four symbiotic ant species colonizing *S. drepanolobium* comprises of two guilds, the hemipteran-tending ants (*C. sjostedti* and *Crematogaster mimosae*) and non-tending ants (*Crematogaster nigriceps* and *Tetraponera penzigi*). Communities associated with these guilds were found to be significantly different in all four diversity indices.

The black cotton ecosystem is species-poor compared to other ecosystem such as forests. The number of insect species that colonizes *S. drepanolobium* and coexists with acacia-ants forms a large proportion of the invertebrate community. Therefore, this ecosystem should be conserved to safeguard this invertebrate community. This will also give scientists a chance to establish how the various insect species coexist with symbiotic ants on tree canopies.

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Abbreviations

Cn – *Crematogaster nigriceps*

Cm – *Crematogaster mimosae*

Cs - *Crematogaster sjostedti*

Tp – *Tetraponera penzigi*

KLEE – Kenya Long-term Exclosure Experiment

Dedication

This thesis is dedicated to my wife Faith Kamande, my sons Ian Kuria and Kevin Ruhiu for their love and patience during the entire period of my studies.

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CHAPTER 1: GENERAL INTRODUCTION

Introduction

Mutualism

The relationships between plants and insects are very diverse and can be complex. Some of these relationships are mutualistic. Biological mutualism refers to associations whereby two species benefit from one another (Howe and Westley, 1988; Molles, 2005). Different types of mutualisms has been described, and examples involving ants include associations with bacteria (Boursaux-Eude and Gross, 2000; Degnan *et al*., 2004), fungi (Bass and Charrett, 1995; Jolivet, 1998; North *et al*., 1999; Currie, 2001; Mueller *et al*., 2001; Aanen *et al*., 2002; Thomas, 2002), lycaenid butterflies (Leimar and Axén, 1993; Travassos and Pierce, 1999; Agrawal and Fordyce, 2000; Petterson, 2002; Pierce *et al*., 2002), hemipteran bugs (Fischer *et al*., 2002; Fagundes *et al*., 2005), myrmecophytic plants (Janzen, 1966; Handel, 1976; Beattie, 1985; Handel and Beattie, 1990; Rickson and Rickson, 1998; Gorb and Gorb, 1999; Brouat *et al*., 2000, 2001; Raine *et al*. 2002; Christianini and Machado, 2004; Gerardo *et al*., 2004; Bruna *et al*., 2005), and pollinators (Howe and Westley, 1988; Gómez and Zamora, 1992; Garcia *et al*., 1995; Puterbaugh, 1998; Gómez, 2000), among others. Ants comprise the highest numbers of species involved in mutualisms (Thompson, 1982; Herrera and Pellmyr, 2002).

In a number of tropical localities, ants have formed symbiotic, cooperative relationships with species of myrmecophytic plants (Buckley, 1982; Beattie, 1985; Vasconcelos and Casimiro, 1997; Renner and Ricklefs, 1998; Djiéto-Lordon *et al*., 2004). Over 465 plant species in 52 families have been recorded as having symbiotic association with ants (Jolivet, 1998; Agosti *et al*., 2000), and thirteen of these families are from tropical Africa (Jolivet, 1998). Most of these ant-plants are distributed in Kenya, Uganda, Ethiopia, Tanzania and Namibia (Jolivet, 1998). Symbiotic plant-ants provide protection against a number of threats to the plant, and in return the plant provides a home and often food sources for the ants (e.g. Heil *et al*., 1997; Oliveira, 1997; Herrera and Pellmyr, 2002; Bruna *et al.,* 2005). Plants having symbiotic associations with ants are referred to as myrmecophytes. These ant-plant interactions are often obligate, in that

participating species depend upon each other in order to exist (Speight *et al*., 1999). Coevolution of ants and plants often seems the only feasible explanation for these relationships (Jolivet, 1998).

Ant-myrmecophyte interactions are intricate. A single tree is usually inhabited by one species of ant and on rare occasions by more species, including obligate and non-obligate associates (Heil and McKey, 2003), with each species exhibiting different behaviours, and potentially different interactions, with other organisms. This was first demonstrated by Janzen (1966) in the *Acacia-Pseudomyrmex* system, in which the plant provides swollen thorn domatia (natural holes or cavities of plants in which animals may live) and food-bodies for its specialist ant-mutualist. In return for this diet and housing, the ants remove a variety of the plant's enemies. Investigations by various workers have sometimes failed to show any measurable benefits to plants by ants (O'Dowd and Catchpole, 1983; Tempel, 1983; Boecklen, 1984; Whalen and Mackay, 1988; Rashbrook *et al*., 1992; Wilmer and Stone, 1997). In fact some studies have shown that the plant is a loser in some of these associations (Mody and Linsenmair, 2004). *Allomerus* cf. *demerarae* castrates its host tree *Cordia nodosa*, reducing fruit production to zero (Yu and Pierce, 1998). However, these studies did not indicate whether their findings were based on symbiotic mutualists, since not all ant species have mutualistic associations with plants. The distinction between true symbionts and ants that facultatively visit extra-floral nectarines is an important one. However, the factors that lead ants to attack some herbivores and allow others on the same myrmecophytic plants are not well understood.

A wide range of plants produce extrafloral nectaries that attract ants and other arthropods (Pemberton and Lee, 1996; Oliveira *et al*., 1999; Heil *et al*., 2001; Moya-Raygoza and Larsen, 2001). Ants have been shown to play an essential role of defensive against herbivores to some myrmecophilic plants (Bentley, 1977; Buckley, 1982; Holldobler and Wilson, 1990; Davidson and McKey, 1993; Gaume and McKey, 1999; Speight *et al*., 1999). Von Wettstien [1889, cited in Beattie (1985)] was among the first workers using exclusion experiments to show that ants attracted to the extrafloral nectaries of two Compositae species reduced seed damage levels.

Myrmecophytes differ with respect to the types of food and/or shelter they provide to resident ant colonies. *Cecropia* trees produce protein and lipid-rich Müllerian bodies, on which *Azteca* ants feed (Janzen, 1969, 1973; Downhower, 1975; Agrawal, 1998). The association between the *Cecropia* trees and *Azteca* ants is obligate. Removal of the ants seriously reduces the fitness of the plant and ultimately it dies (Agrawal, 1998). *Piper* trees also produce food bodies that *Pheidole* ants eat (Risch and Rickson, 1981; Letourneau, 1990). The relationship between myrmecophytic *Macaranga* and *Crematogaster* ants is regarded as obligatory, as the associated ants nest only in plants of *Macaranga* (Fiala and Maschwitz, 1990).

The best-known Neotropical symbioses are between *Acacia* trees and *Pseudomyrmex* ants (Hölldobler and Wilson, 1990). Thirteen Neotropical *Acacia* species are specialized myrmecophytes that house ants in their domatia and provide ants with extrafloral nectaries and nutritious Beltian bodies (Seigler and Ebinger, 1995). In exchange for food and shelter from the *Acacia* in which they live, some *Pseudomyrmex* species fiercely attack leaf-eating insects and keep the base of their tree clear of competing vegetation (Janzen, 1966; Cronin, 1998). *Acacia collinsii* has a mutualistic relationship with the three species of stinging ants, *Pseudomyrmex spinicola*, *P. nigrocinctus*, and *P. flavicornis* (Keeler, 1981). As with most New World ant-acacias, this species provides resident ants with extrafloral nectaries and protein-rich Beltian bodies. In contrast, ant-acacias in Africa produce only extrafloral nectaries, so most of their symbiotic ants must forage away from the host tree for protein sources (Palmer, 2003).

Acacia-ants as keystone species

The term 'keystone species' was first used by Paine [1966, cited by Payton *et al*. (2002)] when he removed starfish (*Pisaster ochraceus*) from a section of a shore, and the original 15-species assemblage was reduced to eight species. Keystone species are defined as those species whose removal has strong effects on community diversity and composition (Price, 1975; Risch and Carrol, 1982; Mills *et al*., 1993). Christianou and Ebenman (2005) and Roughgarden [1983, cited in Tanner *et al*. (1994)] described keystone species as those species whose loss is likely to trigger a relatively large number of secondary extinctions. In this thesis, a keystone species will be defined as a species that directly or indirectly influences the community structure and whose elimination would result in a rapid decline or increase in the number of species in the community.

Some characteristics of a species can influence its status as a keystone species, in particular its trophic position and the strength of its interactions with other species (Ebenman and Johnson, 2005). Christianou and Ebenman (2005) indicated that both weakly- and strongly-interacting species can be keystone species, in the sense that their loss can cause a cascade of secondary extinctions. Interdependence among species, and a loss of one species, may activate a cascade of secondary extinctions affecting the stability of the community (Mills *et al*., 1993; Christianou and Ebenman, 2005; Ebenman and Jonsson, 2005). In the worst case, loss of a single species may result in a community collapse (Ebenman and Jonsson, 2005). The army ant, *Eciton burchelli,* is a keystone species in certain Neotropical rainforest ecosystems; many species of vertebrates and invertebrates associate with them and would face extinction if the army ant disappeared (Boswell *et al*., 1998). Risch and Carrol (1982) showed that *Solenopsis geminata* is a keystone predator whose removal in agroecosystem in southern Mexico resulted in an increase in arthropod species. Ants of the genus *Atta* are regarded as keystone species for their ability to modify the environment and could be used as environmental indicators for natural ecosystems (Fowler *et al.*, 1989; Perfecto and Vandermeer, 1993). Banner-tailed kangaroo rats found in Chihuahuan desert grassland (Krogh *et al*., 2002), *Anadromous* salmon in British Columbia (Hyatt and Godbout, 1999) and *Sphyrapicus nuchalis* (*Piciformes*: Picidae) in a subalpine ecosystem in the Rocky Mountains (Daily *et al*., 1993) are examples of keystone species. Other examples include *Sphagnum* moss occurring in most Canadian peatlands (Rochefort, 2000) and the cicada *Diceroprocta apache* Davis in Arizona, USA (Andersen, 1994).

Batabyal (2002) indicated that human activities such grazing and tourism, among others, can influence the survival and well-being of keystone species. The Kenyan black cotton ecosystem is currently under the influence of human activities and in particular livestock grazing. Therefore, there is need to conserve and manage this ecosystem in order to retain the biodiversity resulting from coexistence of the four ant species and other related arthropods. The acacia-ants are likely to play an unusually important role because over 95% of the canopy cover is *S. drepanolobium*, and the whole community is relatively species-poor (Stanton, personal communication).

Acacia-ants form an integral part of the mutualistic association between ants and *Acacia* plants in Africa and New world. Although a lot of literature is available covering the various aspects of

these associations, there is no documented study indicating whether some of the acacia-ants are keystone species. Therefore, one goal of this study was to determine whether one or more of the four acacia-ants colonizing *S. drepanolobium* are keystone species for the community of arthropod species that live in the canopies of the trees. If so, then the loss of one or more ant species due to natural factors or as a result of anthropogenic activities could result in secondary extinctions of some canopy arthropods that coexist with them, or even a collapse of the whole community. The other possibility would be the loss of one or more of the ant species may result in an increase of the arthropod species.

The S. drepanolobium ecosystem

Senegalia drepanolobium (Harms) Sjostedt trees inhabiting the Laikipia ecosystem in Kenya are known to have mutualistic association with four ant species at fine spatial scales (Young *et al*., 1997; Stanton *et al*., 2002). Research has shown that these ant species behave differently and modify the host tree canopy differently (Young *et al*., 1997; Stanton *et al*., 1999; Palmer *et al.*, 2000; Palmer *et al*., 2002). The ants have also been shown to associate with different invertebrate species (Young *et al.*, 1997). However, no detailed study has been carried out to document this, and therefore the invertebrate communities coexisting with these acacia-ants are not well understood.

S. drepanolobium is a small single-stemmed tree or shrub that occurs in East Africa on soils of impeded drainage (Taiti, 1992). To reduce browsing by herbivores, the tree has stipular thorns (Young, 1987; Milewski *et al*., 1991), symbiotic ants (Madden and Young, 1992; Young *et al*., 1997; Stapley, 1998), and sometimes accumulates tannins on its leaves (Ward and Young, 2002). Roughly one node out of every 10 – 20 has a swollen structure, situated at the base of the spine pair, that generally houses resident ants that feed in part from extrafloral nectaries (Hocking, 1970; Young *et al*., 1997). In return, the ants confer defence against other insects or larger herbivores that attempt to browse on it.

In the Laikipia region in Kenya, *S. drepanolobium* occurs mostly on black cotton soils and supports at least ten ant species (personal observation). These include three species of *Crematogaster,* two species of *Camponotus*, and one each of *Tetraponera, Technomyrmex,*

Tetramorium, Monomorium and *Polyrhachis*. Four of these species of ants (*Crematogaster nigriceps* Emery*, C. sjostedti* Mayr*, C. mimosae* Santschi and *Tetraponera penzigi* Mayr) are known to coexist at fine spatial scale on these trees throughout East Africa and in the Laikipia area (Stanton *et al*., 2002). The four ant species commonly dominate the canopy while the others tend to occur in small "satellite" colonies on trees, or parts of trees, where the four primary symbionts are less active.

All four species of primary symbionts usually live on *S. drepanolobium*, although never at the same time on the same tree, due to violent intolerance of one another. More than 99% of trees over one metre tall are occupied by ants, and forceful interspecific takeovers of host trees by neighbouring colonies are common (Palmer *et al*., 2000), occurring both via the ground and when canopies of neighbouring trees grow together (Stanton *et al*., 1999). Based on experiments and observations, Palmer *et al*. (2000) classified the four ant species coexisting on Mpala ranch into two groupings, subordinate (*C. nigriceps* and *T. penzigi*) and dominant (*C. mimosae* and *C. sjostedti*) species. They also found that trees that have been deserted by dominant ants are frequently taken over by subordinate ants. Subordinate ant species may also colonize new saplings. Young *et al.* (1997) classified *C. nigriceps* and *T. penzigi* as early successional species while *C. sjostedti* and *C. mimosae* as late successional species.

Crematogaster mimosae Santschi (Myrmicinae) is the most common resident ant species in Mpala Ranch, Laikipia, Kenya (Young *et al*., 1997). The workers vigorously defend the tree, especially at the young shoots, with greater vitality than those of the other ant species. It also tends *Ceroplastes* scale insects both inside the swollen thorns and on the undersides of young branches. It uses the swollen thorns for nesting.

Crematogaster sjostedti Mayr (Myrmicinae) is the most competitively dominant ant among the four acacia-ant species (Palmer *et al*., 2000). It is the second most common ant species at the study site (Young *et al*., 1997). It does not raise brood inside the swollen thorns, favouring cavities in dead wood on older plant parts or on the ground around the bases of trees, and tends *Ceroplastes* scale insects within twig cavities.

Crematogaster nigriceps Emery (Myrmicinae) removes practically all axillary buds apart from swollen thorns, effectively sterilizing the tree (Palmer *et al*., 2000). This results in the tree having more branches and its canopy appearing denser. It does not tend scale insects and uses swollen thorns to rear its brood.

Tetraponera penzigi Mayr (Pseudomyrmecinae) is the least competitively dominant ant species at Mpala Ranch (Young *et al*., 1997; Palmer *et al*., 2002). It eats the extrafloral nectaries on the leaves, and the swollen thorns on its trees have entry holes that are smaller in accordance to their smaller body size, than those created by the *Crematogaster* species, which must widen them to gain entry whenever a takeover occurs (Palmer *et al*., 2002). It does not tend scale insects.

Interactions of acacia-ants and *S. drepanolobium* trees in the black cotton ecosystem of Laikipia, Kenya are well studied (Young, 1987; Milewski *et al*., 1991; Madden and Young, 1992; Young *et al*., 1997; Young and Okello, 1998; Stanton *et al*., 1999; Palmer *et al*., 2000; Palmer *et al*., 2002; Ward and Young, 2002). However, information on arthropod communities sharing the acacia canopies with ants is minimal. The same is true for insect herbivores that feed on other ant-defended plants (Jolivet, 1991; Eubanks *et al*., 1997). Young *et al*. (1997) found that different resident acacia-ants also had characteristic relationships with other insects. At Mpala Ranch, *C. sjostedti* was found associating with two species of *Camponotus* ants, and the trees inhabited by this acacia-ant species were far more heavily infested with leaf galls than were trees occupied by other ant species.

Similarly, Young *et al.* (1997) identified aphids, spiders and mantids associated with *S. drepanolobium* within the Laikipia ecosystem. Other invertebrate community living together with ants includes scale insects, sap-sucking insects, spiders, butterflies and grasshoppers (Hocking, 1970; personal observation). Moreover, casual field observations by Young and colleagues suggest that different arthropod communities are found on trees occupied by different acacia-ant species. However, no detailed studies have been carried to characterize the invertebrate communities that are found associating with each of the four ant species. It was based on these observations that the current study was undertaken.

During the last two decades, some research has focused on the insect diversity in tropical forest tree canopies (Moran and Southwood, 1982; Basset and Kitching, 1991; Basset, 1996; Chey *et al*., 1998). However, arthropod community structure in tree canopies of savannah ecosystems, particularly the ant-acacias, is not well known, and information concerning the coexistence with acacia-ants and other arthropods is scarce (Krüger and McGavin, 1997). Hocking (1970) described the rich invertebrate fauna associated with *S. drepanolobium* and its ant symbionts, and noted that several ant species were mutually exclusive to *S. drepanolobium* trees.

Terrestrial ants as bioindicators

Paoletti (1999a, b) defined a biological indicator or bioindicator as a species or assemblage of species that is largely well synchronized to specific features of the landscape and responds to impacts and changes. However, de la Torre *et al*. (2000) defined bioindicators as key species in an ecosystem that are monitored to improve human capabilities for detecting and predicting the effects of environmental stress. In this thesis, a bioindicator will be defined as a species or assemblage of species that are sensitive to natural and anthropogenic changes and can be used to monitor changes occurring in the environment. Studies on the use of invertebrates as bioindicators include those of ants (Lobry de Bruyn, 1999; Andersen *et al*., 2002), spiders (Marc *et al*., 1999; Warui, 2005), spiders and beetles (Perner and Malt, 2003), beetles (Bohac, 1999) and Syrphidae (Sommaggio, 1999), among others.

The sensitivity of ant-species composition to changes in vegetation structure and disturbance, has led to their increasing use as ecological indicators, particularly in relation to mine-site rehabilitation (Andersen, 1993; Andersen *et al*., 2003; Hoffman and Andersen, 2003; Herrera and Pellmyr, 2002). In Australia ant communities are also used in monitoring the environmental effects of rangeland pastoralism on arid and semi-arid regions (Wilson, 1990; Nash *et al.* 2001; Andersen *et al*., 2004). However, studies on the effects of livestock grazing on ant communities in the eastern Mojave Desert, USA, showed that ant community metrics had little potential to serve as bioindicators of rangeland conditions (Nash *et al*., 2004). Similar results were obtained in the Southern Australia arid zone (Read and Andersen, 2000). This was because differences were evident in severely degraded localized conditions rather than in intermediate, widespread conditions (Nash *et al*., 2004).

The present study is intended to characterize arthropod communities coexisting with acacia-ants on the canopies of *S. drepanolobium* and therefore it was necessary to document the ant species diversity in this ecosystem. Most of Laikipia region is exposed to livestock grazing and wildlife, therefore, there is need for indicators that are sensitive and can be consistently applied across large areas. The current study therefore proposed to elucidate the role of terrestrial ants as opposed to canopy ants in this ecosystem as bioindicators and their potential as a tool for management. The study was carried out at Mpala Research Centre both inside and outside the Kenya Long-term Exclosure Experiment (KLEE) plots. The ultimate goal was that, while tackling the above objectives, the study also evaluated the impact of exclosures on arthropod communities.

Effect of grazing on invertebrates

The major commercial activity in Laikipia is livestock farming (Georgiadis *et al*., 2003; Warui, 2005). Studies on the effects of grazing on grasshopper communities have documented differences in species composition as a result of livestock grazing (Capinera and Sechrist, 1982). Morris (1978) showed that temporal patterns of grazing can affect insect abundance and species richness. The current study will therefore determine whether livestock grazing has any effect on canopy insect abundance and species richness in Laikipia ecosystem. The current study was carried out in three different grazing systems: i) all herbivores were allowed to feed: ii) only cows were allowed to graze: and iii) all herbivores were excluded (wildlife and livestock).

Kenya Long-term Exclosure Experiment (KLEE)

KLEE is a multi-disciplinary project that examines the interactions between livestock and local flora and fauna with a series of herbivore barriers (Young and OKello, 1998). The exclosures were set up in September 1995. The current study is part of the on-going research programme and aims to elucidate the role of the acacia-ants in structuring arthropod community inhabiting canopies of *S. drepanolobium* and the role of ant communities as potential indicators and a tool for management.

Motivation

The canopy arthropods of *S. drepanolobium* occurring on the black cotton soils of the Laikipia ecosystem are not well known. Although they are poorly known, canopy arthropods may represent a large fraction of invertebrate species within tropical communities. At the moment, arthropods sampled from tropical vegetation represent a small proportion of the total known arthropod community (Janzen and Schoener, 1968; Erwin and Scott, 1980).

Casual observation by previous workers had indicated that host trees occupied by different ant species are associated with different invertebrate communities. However, there is little information on species diversity and abundance of these arthropod communities on *S. drepanolobium* trees at Mpala Ranch Laikipia, Kenya. Previous studies concentrated mainly on mutualistic association between the ants and vertebrate herbivores (Young, 1987; Young and Okello, 1998) and factors that lead to coexistence of the four acacia-ants at a fine spatial scale (Stanton *et al*., 1999, 2002; Palmer *et al*., 2002).

Scope and Aims

The aim of this study was to document the different arthropod communities that coexist with the four species of ants and to understand some of the mechanisms shaping this community structure, since previous studies (Young *et al*., 1997; Stanton *et al*., 1999; Palmer *et al.*, 2000; Palmer *et al*., 2002) had shown that the four ant species behave differently. If these different behaviours support different invertebrate communities, then it is likely that coexistence of the four acacia-ant species may significantly enrich the diversity of canopy invertebrates in black cotton habitats.

The fundamental objective of this study is to characterize and to document the various arthropods communities that coexist with acacia-ants on *S. drepanolobium*. The findings will elucidate whether they are ant-specific and if so, what are some of the factors involved.

The specific objectives of this study are as follows:

- To determine the composition and structure of the ant species assemblage, both terrestrial and arboreal, and investigate their potential as bioindicators for livestock management
- To determine the structure of insect communities found on canopies of *S. drepanolobium* and the efficacy of mist-blowing and beating in sampling canopy arthropods
- To establish a checklist of the insect species that coexists with the four acacia-ants on *S. drepanolobium*
- To determine the effect of block location (North, Central and South), grazing patterns, acacia-ants and ant-hemipteran mutualism on community structure and composition of canopy insects
- To determine what happens to insect communities inhabiting canopies of *S. drepanolobium* whenever takeover of host trees occurs between the four ant species

CHAPTER 2: GENERAL MATERIALS AND METHODS

Study area

The study was carried out at the Kenya Long-term Exclosure Experiment and its immediate environs (KLEE: Young *et al*., 1995, 1997) at Mpala Research Centre in the semi-arid Laikipia ecosystem (37˚ E, 0˚ N; 1800m elevation) in north-central Kenya, approximately 190 km from Nairobi (Figure 2.1). The exclosures were set up in September 1995 on a flat terrain of black cotton soils to study the effects of different grazing and browsing patterns on the savannah ecosystem, and so had been in place for 10 years when this study was conducted. Mpala Ranch has a high diversity of wild mammals which includes elephants, zebras, giraffes, hartebeests, impalas, cheetahs, leopards and lions, among others. It also has more than 200 species of birds (Mpala Research Centre database). Rainfall in this area varies from year to year and averages 500mm (in the north) to 650mm (in the south), with peaks in April, July, and November (Young *et al*., 1998). The current study was carried out between September 2003 and June 2005.

The KLEE experiment categorized the various large herbivores occurring in the study area into three classes, mesowildlife (mesoherbivores) which included buffaloes and other smaller ungulates, megawildlife (megaherbivores) which included giraffes and elephants, and cattle (Young *et al*., 1998; Gadd *et al*., 2001). The KLEE experiment has six different treatments C, W, MW, MWC, WC and 0 (Figure 2.2). In treatment C only cattle are allowed to graze; in W only mesoherbivores are allowed to feed; in MW both mesoherbivores and megaherbivores are allowed to feed; in MWC mesoherbivores, megaherbivores and cattle are allowed to feed; in WC mesoherbivores and cattle are allowed to feed; and in 0 (control) no large herbivores are allowed (Young *et al*., 1998; Warui, 2005). However, small mammals like steinbok, baboons, hares, mice, etc could still gain access to the 0 treatment exclosures. The treatments are arranged into three blocks (referred to as "North", "Central" and "South"), and within each block, treatment exclosures are 200m x 200m. Monitoring of KLEE by other investigators has revealed a number of significant treatment-associated changes; relaxation of induced defence on *S. drepanolobium* (Young, 1987; Young and Okello, 1998), rodent abundance and diversity (Keesing, 1998), survival of *Acacia* seedlings (Goheen *et al*., 2004) and spider diversity (Warui *et al*., 2005).

For this particular study, which mainly focused on canopy arthropods of *S. drepanolobium*, only the C and 0 treatments were used, while a third treatment area termed 'E', which was accessible to all herbivores including cattle, was marked adjacent to the KLEE plots. It was felt that these three treatments should give a general representation of the various insects found on the canopies of *S. drepanolobium*. The choice of control (0) was meant to elucidate whether by excluding all herbivores there was any effect on canopy arthropods, in case this was to happen in the future of this particular ecosystem. It was assumed that ten years was long enough that if herbivore exclusion had any effect on canopy insects, it should have become measurable. On the other hand the choice of treatment C was meant to determine what would happen to canopy insects if all the wildlife was eliminated from this ecosystem and only livestock was left.

Sampling Methods

Most ecological studies on invertebrates involve sample collection in the field. However, the choice of method to use depends on whether the study aims to collect samples from arboreal, terrestrial or from both habitats. In this particular study insect samples were collected from canopies of *S. drepanolobium*. To ensure that a sizeable number of insects were collected from the canopies, two different sampling methods were used: beating/jarring and mist-blowing. Pitfall trapping was also used to sample terrestrial ants. The objective of pitfall trapping was to determine if there were terrestrial ants that coexisted in this ecosystem with those that were found on the canopies.

Pitfall trapping

Pitfall trapping is the most commonly used method in sampling ground active arthropods (Koivula *et al*., 2003; Cote *et al*., 2005; Dauber *et al*., 2005; Lensing *et al*., 2005). Most studies on ground active spiders (Brennan *et al*., 1999; Chatzaki *et al*., 2005; Clough *et al*., 2005; Pétillon *et al*., 2005; Varol and Kutbay, 2005; Warui, 2005), and beetles (Bertone *et al*., 2005; Bertrand, 2005; Eyre, 2005; Feer and Hingrat, 2005; Gudleifsson, 2005; Kanda *et al*., 2005; Purtauf *et al*., 2005) are carried out using pitfall traps. Most studies on terrestrial ants communities have often used pitfall traps as the sampling device (James, 2004; Bestelmeyer, 2005; Holec and Frouz, 2005; Holway, 2005).

Pitfall trapping was carried out in all nine treatment plots. In each plot 10 pitfall traps were set on a line transect at an interval of 10 meters. In total 90 pitfall traps were used. A trap consisted of two PVC (polyvinylchloride) containers having a diameter of 96 mm, one container fitting into the other. This design allowed the inner trap to be removed and minimized disturbance effects during subsequent sampling sessions (Hsieh *et al*., 2003). The trap had a volume of 750 ml and was partially filled with 250 ml of water. Detergent was added to the water to break the surface tension and prevent ants from crawling out. The traps were inserted into the ground so that the top was flush with the soil surface. These traps were left uncovered when in operation. Traps were emptied after 48 hours and sampling was repeated every three months.

Samples were collected from 08:00 hrs to 10:30 hrs, washed with water and sieved in the field using a domestic sieve, and later taken to the laboratory for sorting. In the laboratory, samples were first rinsed with 70% ethyl alcohol and later stored in 70% ethyl alcohol. Samples were sorted to subfamily and, when possible, to morphospecies using taxonomic guides. Most of them were later identified to generic and species level by R.R. Snelling from the Natural History Museum, Los Angeles, and by N. Mbanyana from Iziko South African Museum, Cape Town.

Beating/jarring Method

This method involves beating a tree several times using a wooden pole or any other device and collecting arthropods falling on the ground. The method is cheap and environmentally friendly, given that it does not contaminate the environment like chemical-based methods. Jenser *et al*. (1999) used beating to collect canopy samples when they tested the effect of broad spectrum and selective insecticides on the structure of phytophagous and zoophagous communities in the IPM apple orchards in Hungary. Seven methods were evaluated for their efficiency in sampling understorey Hemiptera. The methods evaluated were beating, chemical knockdown, sweeping, branch-clipping, hand-collecting, vacuum sampling and sticky trapping. Results showed chemical knockdown, vacuum sampling and beating performed better compared to the other methods (Moir *et al*., 2005). Costello and Daane (2005) also used beating and vacuum sampling to collect spiders when they compared day and night sampling in a California vineyard. However, beating has limitations since it damages the trees (Vincent *et al*., 1999) and is usually biased against winged and highly mobile insects which escape during sampling (Suckling *et al*., 1996).

Eighty trees were semi-randomly marked using aluminium tags in each plot. This was carried out by following a compass direction on a straight line and tagging trees within 20m range. Their heights and diameter of the girth at 20cm from the ground was measured to the nearest centimetres. Only trees with heights ranging between 1.0 to 2.5 metres were tagged. This was due to the fact that trees within this range were colonized by all four of the focal ant species, while most tall trees beyond 2.5 metres were colonized mainly by *C. sjostedti*, and small trees below 1.0 metres were inhabited mainly by *T. penzigi* (Young and Stubblefield, 1997; Palmer *et al*., 2000). A total of 720 trees were tagged in the nine plots. Random numbers were used to assign the trees to one of four groups for each of the four sampling sessions (Zar, 1974). Twenty trees occupied by each of the four acacia-ants (*C. sjostedti, C. mimosae, C. nigriceps* and *T. penzigi*) were marked in each plot.

For every sampling session five trees occupied by each of the four acacia-ants were sampled. This involved beating a tree twenty times using a wooden pole and collecting all falling arthropod samples using four light blue sheets (each 1 m^2) spread under the tree. Samples from the sheets were pooled to make one sample, labelled and placed in a polythene bag. It took one person approximately 30-40 minutes to sample one tree, which was regarded as one sampling unit.

Samples were later transported to the laboratory and placed in a deep freezer overnight to immobilize the insects, and eventually sorted to order, family and finally to morphospecies. These groupings were later confirmed at the National Museums of Kenya, Iziko South African Museum, Plant Protection Research Institute (Pretoria), and The Natural History Museum (London). Four sampling sessions were carried out with intervals of three-month in between them.

Mist-blowing method

Mist-blowing is commonly applied in sampling canopy arthropods (Kitching *et al*., 1993; Tassone and Majer, 1997 Chey *et al*., 1998). The mist-blowing method works by producing a fine mist of chemical insecticide droplets. These drops are boosted into the target canopy by an air-stream generated by either a back-pack petrol engine or a hand pumped knap-sack sprayer.

Arthropods coming into contact with the chemical are killed or rendered motionless and fall to the ground, where they are collected.

The same number of trees and of similar heights to those used for the beating method were tagged in all nine plots, a total of twenty trees occupied by each of the four ant species in each experimental plot. During each sampling session five trees occupied by each ant species were sampled, making a total of twenty samples.

During the current study a hand pumped knap-sack sprayer was used (Solo 425, made in Germany). The chemical used was Alphacypermethrin 100g/l from Bilag Industries Ltd (traded as Alfix® 10EC). It was diluted with water in the ratio of 5ml to 10 litres. Approximately 300ml of the diluted insecticide was used to spray one tree. Mist-blowing was carried out in the mornings (07:30 - 10:30hrs) when winds were slight, and only in dry conditions. Each tree was sprayed for 30 - 40 seconds, making sure the mist from the mist-blower penetrated the canopy. All arthropods falling from the canopy were collected on four light blue sheets (each 1 m^2) placed under the tree. After 40 - 50 minutes the catch was removed from the sheets and placed in polythene bags. Samples were later transported to the laboratory and placed in a deep freezer to immobilize the insects, although most of them were already dead due to the insecticide. Sorting followed the same regimen as for the beating method. All sorted specimens were preserved in 70% ethanol. Specimens that were different from those collected using beating were also sent to the above named Museums either to confirm their identity or to have them identified. Four sampling sessions were carried out with three-month intervals between them.

Diversity indices

Species diversity is a function of the number of species present and the evenness with which the individuals are distributed among these species (Hurlbert, 1971). However, Hurlburt (1971) argued that diversity had been defined in so many ways that it risked becoming a meaningless concept but still recommended the continued use of richness and evenness when measuring diversity. According to Hurlbert (1971) “diversity per se does not exist”. Peet (1974) suggested that if diversity was to continue to play a productive role in ecological investigations, agreement was needed on the definitions of the many constituent concepts included in its current

application. Noss, (1990) argued that diversity indices lose information, are heavily dependent on sample size, and generally have fallen out of favour in the scientific community.

Several diversity indices were selected and used during the current study. These included total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′). The original insect abundance data were converted into these indices and later subjected to various statistical analyses to address the various objectives. Even though there is still argument as to how the various different diversity indices work (Hurlbert, 1971: Peet, 1974), diversity indices still continue to be used to describe ecological communities until better replacements are found or consensus on their use is achieved. The indices chosen for the current study are those commonly used (Warwick *et al*., 1990; Vetter and Dayton, 1998) and some have also been used previously on studies carried out on the same study area (Keesing, 1998; Keesing, 2000; Warui, 2005).

Communities can be analysed using the abundances of the various taxa as data. This approach tends to be very rich in variables, since each taxon forms a separate variable, and this can make analysis complicated. One method of simplifying the data before analysis is to calculate summary indices of the diversity of the communities. Many diversity indices exist, each with its own strengths and weaknesses (Roth *et al*., 1994). No single index includes all of the characteristics of an ideal index with high discriminant ability, low sensitivity to sample size, and ease of calculation; therefore, it is best to use a combination of them (Roth *et al*., 1994). Diversity indices are usually classified into three groups; richness, heterogeneity and equitability indices (Peet, 1974). The simplest and most basic measure is the number of species or species richness (S) and is currently the most widely used diversity measure (Peet, 1974; Whittaker, 1975; Stirling and Wilsey, 2001; Spellerberg and Fedor, 2003; Andrew and Hughes, 2004). As an index, S is easily conceptualized and comparable across habitats (Noss, 1990). Ecological diversity indices such as the Shannon-Wiener diversity index and the Simpson index summarize the information about the relative abundances of taxa within a sample or community (Ricotta, 2002). These are examples of heterogeneity indices. The most commonly used is the Shannon-Wiener diversity index (H′), even though its performance and meaning are contentious (Hurlbert, 1971; Stirling and Wilsey, 2001; Spellerberg and Fedor, 2003).

$$H' = -\Sigma(P_i \log_e(P_i))$$

P_i is the proportion of the *i*th species in the total sample (Price, 1975). Thus number of species in the community and their evenness in abundance are the two parameters that define H′. The Shannon-Wiener diversity index is sensitive to both species richness and evenness and is the best measure of their joint influence and also is not strongly affected by rare species (Stirling and Wilsey, 2001). It is also sensitive to changes in the rare species (Peet, 1974). However, Pielou [1967 quoted in Peet (1974)] argued for use of the Brillouin index in preference to the Shannon formula on the grounds that the latter does not reflect the sample size.

Simpson's index was the first of the heterogeneity indices used in ecology (Peet, 1974). The index measures the probability that two individuals selected at random from a sample will belong to the same species (Peet, 1974).

Examples of equitability indices include Pielou's index, the Redundancy (Patten) index, and the V Simpson index, among others (Peet, 1974). Among the equitability indices, the mostly commonly used is Pielou's evenness index, J′.

$$J' = \frac{H'}{H'_{\max}} = \frac{H'}{\log_e S}$$

where S is the number of species present. Stirling and Wilsey (2001) showed that number of species (S), Pielou's evenness index (J') and the Shannon-Wiener diversity index (H') were positively and highly correlated.

Figure 2.1. A map of Laikipia District, Kenya showing the location of Mpala Ranch (in black). Mpala Research Centre, where the project was carried out, lies near the south east corner of Mpala Ranch.

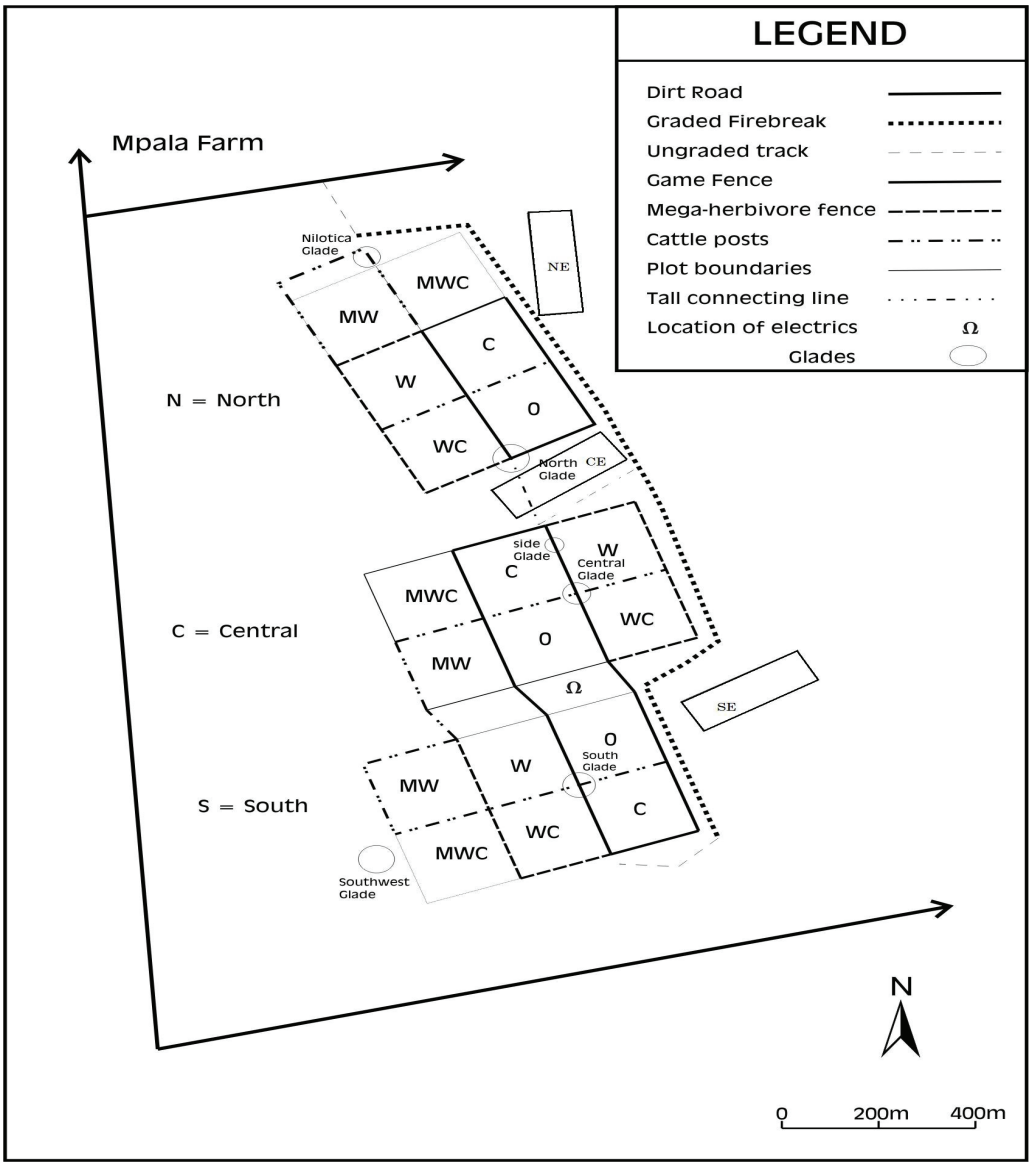


Figure 2.2. Study design showing KLEE plots and three other plots which were added during this study. "MWC" represents plots in which megaherbivores, mesoherbivores and cattle were allowed to feed; "WC" represents plots in which mesoherbivores and cattle were allowed to feed; "C" represents plots in which only cattle were allowed to feed; "MW" represents plots in which megaherbivores and mesoherbivores were allowed to feed; "W" represents plots in which only mesoherbivores were allowed to feed; and "0" represents plots in which all herbivores were excluded. In addition, "NE", "CE" and "SE" represent nearby plots in which all herbivores and cows were allowed to feed.

CHAPTER 3: DIVERSITY OF ANTS IN THE BLACK COTTON ECOSYSTEM AND THEIR POTENTIAL AS INDICATORS

Introduction

The black cotton soil ecosystem of Laikipia, Kenya is known to be home to several canopy-dwelling ant species. Young *et al*. (1997), working on acacia-ants and their coexistence on Mpala Ranch, identified nine ant species inhabiting *Senegalia drepanolobium* and *S. seyal.* These included five species of *Crematogaster*, two species of *Camponotus*, and one each of *Tetraponera* and *Lepisiota*. The present study was intended to characterize arthropod communities coexisting with acacia-ants on canopies of *S. drepanolobium* and therefore it was necessary to document the ant species diversity in this ecosystem. This aspect of the study was meant to show that there are other ant species, both arboreal and terrestrial, in this ecosystem. Another goal is to determine the potential of the ant community as an indicator of grazing systems in the management of this ecosystem.

Land-use and land-cover change often leads to changes in species' abundances, which affect ecosystem function and the ability of ecosystems to recover after disturbance (Verchot *et al*., 2003). Habitat disturbance often has little direct impact on ants, especially those nesting in soil, but acts indirectly on ant communities through effects on vegetation structure, food supplies and competitive interactions (Hoffmann and Andersen, 2003). Presence of livestock and wildlife on arid and semi-arid land has continued to exert pressure on this environment and there is need to develop methods for assessing and monitoring the environmental impact of these large animals (Bernard *et al*., 1989; Western and Pearl, 1989; Georgiadis *et al*., 2003; Lamprey and Reid, 2004; Warui, 2005; Young *et al*., 2005). Therefore, indicators are needed that are sensitive to disturbance (in particular grazing, which is the major commercial activity in this ecosystem) and that can be applied in large areas. Not much has been done on use of faunal indicators in evaluating ecological condition in rangeland systems (Nash *et al*., 2004).

Ants possess a number of characteristics that may make them particularly useful as indicators of ecosystem change, as they are extremely abundant, live in stationary colonies, have relatively high species richness, are easily sampled, are easy to identify and are responsive to

environmental conditions (Agosti *et al*., 2000; Nash *et al*., 2004). Paoletti (1999a, b) defined a bioindicator as a species or assemblage of species that is well matched to particular features of the landscape and responds to impacts and changes.

Of all terrestrial invertebrates, ants are the most widely used bioindicators in Australia (Hoffmann and Andersen, 2003), and particularly in monitoring mine-site restoration (Majer, 1983; Majer and Nichols, 1998; Andersen, 1993; Jackson and Fox, 1996). They have been used to monitor the environmental effects of rangeland pastoralism on arid and semi-arid regions of Australia (Wilson, 1990; Hoffman and Andersen, 2003; Andersen *et al*., 2004; James, 2004). They owe this to their relative stability, modest diversity, and sensitivity to microclimate (Agosti *et al*., 2000). The effects of grazing on invertebrates include studies of ant communities (Whitford *et al*., 1999; Kerley and Whitford, 2000; Read and Andersen, 2000), spiders (Lowrie, 1963; Rushton *et al*., 1989; Gibson *et al*., 1992; Dennis *et al*., 2001; Warui, 2005) and beetles (McGeoch, 2002; Vohland *et al*., 2005). Livestock grazing was also shown to affect species composition on grasshopper communities (Capinera and Sechrist, 1982).

On the black cotton soils of the Laikipia ecosystem four species of acacia-ants have a mutualistic association with *S. drepanolobium* and *S. seyal* (Young *et al*., 1997; Palmer *et al*., 2000). A number of studies have been conducted on this ecosystem particularly on these symbiotic ants (Young, 1987; Young and Okello, 1998; Young *et al*., 1997, 1998; Palmer *et al*., 2000, 2002, Palmer, 2004; Stanton *et al*., 2002; Ward and Young, 2002) but none of these studies examined the effect of feeding by livestock and other herbivores on the terrestrial ant community. However, the effect of grazing on spider community in this ecosystem has been reported (Warui, 2005). Vegetation changes resulting from drought, rainfall or overgrazing are likely to affect the temporal availability, quality, and quantity of food for these ant species and for the entire ant community in this ecosystem.

The ultimate goal of the current study is to elucidate whether assemblages of ant species can be used as indicators in a savannah ecosystem to monitor different grazing patterns and therefore serve as a management tool. This study was designed at Mpala Research Centre to examine the effect of different grazing patterns on ant communities at the KLEE experimental plots (Young *et*

al., 1995) and its immediate environs. A secondary goal was to produce a checklist of ant species on this ecosystem, particularly for those found on the ground, since these species have not been surveyed systematically previously.

Objectives

Objectives of this study were:

i) To establish and document the abundances of different ant species occurring in this savannah ecosystem

ii) To determine if ant community structure was affected by either location of the blocks or treatments

iii) To determine whether different grazing systems have any effect on diversity, species richness and species evenness within the ant community

Hypotheses

i) The distribution pattern of the ant community was not affected by block location and the different treatments

Blocks are approximately 200 meters from each other, with the furthest plots approximately 5 km apart. Therefore, structure of ant communities was expected to be affected by the location of the different blocks. Different treatments had different feeding pressure and therefore different distribution patterns were expected to be found in different treatments. Principal component analysis (PCA) and non-multidimensional scaling (MDS) were used to describe the community pattern.

ii) The location of the blocks (North, Central and South) had no effect on the ant community. There is also no difference between the three different treatments. The treatments were C (only cattle present), 0 (all herbivores excluded) and E (all herbivores and cattle present).

Since the blocks were wide apart, approximately 200 metres from each other, and the furthest plots approximately 5 kilometres apart, it was hypothesized that total number of taxa, the Shannon-Wiener diversity index, Margalef's richness index and Pielou's evenness index would be significantly different between the plots. The different grazing patterns were expected to have

an impact on the ant community. It was hypothesized that total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) would be significantly different in the different treatments. Treatment plots with high feeding pressure would have low diversity indices compared to control plots.

Materials and Methods

See Chapter Two.

Data analysis

Data analysis was performed using PRIMER 5 for widows (Version 5.24) Plymouth, PRIMER-E Ltd. (Clarke and Gorley, 2001) and PERMANOVA v. 1.6 (Anderson, 2005). Permutational Multivariate Analysis of Variance (PERMANOVA) is a better method compared to the Kruskal-Wallis test because it can also test interaction effects. PERMANOVA test using permutations assumes only that the observations units are exchangeable under a true null hypothesis. The original variables are not assumed to be normally distributed as in ANOVA. PRIMER was used in generating diversity indices which were later subjected to PERMANOVA. PRIMER was also used in performing principal component analysis (PCA) and non-metric multidimensional scaling (MDS). These two methods were used to determine variation between samples collected from the different blocks and the different treatments. Counts of ant species abundances are often transformed in order to reduce distortions caused by large numbers of ants falling into a few traps when traps are placed beside colony entrances or along foraging trails (Andersen, 1990). The original ant data were therefore first log-transformed (log(x +1)) using the transformation module of the PRIMER program to down-weight the importance of the very abundant species, so that the less dominant, and even the rare species, play some role in determining the similarity of two samples. The transformed data were subjected to PCA analysis to explore if the ant community pattern was affected by either the location of the block or the grazing treatments. The same ant community data were subjected to the MDS module of PRIMER program. The original data matrix was first log-transformed (log (x + 1)) and later subjected to the similarity module of the PRIMER program to generate similarity matrix using Bray-Curtis similarity coefficient. The

similarity matrix was submitted to MDS module to generate a two-dimensional configuration of the ant community collected using pitfall traps. The fitting process was iterated 10 times.

The raw data collected from the pitfall traps was also used to calculate the various diversity indices. A pitfall trap was taken as a sampling unit. The indices included the Shannon-Weiner diversity index (H′), total number of taxa (S), Margalef's richness index (d) and Pielou's evenness index (J′). The diversity matrices obtained after subjecting the raw data to the PRIMER program using the DIVERSE module were later subjected to the PERMANOVA. The indices were used to determine if location of the blocks and the different treatments had any effect on the ant community.

Results

A total of 4369 ants of sixteen species belonging to six subfamilies were found in this ecosystem. Ten species inhabited the canopies of *S. drepanolobium*. All sixteen species occurred on the ground, but a number of species found in pitfall traps were never encountered in canopy samples (Table 3.1). Between the two methods used in sampling the canopies of *S. drepanolobium*, beating yielded the higher number of species (Table 3.1). For the pitfall trap samples subfamilies Myrmicinae and Formicinae accounted for 61.64% and 30.12% of the total individuals (Table 3.1). *Camponotus* cf. *flavomarginatus* and *Pheidole crassinoda* had more than one thousand individuals each (Table 3.1).

Community structure

Effects of block location on terrestrial ants

The first two axes of the PCA captured 49.9% of the total variation. Assessment of the Eigenvectors revealed that the first axis was mainly affected by *Technomyrmex* sp. A, *Lepisiota* sp. A, *Monomorium bicolor* and *C. mimosae* (Table 3.2). The second axis was mainly influenced by *Polyrhachis viscosa*, *C. sjostedti*, *T. penzigi*, *Tetramorium sericeiventre*, *Camponotus maculatus* and *P. crassinoda* (Table 3.2). These two dimensions showed that the blocks were different. There was a tendency for samples collected from the south block to cluster in one

direction and those from Central block in the opposite direction and those from north block to occur in between, but not consistently (Figure 3.1a). A two-dimensional PCA plot showed that convex hulls for central block did not overlap with convex hulls of south block (Figure 3.1a). However, there was overlap between convex hulls for north and central blocks and also for south and north blocks (Figure 3.1a).

Results of PERMANOVA performed on principal scores showed that there was a significant difference between blocks. Further analysis using pairwise comparisons revealed that central and south blocks were significantly different (Table 3.3). When the same data set were subjected to the MDS a two-dimensional MDS ordination generated was similar to that obtained using PCA, convex hulls for central and south blocks did not overlap. The stress value of 0.1 was not good and therefore there was no need for further interpretation (Figure 3.1b). PERMANOVA results did show any significant difference between sampling events.

Effects of treatments on terrestrial ants

The first two axes of the PCA explained 48.7% of the total variation (Table 3.2). Examination of the Eigenvectors showed that the first axis was mainly affected by *C. flavomarginatus*, *M. bicolor*, *Technomyrmex* sp. A and *C. mimosae*; the second axis was a gradient between (*Lepisiota* sp. A + *Technomyrmex* sp. A) and *C. flavomarginatus* (Table 3.4). These two dimensions showed that treatments were not significantly different, and convex hulls for the three treatments overlapped (Figure 3.2a). Samples collected from the central block under treatment 'E' in the second and fourth replicates were isolated from the rest of the ant samples (Figure 3.1).

Principal component scores generated from PCA were analysed using PERMANOVA to test whether sampling events and treatments had any effect on the ant community. Results showed that there was a significant effect on treatments and sampling events but there was no interaction effect between treatments and sampling events (Table 3.5). However, pairwise comparisons using PERMANOVA did not reveal significant differences between treatments, but there was a significant difference between the fourth sampling event and the first, second and third events (Table 3.5).

The same data were subjected to MDS. A two-dimensional MDS ordination obtained was not very different from that generated using PCA (Figure 3.2b). However, the MDS stress value of 0.21 was too high and therefore there was no need for further interpretation. The groupings did not represent any distinct pattern and this was interpreted to mean that the different treatments were not different from each other. The other explanation was that there was a pattern which was highly complex and could not be revealed by this type of ordination.

Diversity Indices

PERMANOVA was performed to determine the effect of treatments, blocks and sampling events on total number of taxa, Margalef's richness index, Pielou's evenness index and the Shannon-Wiener diversity index. Results showed that there were no significant effects of treatments, blocks or sampling events on all four diversity indices (Tables 3.6 - 3.9). There was also no significant interaction effect on all four diversity indices between treatments, blocks and sampling events (Tables 3.6 - 3.9). But there was a significant difference between sampling events on Margalef's richness index (Table 3.7) and the Shannon-Wiener diversity index (Table 9). Further analysis using pairwise comparisons on Margalef's richness index revealed that the third and fourth sampling events were significantly different (Table 3.7). Pairwise comparisons on the Shannon-Wiener diversity index revealed that the fourth sampling session was significantly different from the first and third sampling events (Table 3.9).

Discussion

Community structure

The current study revealed that, apart from those ants occurring on canopies of *S. drepanolobium* and *S. seyal* that were reported by Young *et al.* (1997), other ant species occur in this ecosystem. During the present study, ant samples were collected from canopies of *S. drepanolobium* and from the ground, and the ground-collected samples included many species that were not found in *Acacia* canopies. However, some of the ant species identified by Young *et al*. (1997) were not among those collected during this study. Therefore, the number of ant species occurring in this ecosystem is higher than the current figure of sixteen. However, the number reported here was

only from the black cotton ecosystem. This number is however, small compared to 232 ant species identified in Mkomazi, Tanzania (Robertson, 1999). More exhaustive studies should be carried out in order to define the community structure and composition of the ant diversity in this ecosystem.

This is the first time the terrestrial ants in this ecosystem have been surveyed. All of those ant species recorded from the canopies were also found on the ground, but several ant species were only found on the ground, including *Aenictus* sp. A, *T. sericeiventre*, *T. weitzeckeri* and *Tetramorium* sp. 4. The dominant ant species on canopies of *S. drepanolobium* are *C. mimosae, C. nigriceps, C. sjostedti* and *T. penzigi* (Young *et al*., 1997), while on the ground the dominant species were *C. flavomarginatus*, *C. mimosae* and *P. crassinoda.* More than 99% of *S. drepanolobium* trees that are more than one metre tall are occupied by one of four acacia-ants (*C. mimosae, C. nigriceps, C. sjostedti* and *T. penzigi*) that comprise thousands and thousands of individuals (Hocking, 1970; Young *et al*., 1997; Palmer, 2004). However, the numbers of these species collected on the ground using three hundred and sixty pitfall traps is very low (Table 3.1). Therefore, it is very likely that several of these ant species or all of them rarely forage on the ground as earlier believed and probably most of their nutrient requirements are met within the canopies. This argument will become clear in the coming chapters.

Ordination analysis carried out using Principal Component Analysis (PCA) and non-metric Multidimensional Scaling (MDS) generated two-dimensional plots indicating that, the ant community sampled by pitfall traps was affected by location of blocks and treatments. There was a pattern which showed samples collected from the south block clustering in one direction and those from central block clustering in the opposite direction, with samples collected from the north block occurring in between (Figure 3.1).

Further analysis of principal components scores generated by PCA revealed that block location and treatments were significantly different. However, further analysis using pairwise comparisons revealed that only the south block was significantly different from the central block, but there was no effect on treatments. There are two explanations to the observed difference between blocks; the Centre database shows that the south block receives more rainfall than the

other two blocks or edaphic factors of the south block may be different from that of the central block (Warui, 2005). Young *et al*. (1998) indicated that there was a north-south gradient and that blocks may be different. The feeding pressure on vegetation on different treatments was not very intense and this might explain why there was no significant difference between treatments. Similar observation was made by Warui (2005) while working on the impact of wildlife and cattle grazing on spider biodiversity. However, results on diversity indices showed that treatments and blocks were not significantly different.

Bioindication

Environmental management has largely depended on invertebrates as monitoring tools because of their great abundance, diversity and functional importance, their sensitivity to disturbances, and the ease with which they can be sampled (Andersen *et al*., 2004). There is increasing evidence that invertebrate species or vertebrate assemblages provide a good indication of changing environments (Bohac, 1999; Lobry de Bruyn, 1999; Marc *et al*., 1999; Read and Andersen, 2000; Kimberling *et al*., 2001; Jeanneret *et al*., 2003; Perner and Malt, 2003; Kampichler and Platen, 2004). Among the invertebrates, ants stand out as the most frequently used group (Majer, 1992; Read and Andersen, 2000; Nash *et al*., 2001), being used as bioindicators in Australia and particularly in monitoring rehabilitation of mine-sites (Majer and Nichols, 1998).

The current study investigated the potential of the ant community in the black cotton ecosystem to serve as an indicator of environmental change due to wildlife or livestock feeding pressure. Grazing was shown to have different effects on grass cover, litter cover, and soil strength in different grasslands and ant communities accordingly show different responses (Hoffmann and Andersen, 2003). In this study, I found a significant effect between treatments using principal scores generated using PCA. However, pairwise comparisons did not reveal any significance difference between long-term grazing treatments on ant communities, contrary to what was expected. However, this could be due to the nature of the experimental plots at the study site. Grazing pressure and browsing pressure are not so intense and therefore, there might not be much effect on the vegetation cover and composition between the different treatments. However, other workers at the KLEE site have reported different observations. The spider community collected through sweep-netting was found to respond to grazing impacts and it was suggested that the

spider community could be used as a bioindicator in this ecosystem (Warui, 2005). The spider data again showed that the south block was different from the other blocks and this was attributed probably to soil factor but not to vegetation cover or rainfall (Warui, 2005). According to data from previous study in this same area by Young *et al*. (1998), there was a north-south gradient, which also suggested that the blocks differ. The current data on terrestrial ants also revealed that blocks were different but portrayed a central-south gradient.

The terrestrial ant community cannot be used as an indicator of grazing effect in this ecosystem, at least with the intensity of sampling used here. Similarly Espira (2001), working on ant communities at the Kakamega Forest in Kenya, could not conclusively show that ants could be used as bioindicators of forest disturbance. Nash *et al*. (2004) concluded that the ant community may not be a good indicator of rangeland condition because community changes are only seen under severely degraded conditions rather than in intermediate, more widespread conditions. This observation supports the findings of the current study. A five-year project in Chihuahuan desert grassland found that grazing affected ant species richness negatively but only in some years (Forbes *et al.,* 2005), whereas other studies have also shown that there is no consistency in the way ant communities respond to grazing pressure (Andersen, 1991a; Read and Andersen, 2000). However, there is need for more studies to fully understand the ecology of this ant community, to identify species that are likely to respond fast to feeding pressure. Temporal and spatial variability of the terrestrial ant community may require the use of intensively replicated sampling schemes, to see the effects of environmental change. This may reduce their value as bioindicators.

Table 3.1. Ant species found in black cotton habitats at the Mpala Research Centre of Laikipia ecosystem. "N", "C" and "S" refer to the North, Central and South experimental blocks, respectively. Within each block, data are pooled across sampling dates and grazing treatments. Sampling was carried out using three different methods. For samples collected from the canopies of *S. drepanolobium*, ant species are recorded as present ("X") or absent. The table also records the number of individuals of each morphospecies collected using pitfall traps within the nine experimental plots (Number of traps = 360). Sampling was carried out using three different methods.

Ant Morphospecies	Sampling techniques								
	Beating			Mist-blowing			Pitfall traps		
	N	C	S	N	C	S	N	C	S
Aenictinae									
1. *Aenictus* sp. A							11	31	0
Dolichoderinae									
1. *Technomyrmex* sp. A (*albipes* group)		X	X				47	97	34
Formicinae									
1. *Camponotus* cf. *flavomarginatus* Mayr	X	X	X	X	X	X	33	980	183
2. *Camponotus maculatus* (Fabricius)	X	X	X	X	X	X	27	14	27
3. *Lepisiota* sp. A							63	50	31
4. *Polyrhachis viscosa* F. Smith			X	X	X	X	1	2	4
Myrmicinae									
1. *Crematogaster mimosae* Santschi	X	X	X	X	X	X	388	220	152
2. *Crematogaster nigriceps* Emery	X	X	X	X	X	X	10	0	12
3. *Crematogaster sjostedti* Mayr	X	X	X	X	X	X	19	19	45
4. *Monomorium bicolor* Emery			X				8	90	10

Ant Morphospecies	Sampling techniques								
	Beating			Mist-blowing			Pitfall traps		
	N	C	S	N	C	S	N	C	S
5. *Pheidole crassinoda* Emery		X	X				326	425	559
6. *Tetramorium sericeiventre* Emery							21	8	45
7. *Tetramorium weitzeckeri* Emery							124	94	92
8. *Tetramorium* sp. 4							2	4	0
Ponerinae									
1. *Platythyrea cribrinodis* (Gerstaecker)							22	4	9
Pseudomyrmecinae									
1. *Tetraponera penzigi* Mayr	X	X	X	X	X	X	0	8	6

Table 3.2. Eigenvectors and Eigenvalues of the correlation matrix generated by PCA from log-transformed ant morphospecies abundance data collected using pitfall traps to test the effect of block location (Central, North and South) and sampling events (First, Second, Third and Fourth) on terrestrial ant communities.

Variable	PC1	PC2	PC3	PC4	PC5
Aenictus sp.	-0.247	-0.016	0.094	-0.044	-0.648
C. mimosae	**-0.311**	-0.005	-0.367	0.066	-0.241
C. nigriceps	0.056	-0.085	-0.525	0.241	-0.345
C. sjostedti	-0.155	**-0.390**	-0.337	0.148	0.241
C. maculatus	0.058	**-0.363**	-0.016	-0.495	0.040
C. flavomarginatus	-0.242	-0.258	0.341	0.275	-0.121
Lepisiota sp. A	**-0.360**	-0.086	-0.153	-0.173	0.054
M.bicolor	**-0.348**	0.041	0.260	0.144	-0.037
P. crassinoda	-0.175	**-0.341**	0.045	-0.039	0.194
P. cribrinodis	0.249	-0.084	-0.101	-0.381	-0.430
P. viscosa	-0.029	**-0.438**	0.238	0.089	-0.193
T. penzigi	0.181	**-0.388**	0.002	0.439	0.022
Technomyrmex sp. A	**-0.365**	0.127	-0.071	-0.150	0.199
T. sericeiventre	0.283	**-0.368**	0.037	-0.255	0.053
Tetramorium sp. 4	-0.281	-0.063	0.293	-0.272	-0.077
T. weitzeckeri	-0.290	-0.109	-0.315	-0.186	0.124
Eigenvalues	5.12	2.87	2.09	1.69	1.30
% Variation	32.0	17.9	13.1	10.6	8.1
Cum % variation	32.0	49.9	63.0	73.6	81.7

Table 3.3. Results of PERMANOVA performed using principal scores generated using ant species data collected using pitfall traps to determine the effect of block location (Central, North and South) and sampling events (First, Second, Third and Fourth). * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	45.793	22.897	2.104	0.030*
Residual	9	97.960	10.884		
Total	11	143.753			
Sampling event	3	52.886	17.629	1.552	0.111
Residual	8	90.867	11.358		
Total	11	143.753			

Block	t	P_{perm}
Central*North	1.286	0.260
Central*South	1.644	0.040*
North*South	1.410	0.110

Table 3.4. Eigenvectors and Eigenvalues of correlation matrix generated by PCA when log-transformed ant data collected using pitfall traps was run through PCA module of PRIMER program to test the effect of treatments and sampling events.

Variable	PC1	PC2	PC3	PC4	PC5
Aenictus sp.	0.201	0.092	-0.171	0.458	-0.196
C. mimosae	**0.304**	-0.293	0.052	0.517	-0.111
C. nigriceps	0.019	0.021	0.153	0.295	0.038
C. sjostedti	0.157	-0.121	0.416	-0.293	0.222
C. maculatus	-0.012	0.090	0.106	0.015	-0.635
C. flavomarginatus	**0.686**	**0.612**	0.037	-0.135	0.172
Lepisiota sp. A	0.241	**-0.421**	0.074	-0.391	-0.391
M. bicolor	**0.367**	-0.036	-0.428	-0.045	-0.227
P. crassinoda	0.110	-0.018	0.275	-0.173	-0.097
P. cribrinodis	-0.086	0.074	0.219	0.289	0.131
P. viscosa	0.018	0.014	-0.035	-0.048	-0.089
T. penzigi	0.000	0.095	0.064	-0.048	0.060
Technomyrmex sp. A	**0.357**	**-0.463**	-0.020	0.008	0.243
T. sericeiventre	-0.065	0.284	0.378	-0.010	-0.398
Tetramorium sp. 4	0.037	-0.028	-0.070	-0.065	-0.072
T. weitzeckeri	0.164	-0.136	0.541	0.234	0.015
Eigenvalues	2.85	1.93	1.35	0.73	0.59
% Variation	29.1	19.7	14.7	7.5	6.0
Cum % variation	29.1	48.7	62.5	70.0	76.0

Table 3.5. Results of PERMANOVA performed using principal scores generated using ant species data collected using pitfall traps to determine the effect of treatments 0 (all herbivores and cattle excluded), C (only cattle present) and E (all herbivores and cattle present) and sampling events (First, Second, Third and Fourth). * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Treatment	2	26.781	13.390	3.150	0.022*
Sampling event	3	87.019	29.006	3.071	0.002*
Treatment*Sampling event	6	25.510	4.252	0.450	0.995
Residual	24	226.677	9.445		
Total	35	365.987			

Treatment	t	P_{perm}
C*E	0.921	0.590
C*0	0.640	0.770
E*0	1.367	0.130

Sampling event	t	P_{perm}
First vs Second sampling	1.306	0.110
First vs Third sampling	1.002	0.350
First vs Fourth sampling	2.839	0.010*
Second vs Third sampling	1.383	0.080
Second vs Fourth sampling	1.595	0.020*
Third vs Fourth sampling	2.540	0.010*

Table 3.6. Results of PERMANOVA to test the effect of treatments 0 (all herbivores and cattle excluded), C (only cattle present) and E (all herbivores and cattle present), location (North, Central and South) and sampling events (First, Second, Third and Fourth) on total number of taxa (S). * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	32.528	16.264	1.620	0.151
Treatment	2	24.194	12.097	1.504	0.179
Sampling event	3	34.833	11.611	0.707	0.726
Location*Treatment	4	90.222	22.556	1.614	0.079
Location*Sampling event	6	60.250	10.042	0.612	0.936
Treatment*Sampling event	6	48.250	8.042	0.490	0.990
Location*Treatment*Sampling event	12	167.667	13.972	0.851	0.748
Residual	36	591.000	16.417		
Total	71	1048.944			

Table 3.7. Results of PERMANOVA to test the effect of treatments 0 (all herbivores and cattle excluded), C (only cattle present) and E (all herbivores and cattle present), location (North, Central and South) and sampling events (First, Second, Third and Fourth) on Margalef's richness index (d). * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	6.399	3.200	1.224	0.313
Treatment	2	3.109	1.555	1.161	0.330
Sampling event	3	12.159	4.053	2.038	0.023*
Location*Treatment	4	11.044	2.761	1.287	0.207
Location*Sampling event	6	15.678	2.613	1.314	0.132
Treatment*Sampling event	6	8.032	1.339	0.673	0.895
Location*Treatment*Sampling event	12	25.745	2.145	1.079	0.343
Residual	36	71.597	1.989		
Total	71	153.764			

Sampling event	t	P_{perm}
First vs Second sampling	0.948	0.449
First vs Third sampling	1.200	0.223
First vs Fourth sampling	1.474	0.069
Second vs Third sampling	1.126	0.297
Second vs Fourth sampling	1.176	0.212
Third vs Fourth sampling	2.247	0.001*

Table 3.8. Results of PERMANOVA to test the effect of treatments 0 (all herbivores and cattle excluded), C (only cattle present) and E (all herbivores and cattle present), location (North, Central and South) and sampling events (First, Second, Third and Fourth) on Pielou's evenness index (J′). * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	1.594	0.797	1.509	0.185
Treatment	2	0.812	0.406	1.238	0.294
Sampling event	3	1.862	0.621	1.294	0.223
Location*Treatment	4	1.877	0.468	0.736	0.782
Location*Sampling event	6	3.168	0.528	1.101	0.317
Treatment*Sampling event	6	1.967	0.327	0.684	0.891
Location*Treatment*Sampling event	12	7.653	0.638	1.330	0.070
Residual	36	17.260	0.479		
Total	71	36.192			

Table 3.9. Results of PERMANOVA to test the effect of treatments 0 (all herbivores and cattle excluded), C (only cattle present) and E (all herbivores and cattle present), location (North, Central and South) and sampling events (First, Second, Third and Fourth) on the Shannon-Wiener diversity index (H′). * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	4.300	2.150	1.268	0.293
Treatment	2	3.058	1.529	2.432	0.060
Sampling event	3	8.522	2.841	2.277	0.011*
Location*Treatment	4	7.566	1.892	1.593	0.095
Location*Sampling event	6	10.177	1.696	1.360	0.114
Treatment*Sampling event	6	3.773	0.629	0.504	0.987
Location*Treatment*Sampling event	12	14.253	1.188	0.952	0.588
Residual	36	44.904	1.247		
Total	71	96.552			

Sampling event	t	P_{perm}
First vs Second sampling	1.230	0.170
First vs Third sampling	0.942	0.530
First vs Fourth sampling	1.902	0.010*
Second vs Third sampling	1.221	0.190
Second vs Fourth sampling	1.106	0.230
Third vs Fourth sampling	2.232	0.020*

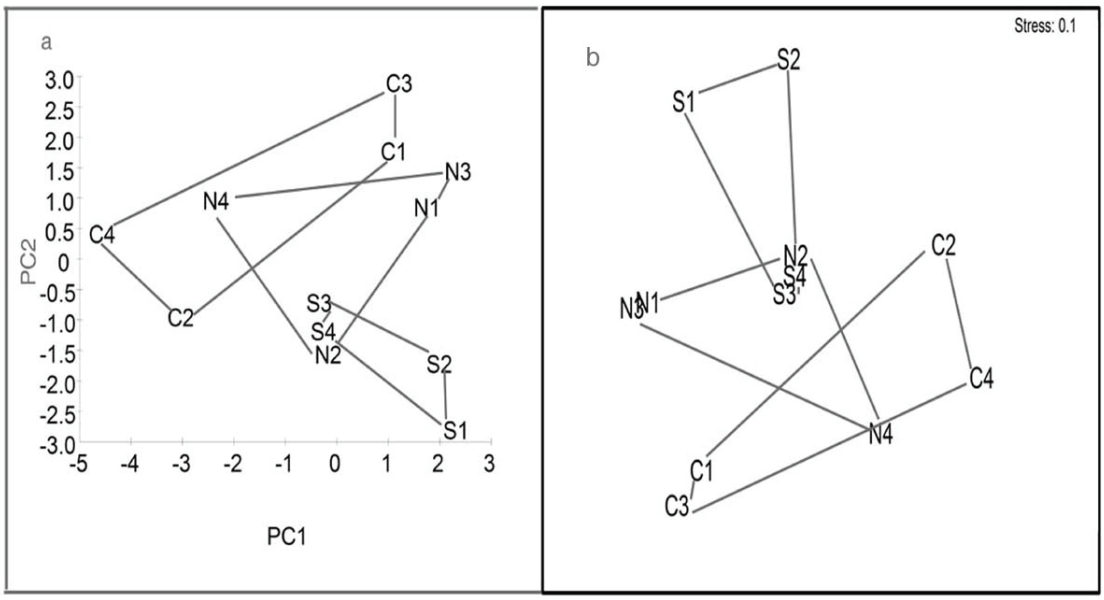


Figure 3.1. Ordinations of log-transformed abundances of ant morphospecies collected using pitfall traps to establish the effect of block location (Central, North and South) on terrestrial ants; (a) First two dimensions of a PCA of abundances of ants (b) Two-dimensional MDS of abundances of ants. The letters represent blocks (N = north, C = central and S = south). The digits represent the sampling sessions.

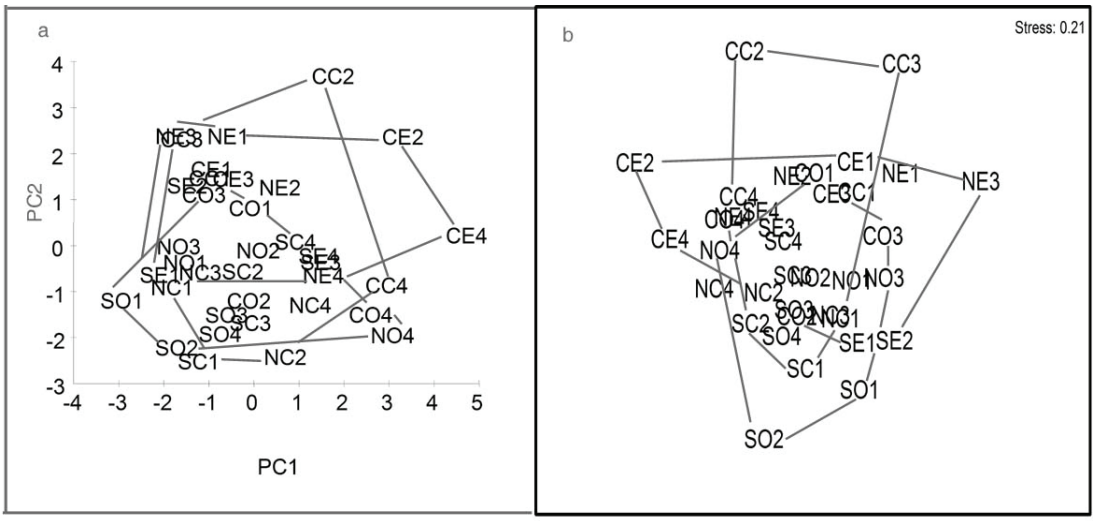


Figure 3.2. Ordinations of log-transformed abundances of ants morphospecies collected using pitfall traps to establish the effect of treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded) on terrestrial ants; (a) First two dimensions of a PCA of abundances of ants (b) Two-dimensional MDS of abundances of ants. The first letters in all cases represent blocks (N = north, C = central and S = south) and the second letters represent treatments. The digits represent the sampling sessions.

CHAPTER 4: A COMPARISON OF INSECT DIVERSITY UNDER TWO SAMPLING METHODS

Introduction

Sampling canopy arthropods

Ecological studies on invertebrates often involve sample collection in the field. However, choice of sampling method depends on what habitats the study aims to sample. Improved access to tree canopies over time has lead to better understanding of arthropod communities occupying these specific habitats (McWilliam and Death, 1998; Werner *et al*., 2004). Some of the techniques used to access canopies include use of rope ladders (Perry, 1978; Perry and Williams, 1981), aerial walkways (Mitchell, 1986), helium balloons (Fukuyama *et al*., 1994) and construction cranes (Parker *et al*., 1992; Morell, 1994; Odegaard, 2000; Basset, 2001).

Different methods are used for collection of arboreal samples, these include insecticide fogging and mist-blowing (Southwood *et al*., 1982; Stork 1987a, b, 1991; Morse *et al*., 1988; Watanabe and Ruaysoongnern, 1989; Majer, 1990; Stork and Brendell, 1990; Blanton, 1990; Basset, 1991a, b; Kitching *et al*., 1993; Russel-Smith and Stork, 1994; Brühl *et al*., 1998; Guilbert, 1998; Chey *et al*., 1998; Kruger and McGavin, 1998; Ellwood and Foster, 2004; Srinivasa *et al*., 2004; Floren and Linsenmair, 2005), branch clipping (Majer and Recher, 1988; Hijii *et al*., 2001; Werner *et al*., 2004), tree felling (Werner *et al*., 2004), light trapping (Kitching *et al*., 2000; Morecroft *et al*., 2002; Orr and Kitching, 2003), beating/jarring (Coddington *et al*., 1991; Wyss, 1996; Marc *et al*., 1999; Pekár, 1999; Stelzl and Devetak, 1999; Memmott *et al*., 2000; Kai and Corlett, 2002; Mizutani and Hijii, 2002; Goolsby *et al*., 2003; Major *et al*., 2003; Costello and Daane, 2005; Miliczky and Horton, 2005; Moir *et al*., 2005) and hand collecting (Basset, 1996; Chen and Tso, 2004), among others.

Structure of arboreal arthropod communities can be highly inconsistent in both time and space, but the observed variation also depends on the sampling method used (Blanton, 1990; Basset, 2001). For instance, canopy fogging tends to catch more rare and sedentary species than flight interception trapping (Basset, 1988). Werner *et al*. (2004) suggested that it may be essential to

sample canopy arthropods using more than one method, in order to collect arthropods having different behaviours. But they cautioned regarding the interpretation of results originating from samples collected by different methods, because all methods have biases and limitations.

Insecticide fogging involves pumping a warm cloud of a fast-acting insecticide into the canopy using a thermal pulse-jet engine and collecting invertebrate samples that fall from the canopy (Godfray *et al*., 1999). Mist-blowing employs ultra-low-volume and occasionally controlled droplet application technology to generate a fine mist of chemical droplets (Chey *et al.*, 1998). These droplets are boosted into the target canopy by an airstream generated by a back-pack petrol engine or a hand-pumped knap-sack sprayer (Chey *et al*., 1998). Both insecticide fogging and mist-blowing work through contact insecticides, whereby arthropods coming into contact with the chemical are killed or rendered motionless, and fall to the ground where they are collected using sheets (Simandl, 1993; Ozanne *et al*., 2000), trays (Basset *et al.*, 1996; Chey *et al*., 1998; Stork *et al*., 2001) or funnel-shaped nylon sheets (Watanabe and Ruaysoongnern, 1989; Tassone and Majer, 1997; Wagner, 2001).

Insecticide fogging has also been carried out in several managed systems (e.g. coffee and various agricultural crops: Stork and Brendell, 1990). Floren *et al*. (2002) used insecticide fogging to investigate the role of ants as predators in tropical lowland rainforest. In Brazil, Majer *et al*. (1994) used insecticide fogging to sample ants from Brazilian cocoa farms. Some of the advantages of canopy fogging include sampling part of the canopy that would otherwise be inaccessible by other methods such as the top of the canopy and it also targets those arthropods living inside the canopies and rarely get attracted to other sampling methods (Lowman and Wittman, 1996). However, insecticide fogging has some disadvantages. Sedentary forms such as scale insects and those grubs living inside tree trunks are difficult to sample using this method (Srinivasa *et al*., 2004), and regular sampling cannot be carried out on the same or surrounding trees (Hijii *et al*., 2001). Mist-blowing has been used broadly in sampling canopy arthropods (Moran and Southwood, 1982; Southwood and Kennedy, 1983; Ozanne, 1991; Kitching *et al*., 1993; Chey *et al*., 1998). Between 1995 and 1996 Kruger and McGavin (1998) used mist-blowing to sample 31 trees belonging to six *Acacia* species at Mkomazi Game Reserve in Tanzania.

Another method frequently used in sampling canopy arthropods is beating or jarring. This method entails beating a tree several times using a wooden pole and collecting arthropods falling on the ground. McCaffrey *et al*. (1984) showed that efficiency of beating was not affected by either season or time of day. The method is also cheap and environmentally friendly, given that it does not pollute the environment like chemical-based methods. However, it has limitations since it damages the trees (Vincent *et al*., 1999) and was also found to favour certain insect groups of low mobility that drop readily from branches (Suckling *et al*., 1996). Beating was found to be biased and usually failed to collect highly mobile winged insects, sessile scale insects, etc (Suckling *et al*., 1996).

This particular study investigated insect communities inhabiting canopies of *S. drepanolobium*, which occurs on the black cotton soils of the Laikipia ecosystem. The study was carried out at the KLEE experimental plots and adjacent areas at Mpala Research Centre. To ensure that a large variety of insects was collected, two methods were used namely beating/jarring and mist-blowing. Sampling was limited to trees that were between 1.0-2.5 meters tall. This aspect of the study also aimed to evaluate the efficacy of the two sampling methods used in collecting canopy arthropods from *S. drepanolobium*. Since different methods exhibit different biases, it was hypothesized that there would be a method-related difference.

Objectives

The objectives of this study were

i) To determine the structure of insect communities found on canopies of *S. drepanolobium*

ii) To determine the efficacy of mist-blowing and beating in sampling canopy arthropods

Hypothesis

The two methods should sample different parts of the insect community. This is because beating would dislodge most arthropods from the canopies, but some might fly away instead of falling to the ground. Borers and scale insects may not even be dislodged. Mist-blowing would kill most of

invertebrates and therefore catch more flying forms, but some are likely to remain trapped within the canopies. It was hypothesized that total number of taxa, the Shannon-Wiener diversity index, Margalef's richness index and Pielou's evenness index would be significantly different between the two methods. Mist-blowing was expected to yield low diversity indices compared to beating, which is commonly used in sampling canopy arthropods, because most of the dead arthropods would remain lodged on the canopies.

Materials and Methods

Study area

For the description of the study area, treatments and tagging of trees see Chapter Two.

The beating method

This involved beating a tree twenty times using a one meter wooden pole and collecting insects falling on the ground using four sheets (each 1 m^2) placed under the tree. A sample consisted of all materials combined from the four sheets and a tree was considered as a sampling unit. During each sampling session twenty trees occupied by acacia-ants were sampled. In total 720 trees were sampled between September 2003 and November 2004. There were nine experimental plots each having 80 trees. Details of this method can be found in Chapter Two. Insect specimens were put in polythene bags and later transported to the laboratory for sorting and identification to different recognizable taxonomic units (RTUs) using a dissecting microscope. Insect samples were preserved in vials using 70% ethanol. Voucher specimens will be placed at the National Museums of Kenya, Nairobi.

The mist-blowing method

Seven hundred and twenty trees were each sprayed with synthetic insecticide (Cypermethrin 100g/l) using a hand-pumped knap-sack sprayer for 20-30 seconds and all arthropods falling onto four sheets (each 1m^2) placed under the tree were collected and placed on the polythene bags. There were nine experimental plots and each had 80 trees. For details on this method see Chapter Two. Samples were later transported to the laboratory and put in a deep freezer overnight to immobilize them though a number of them were already dead. They were later sorted to different recognizable taxonomic units (RTUs) using a dissecting microscope. Samples were preserved in

vials using 70% ethanol. Voucher specimens will be deposited at the National Museums of Kenya, Nairobi.

Data analysis

Non-metric multidirectional scaling (MDS) and principal components analysis (PCA) were used to describe the insect community collected using the two sampling methods, both at order and family levels. At the morphospecies level only MDS was carried out because PCA cannot handle effectively data with more than 30 variables (Clarke and Warwick, 1994). For the PCA the resulting frequency matrix was first log-transformed (log (x + 1)) to weight the contributions of common and rare species and later subjected to ordination.

For the MDS analysis the log-transformed data was first submitted to the similarity module of the PRIMER program to generate a Bray-Curtis similarity matrix (Clarke and Warwick, 1994). The similarity matrix was subjected to the MDS module of the PRIMER program (Clarke and Warwick, 1994) to generate a two-dimensional configuration of the insect samples collected using beating and mist-blowing. The fitting process was iterated 10 times.

In order to compare the two sampling methods, four diversity indices were used: total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′). The choice of the four diversity indices is justified in Chapter Two. Green (1999) used diversity indices (Simpson's and the Shannon-Wiener diversity indices and the Morisita-Horn similarity index) to compare vacuum and pitfall trapping methods in sampling spiders. Suckling *et al*. (1996) had also used the Shannon-Wiener diversity index to evaluate beating tray and suction sampler methods in sampling arthropods from apple trees. Diversity indices were computed for each tree from the raw frequencies of the insect taxa using the DIVERSE module of the software program PRIMER (Clarke and Warwick, 1994). Indices were generated at three taxonomic levels: orders, families and morphospecies. The indices were analysed using the permutational multifactor analysis of variance (PERMANOVA) software program PERMANOVA (Anderson, 2005) to compare the collecting methods. For all analysis 999 permutations were used to generate the p-value. However, for pair-wise comparisons 99 permutations were performed. Almost all community data do not fulfil the normal distribution

assumptions of the ANOVA even after transformation (PRIMER manual). However, PERMANOVA works on the same principles as ANOVA but has very few assumptions regarding the distribution of data. Since the community data collected during this study was not normally distributed, PERMANOVA was chosen because it tests several factors together, unlike Kruskal-Wallis which compares one factor at a time. Correlation coefficients were calculated between samples collected using the two sampling methods at the morphospecies level.

Results

Insect community structure and composition

A total of 10145 individuals were caught using the two methods and 62.63% of these were sampled by mist-blowing (Table 4.1). Both methods collected samples from seven insect orders. However, mist-blowing collected samples from twenty four families while beating collected from twenty two families (Table 4.1). In total the two methods collected samples from twenty five insect families.

Ordinal level

Seven orders were identified. The two sampling methods caught relatively similar proportions of individuals belonging to the orders Mantodea, Orthoptera and Phasmida (Figure 4.1). However, mist-blowing caught higher percentages of individuals than beating in the orders Blattodea, Coleoptera, Hemiptera and Hymenoptera (Figure 4.1).

The first two axes of the PCA captured 66.3% of the total variation (Table 4.2). An examination of the Eigenvectors showed that the first axis emphasised the abundances of most orders except Orthoptera and Mantodea; the second axis represented a gradient between (Mantodea + Phasmida + Coleoptera) and Blattodea, with little influence from Hymenoptera, Hemiptera and Orthoptera (Table 4.2). These two dimensions revealed that the two methods differed slightly from one other in that their convex hulls barely overlapped (Figure 4.2a). The differences tended to be consistent within sampling events, because the score of each beating sample was generally lower on axis 1 and higher on axis 2 than the score for the associated mist-blowing sample, but this was not always the case (Figure 4.2a). However, the samples did not cluster convincingly according to the

methods, because a sample's nearest neighbour was often from a different collecting method (Figure 4.2a). There was a pattern which reflected the sampling periods (Figure 4.2a), suggesting that much of the variation was due to sampling events. The five principal component scores were subjected to PERMANOVA, and no significant difference between the two methods was found (Table 4.4). However, there was a significant effect on sampling events (Table 4.4). Further analysis using pairwise comparisons did not reveal any significant differences between the sampling events (Table 4.5). There was no interaction effect between method and sampling event because whenever the second factor was considered it resulted in a single replicate and PERMANOVA does not accept data when a factor has a single replicate.

The very low stress of 0.04 of a two-dimensional MDS ordination of the same data justified further interpretation. The convex hulls of the two methods overlapped and samples from the same sampling event were not consistently placed relative to one another (Figure 4.2b). Samples collected using beating during the first sampling session and those collected by mist-blowing during the third sampling session were isolated from the rest of the samples (Figure 4.2b). Samples collected during the second sampling session formed one group while those collected during the fourth sampling session formed another group (Figure 4.2b). There was therefore a difference in grouping between the MDS and PCA plots.

Familial level

Twenty-five families were caught. Formicidae consisted of other ants collected from the canopies apart from the four primary symbionts species found on *S. drepanolobium*. Members of the families Curculionidae and Blattidae contributed 22.47% and 13.91% respectively of all insect samples collected by both methods (Table 4.1). Samples of Scarabaeidae, Meenoplidae and Staphylinidae were only collected by mist-blowing with a single specimen each (Table 4.1).

The first two axes of the PCA explained 50.2% of the total variation (Table 4.3). Examination of the Eigenvectors showed that the first axis was a gradient between (Curculionidae + Diapheromeridae + Cerambycidae) and Bostrichidae; the second axis represented a gradient between (Cleridae + Pentatomidae + Blattidae) and (Mantidae + Pamphagidae) with little influence from the other families (Table 4.3). These two dimensions showed that the two

methods differed from one another in that their convex hulls barely overlapped (Figure 4.2c). Beating sample scores were consistently higher on both axes relative to the associated mist-blowing sample scores (Figure 4.2c). However, the distance between them was not consistent, and clustering did not emphasize method or sampling event. The five principal component scores were subjected to PERMANOVA. There was no significant difference between the insect samples collected using the two methods (Table 4.4). However, there was a significant difference between sampling events (Table 4.4). Pairwise comparisons did not reveal any significant differences between the sampling events (Table 4.5).

When the same data were ordinated by two-dimensional MDS, the stress of 0.09 was good and the pattern was a good representation of the insect community. The pattern was slightly different from that generated using PCA, with convex hulls overlapping (Figure 4.2d). However, there was no consistent pattern reflecting sampling methods or sampling events.

Morphospecies level

A total of 117 morphospecies were identified (Table 4.1). Both beating and mist-blowing methods each missed 20.0% of the morphospecies (Table 4.1). Most of the morphospecies collected were in the orders Orthoptera and Coleoptera (Table 4.1). Beating missed five morphospecies from the order Orthoptera, one species from the order Hemiptera, fourteen species from the order Coleoptera and three species from the order Mantodea. Mist-blowing missed two species from the order Hymenoptera, eight species from the order Orthoptera, one species from the order Hemiptera, nine species from the order Coleoptera and two species from the order Mantodea.

A two-dimensional MDS plot generated using morphospecies abundance data had a stress value of 0.06, which was good and therefore this configuration realistically represents the similarities between the insect samples collected using the two methods. Again, samples separated mainly based on the sampling sessions (Figure 4.2e), and a relationship between samples based on methods was usually observed within sampling events (Figure 4.2e). All of the points separated from each other, which means that the sampling methods could have effects on the insect

community. However, insect samples collected during the same sampling sessions using the two methods were closer to each other than those collected during different sampling periods.

Diversity indices

Ordinal level

PERMANOVA of total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) showed that the two methods were not significantly different. There was no significant difference between the methods for all four diversity indices but there was a significant difference between sampling events for all four diversity indices (Table 4.6). There was also an interaction effect between sampling event and method for total number of taxa and the Shannon-Wiener diversity index (Table 4.6). Pairwise comparisons revealed that there was a significant difference between the first sampling session and the second, third and fourth sampling sessions for total number of taxa, the Shannon-Wiener diversity index and Pielou's evenness index (Table 4.7). The first sampling event was significantly different from the second and third sampling events for Margalef's richness index (Table 4.7). Further analysis on interaction effect between sampling event and method showed that the first sampling session was significantly different from the second and fourth sampling sessions for total number of taxa and the Shannon-Wiener diversity index for samples collected by beating (Table 4.8). For samples collected using mist-blowing all sampling events were significantly different from each other except between the second and fourth sampling events for total number of taxa and the Shannon-Wiener diversity index (Table 4.8).

Familial level

At the level of families, the two methods were not significantly different for all four diversity indices (Table 4.9). However, there was a significant difference between sampling events and an interaction effect between method and sampling event for all four diversity indices (Table 4.9). Pairwise comparisons between sampling events revealed that the first sampling session was significantly different from the second, third and fourth sampling events for total number of taxa and the Shannon-Wiener diversity index (Table 4.10). The first sampling event was also significantly different from the second and third sampling sessions for Margalef's richness index

while for Pielou's evenness index only the first sampling event was significantly different from the second sampling session (Table 4.10). Pairwise comparisons on interaction effect revealed that for beating samples, the first sampling event was significantly different from the second and fourth sampling sessions for total number of taxa and the Shannon-Wiener diversity index (Table 4.11). All sampling sessions were significantly different for Pielou's evenness index for samples collected using mist-blowing (Table 4.11). However, the second, third and fourth sampling sessions were significantly different from the first sampling event, and also the third and fourth sampling events were significantly different for total number of taxa, the Shannon-Wiener diversity index and Margalef's richness index for samples collected using mist-blowing (Table 4.11).

Morphospecies level

At morphospecies level, there was no significant difference between the two methods for all four diversity indices (Table 4.12), but there was a significant effect between sampling events for total number of taxa, the Shannon-Wiener diversity index and Margalef's richness index (Table 4.12). There was an interaction effect between method and sampling event for all four diversity indices (Table 4.12). Further analysis of sampling events revealed that the first sampling session was significantly different from the second, third and fourth sessions for total number of taxa and the Shannon-Wiener diversity index (Table 4.13). First sampling event was also significantly different from the second and third sessions for Margalef's richness index (Table 4.13). Pairwise comparisons showed that there was no significant difference between sampling sessions for those samples collected using beating except for the first and second sampling events for total number of taxa (Table 4.14). However, for samples collected using mist-blowing all sampling events were significantly different except between the second and fourth sampling sessions for total number of taxa and the Shannon-Wiener diversity index (Table 4.14). There was a significant difference between the first and third, second and fourth, and third and fourth sessions for Pielou's evenness index (Table 4.14). The first sampling event was significantly different from the second, third and fourth sessions and also there was a significant difference between the third and fourth sampling events for Margalef's richness index for samples collected by mist-blowing (Table 4.14).

Discussion

Both methods were successful in collecting a wide range of taxonomic groups. Kruger and McGavin (1998) identified 133 insect families and 492 morphospecies from specimens collected from 31 trees belonging to six *Acacia* species in Mkomazi Game Reserve, Tanzania. It is feasible that the lower number of morphospecies on *S. drepanolobium* in Mpala Ranch may be due to its symbiotic association with ants. Another explanation is that the different *Acacia* species sampled at Mkomazi contributed morphospecies that were specific to those tree species. During the current studies all insect samples were collected from *S. drepanolobium*. However, some morphospecies are likely to have been missed out by both methods. Scale insects were seen on trees colonized by *C. sjostedti* and *C. mimosae* but the two methods did not collect them. Also, butterflies were occasionally seen perching on trees but again no sample was collected by the two methods.

However, the two sampling methods used during the current study had three disadvantages: i) they could not be used when conditions were wet, ii) they failed to collect some insect orders though they were present on the canopies and iii) some of the insects would fall down on the sheets and crawl away. Improvement of the collecting device and addition of other sampling methods such as light trapping might improve the catches from this ecosystem.

Community structure

Although two *Camponotus* species and two *Clonaria* species were identified from the canopies, they were initially wrongly identified and put together; samples were therefore lumped together and referred to as *Camponotus* species and *Clonaria* species.

Non-metric multidimensional scaling (MDS) at family level showed samples separating out based on the sampling methods. However, at the order and species levels there was no clear separation that could be related to sampling methods. However, samples were grouping together reflecting sampling events. The community composition of samples collected by the two methods was not very different, as shown by the PERMANOVA carried out using principal component scores at order and family levels.

These results show the importance of using different taxonomic levels during data analysis. Therefore, depending on the objectives of the study and the availability of funds and manpower, it may be feasible to carry out data analysis using higher taxonomic groupings which can be easily obtained compared to the time-consuming and difficult task of identifying specimens to genus or species. Warwick (1988) showed that at the family level there was no substantial loss of information when he related benthic assemblages to pollution levels using five data sets collected at different times. This was again demonstrated by Warwick *et al*. (1990) when they analysed macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda. Other studies have also come up with similar observation and supports use of higher taxonomic units other than identifying specimens up to species level (Herman and Heip, 1988; Olsgard and Somerfield, 2000).

Comparison of methods

Catches were mainly dominated by coleopterans, orthopterans and blattodeans. *Myllocerus* sp. A and *Periplaneta* sp. 1 were the two most abundant morphospecies on the canopies of *S. drepanolobium*. The two methods collected relatively similar proportions of individuals belonging to the orders Orthoptera and Mantodea, but mist-blowing collected a higher proportion of individuals in the orders Hemiptera and Coleoptera than beating. The two methods performed equally well at collecting insects when compared at the order level. Results of diversity indices at the three taxonomic levels did not reveal any significance difference between the two methods.

Nevertheless, both methods were not efficient, especially in collecting dipterans and lepidopterans. Although immature stages of these two groups of insects were collected by both methods, no adults were collected. However, immature stages were not included in the analysis because it was difficult to classify them particularly at family level. A similar phenomenon was observed by Suckling *et al*. (1996) while comparing suction sampler and beating trays for apple pests: the methods were both deficient in collecting leafhopper nymphs. Interpreting data collected by light trapping and chemical knockdown was a problem because the two methods collected different quantities of the same insects at different times (Gibbs and Leston, 1970). Spider assemblages collected by vacuum and pitfall traps were significantly different, implying that different methods have different efficacies (Green, 1999). Suction samplers performed better

than other methods in collecting spiders from maize plots (Meissle and Lang, 2005), while sweep-netting caught different spider species from pitfall traps (Warui, 2005). Although different sampling methods collect different insects or different number of the same insects, the two methods used during the current study were not significantly different, even though they collected several morphospecies that were different. Correlation analysis showed that the samples collected by the two methods were highly correlated ($r = 0.93$).

After considering those morphospecies missed out by the two methods, it appears as if there was no predictable pattern for groups missed by any of the two methods. The two methods performed equally well in collecting canopy arthropods. However, beating was easier to use, cost-effective and environmentally friendly with no chemical residues remaining in the ecosystem. It is generally best for slow-moving arthropods that dislodge from plants when disturbed such as beetles (Suckling *et al*. 1996). Since, the two methods missed equal number of morphospecies, it would be better to use the two of them together in order to improve on the diversity of specimens collected.

This study highlights the importance of using multiple collection methods to determine the fauna of a site. In the case where one wanted to combine samples collected by different methods, different biases in each method would force one to reduce the quantitative measurements to categorical presence/absence data before combining it together for further analysis (PRIMER manual). However, for the current study it was felt that analysing the data collected using the two methods separately without combining it would still address the proposed objectives adequately. It was clear by comparing the two methods that none alone was able to catch all of the arthropod species. Therefore, it is left to the researcher to determine which method/s to use depending on the ecological question/s to be addressed and the type of habitat/s to be sampled.

However, it was evident that sampling events played a major role on canopy arthropod community. This shows the effect of seasonality on arthropod community (Denlinger, 1980; Wolda, 1980; Recher *et al*., 1996; McWilliam and Death, 1998; Wagner, 2001; Kai and Corlett, 2002). During the current study samples were collected at intervals of three months and although seasonality was not taken into consideration, different sampling sessions must have interacted

with different seasons. There was also an interaction effect between method and sampling event. Further analysis using pairwise comparisons showed that sampling events responded differently between the two methods, implying that methods might be slightly different from one another.

In conclusion, both mist-blowing and beating collected sufficient numbers of insects to permit estimation of the various diversity indices, which in turn would be used to determine if the four symbiotic acacia-ants inhabiting *S. drepanolobium* supports different insect assemblages. While each method had its unique biases, in concert they provided a broad picture of the communities they were intended to sample.

Table 4.1. Number of individual insects at three taxonomic levels sampled from canopies of *S. drepanolobium* at the KLEE plots and its immediate environs at Mpala Research Centre using mist-blowing and beating.

Taxonomic level			Numbers of specimens	
Order	Family	Morphospecies	Beating	Mist-blowing
Hymenoptera			**397**	**832**
	Formicidae		397	832
		Camponotus sp.	383	823
		Polyrhachis sp. A	3	9
		Technomyrmex sp. A	9	0
		Pheidole crassinoda	2	0
Orthoptera			**982**	**931**
	Acrididae		330	412
		Acrididae sp. 1	36	66
		Acrididae sp. 2	134	156
		Acrididae sp. 3	26	37
		Acrididae sp. 4	34	46
		Acrididae sp. 5	46	51
		Acrididae sp. 8	1	0
		Acrididae sp. 9	1	0
		Acrididae sp. 10	1	0
		Acrididae sp. 11	4	13
		Acrididae sp. 12	5	8
		Acrididae sp. 14	13	22
		Acrididae sp. 15	3	3
		Acrididae sp. 16	16	7
		Acrididae sp. 17	0	1
		Acrididae sp. 19	2	1
		Acrididae sp. 20	1	1
		Acrididae sp. 21	1	0
		Acrididae sp. 23	0	1

Taxonomic level			Numbers of specimens	
Order	Family	Morphospecies	Beating	Mist-blowing
		Acrididae sp. 24	0	1
		Acrididae sp. 26	0	1
		Acrididae sp. 27	1	0
		Acrididae sp. 28	4	0
		Acrididae sp. 30	0	1
		Acrididae sp. 31	1	0
	Gryllacrididae		2	5
		Gryllacris sp. A	2	5
	Gryllidae		639	502
		Gryllodes sp. A	4	4
		Ectatoderus sp. A	635	498
	Pamphagidae		11	8
		Pamphagidae sp.1	3	3
		Pamphagidae sp. 2	1	0
		Pamphagidae sp. 3	6	3
		Pamphagidae sp. 4	1	2
Hemiptera			**222**	**601**
		Hemiptera sp. 5	1	5
		Hemiptera sp. 11	6	0
	Pentatomidae		8	16
		Aeliomorpha? *simulans*	2	3
		Aeliomorpha senegalensis	2	3
		Pentatomidae sp. 1	4	10
	Miridae		207	579
		Miridae sp. 1	82	513
		Miridae sp. 2	93	53
		Miridae sp. 3	32	13
	Meenoplidae		0	1
		Anygrus ochreatus	0	1

Taxonomic level			Numbers of specimens	
Order	Family	Morphospecies	Beating	Mist-blowing
Coleoptera			**1458**	**2864**
	Buprestidae		73	149
		Agrilus sp. A	3	3
		Agrilus sp. B	1	9
		Agrilus sp. D	1	0
		Agrilus sp. G	0	1
		Buprestid sp. 1	7	36
		Buprestid sp. 2	0	6
		Chrysobothris sp. A	4	4
		Hoplistura sp. A	44	74
		Sjoestedtius sp. A	0	2
		Sjoestedtius sp. B	0	1
		Sjoestedtius sp. C	13	13
	Anthicidae		269	594
		Anthicidae sp. A	269	593
		Anthicidae sp. D	0	1
	Scarabaeidae		0	1
		Aphodius sp. A	0	1
	Carabidae		38	53
		Arsinoe sp. A	0	1
		Carabidae sp. 1	32	50
		Carabidae sp. 2	5	0
		Carabidae sp. 3	1	2
	Bruchidae		8	11
		Bruchid sp. 1	5	9
		Bruchid sp. 2	0	1
		Bruchid sp. 3	2	0
		Bruchid sp. 4	1	1
	Bostrichidae		8	6

Taxonomic level			Numbers of specimens	
Order	Family	Morphospecies	Beating	Mist-blowing
		Bostrichidae sp. 1	8	6
	Chrysomelidae		55	114
		Chrysomelidae sp. 1	0	1
		Chrysomelidae sp. 3	1	1
		Chrysomelidae sp. 4	17	18
		Chrysomelidae sp. 5	1	1
		Chrysomelidae sp. 6	3	2
		Cryptocephalus sp. A	0	1
		Cryptocephalus sp. B	1	0
		Dorcathispa sp. A	1	0
		Hispa sp. A	2	6
		Lema sp. A	3	2
		Megalognatha sp. A	0	4
		Monolepta sp. A	13	52
		Monolepta sp. B	10	24
		Monolepta sp. C	1	2
		Monolepta sp. D	2	0
	Cleridae		105	407
		Cleridae sp. 1	105	407
	Curculionidae		840	1485
		Myllocerus sp. A	801	1440
		Neosphrigodes sp. A	1	18
		Systates sp. A	21	7
		Curculionidae sp. 1	5	13
		Curculionidae sp. 2	5	1
		Curculionidae sp. 4	2	2
		Curculionidae sp. 5	2	2
		Curculionidae sp. 6	0	2
		Curculionidae sp. 7	1	0

Taxonomic level			Numbers of specimens	
Order	Family	Morphospecies	Beating	Mist-blowing
		Curculionidae sp. 8	1	0
		Curculionidae sp. 9	1	0
	Cerambycidae		11	14
		Enaretta sp. A	11	14
	Coccinellidae		2	5
		Micraspis sp. A	2	2
		Scymnus sp. A	0	3
	Tenebrionidae		49	24
		Lagria sp. A	49	24
	Staphylinidae		0	1
		Philonthus sp. A	0	1
Phasmida			**106**	**123**
	Diapheromeridae		106	123
		Clonaria sp.	106	123
Mantodea			**110**	**98**
	Mantidae		110	98
		Cilnia sp. A	11	15
		Galepsus sp. A	8	13
		Miomantis sp. A	15	16
		Parasphendale sp. A	63	42
		Popa sp. A	7	5
		Mantidae sp. F	1	1
		Mantidae sp. G	0	1
		Mantidae sp. H	1	0
		Mantidae sp. J	3	3
		Mantidae sp. K	0	1
		Mantidae sp. L	0	1
		Mantidae sp. P	1	0
Blattodea			**516**	**905**

Taxonomic level			Numbers of specimens	
Order	Family	Morphospecies	Beating	Mist-blowing
	Blattidae		506	905
		Cyrtotria sp. A	28	9
		Periplaneta sp. 1	478	896
	Polyphagidae		10	0
		Derocalymma sp. A	10	0

Table 4.2. Eigenvalues and Eigenvectors of the correlation matrix generated by PCA from log-transformed insect order abundance data collected using beating and mist-blowing.

Variable	PC1	PC2	PC3	PC4	PC5
Blattodea	**0.302**	**-0.565**	-0.097	-0.007	0.639
Coleoptera	**0.474**	**0.386**	0.006	-0.144	0.405
Hemiptera	**0.529**	-0.163	0.015	-0.236	-0.617
Hymenoptera	**0.421**	-0.005	-0.358	0.783	-0.147
Mantodea	-0.238	**0.496**	-0.514	0.102	0.108
Orthoptera	0.013	-0.175	-0.761	-0.487	-0.081
Phasmida	**0.413**	**0.477**	0.137	-0.250	0.074
Eigenvalue	2.79	1.85	1.41	0.51	0.34
% of total variance	39.9	26.4	20.1	7.3	4.9
Cum % of total variance	39.9	66.3	86.4	93.8	98.7

Table 4.3. Eigenvalues and Eigenvectors of correlation matrix generated by PCA from log-transformed insect family abundance data collected using beating and mist-blowing.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	0.267	0.136	0.102	-0.336	-0.015
Anthicidae	-0.009	0.211	0.336	0.232	0.045
Diapheromeridae	**-0.324**	0.073	-0.045	0.235	0.090
Blattidae	0.082	**0.384**	-0.017	-0.154	-0.029
Bostrichidae	**0.310**	-0.067	0.143	-0.182	0.144
Bruchidae	0.172	0.166	0.344	-0.023	0.190
Buprestidae	-0.144	0.131	0.204	-0.185	0.106
Carabidae	0.181	0.244	0.064	0.040	0.371
Cerambycidae	**-0.306**	-0.081	-0.070	-0.177	-0.211
Chrysomelidae	-0.290	0.021	0.196	-0.190	0.232
Cleridae	0.009	**0.348**	0.041	-0.063	-0.124
Coccinellidae	0.146	0.093	-0.107	-0.414	-0.273
Curculionidae	**-0.307**	0.119	-0.086	-0.047	0.244
Formicidae	-0.197	0.223	-0.005	-0.180	-0.269
Gryllacrididae	-0.056	-0.156	0.448	-0.148	0.013
Gryllidae	-0.104	0.002	-0.338	-0.374	0.130
Mantidae	-0.160	**-0.321**	0.004	-0.231	-0.086
Meenoplidae	0.065	0.028	0.161	0.190	-0.510
Miridae	-0.141	0.287	-0.170	0.021	0.216
Pamphagidae	-0.038	**-0.309**	0.298	0.101	-0.041
Pentatomidae	0.016	0.317	0.088	0.116	-0.219
Polyphagidae	0.120	-0.189	-0.166	0.127	0.266
Scarabaeidae	-0.287	0.002	0.245	-0.128	0.032
Staphylinidae	-0.287	0.002	0.245	-0.128	0.032
Tenebrionidae	0.245	-0.180	0.109	-0.288	0.102
Eigenvalues	6.93	5.63	3.76	3.16	2.80
% of total variance	27.7	22.5	15.0	12.7	11.2
Cum % of total variance	27.7	50.2	65.3	77.9	89.2

Table 4.4. Results of PERMANOVA test carried out using principal scores generated using order- and family-level data collected using beating and mist-blowing to test the effect of sampling methods and sampling events. * Significant at $\alpha = 0.05$.

Taxa	Source	df	SS	MS	F	P_{perm}
Order	Method	1	8.308	8.308	1.245	0.318
	Residual	6	40.034	6.672		
	Total	7	48.342			
	Sampling event	3	33.325	11.108	2.959	0.014*
	Residual	4	15.017	3.754		
	Total	7	48.342			
Family	Method	1	30.268	30.268	1.444	0.150
	Residual	6	125.780	20.963		
	Total	7	156.048			
	Sampling event	3	89.392	29.797	1.788	0.035*
	Residual	4	66.656	16.664		
	Total	7	156.048			

Table 4.5. Results of PERMANOVA t-tests to test the effect of sampling methods and sampling events carried out on principal scores generated using order- and family-level data collected using beating and mist-blowing. * Significant at $\alpha = 0.05$.

Taxa	Sampling event	t	P_{perm}
Order	First vs Second sampling	1.950	0.290
	First vs Third sampling	1.356	0.470
	First vs Fourth sampling	1.756	0.260
	Second vs Third sampling	1.527	0.330
	Second vs Fourth sampling	2.957	0.270
	Third vs Fourth sampling	1.533	0.340
Family	First vs Second sampling	1.394	0.290
	First vs Third sampling	1.023	0.690
	First vs Fourth sampling	1.244	0.260
	Second vs Third sampling	1.372	0.330
	Second vs Fourth sampling	1.683	0.270
	Third vs Fourth sampling	1.294	0.340

Table 4.6. Results of PERMANOVA to test the effect of sampling methods (beating and mist-blowing) and sampling events (First, Second, Third and Fourth) on total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) at order level. * Significant at $\alpha = 0.05$.

Variable	Source	df	SS	MS	F	P_{perm}
S	Method	1	47.441	47.441	2.776	0.188
	Sampling event	3	134.934	44.978	6.234	0.001*
	Method*Sampling event	3	51.267	17.089	2.369	0.006*
	Residual	280	2020.139	7.215		
	Total	287	2253.781			
H′	Method	1	3.775	3.775	2.027	0.236
	Sampling event	3	12.995	4.332	4.534	0.001*
	Method*Sampling event	3	5.588	1.863	1.950	0.025*
	Residual	280	267.501	0.955		
	Total	287	289.858			
J′	Method	1	1.355	1.355	1.612	0.249
	Sampling event	3	4.575	1.525	2.533	0.004*
	Method*Sampling event	3	2.521	0.840	1.396	0.145
	Residual	280	168.546	0.602		
	Total	287	176.996			
d	Method	1	1.550	1.550	0.874	0.446
	Sampling event	3	9.278	3.093	1.801	0.034*
	Method*Sampling event	3	5.322	1.774	1.033	0.430
	Residual	280	480.782	1.717		
	Total	287	496.932			

Table 4.7. Results of PERMANOVA t-tests to test the effect of sampling methods (beating and mist-blowing) and blocks (North, Central and South) on total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) at order level. * Significant at $\alpha = 0.05$.

	S		H′		J′		d	
Sampling events	t	P_{Perm}	t	P_{perm}	t	P_{perm}	t	P_{perm}
First vs Second sampling	3.588	0.010*	2.688	0.010*	1.755	0.010*	1.666	0.010*
First vs Third sampling	3.729	0.010*	3.139	0.010*	2.041	0.020*	1.879	0.020*
First vs Fourth sampling	3.050	0.010*	2.846	0.010*	2.103	0.020*	1.698	0.060
Second vs Third sampling	0.865	0.620	0.929	0.500	1.178	0.170	0.709	0.770
Second vs Fourth sampling	0.589	0.920	0.446	0.960	0.766	0.710	0.635	0.810
Third vs Fourth sampling	0.972	0.420	0.672	0.760	0.774	0.650	0.512	0.920

Table 4.8. Results of PERMANOVA t-tests to test the effect of sampling methods (beating and mist-blowing) and sampling events (First, Second, Third and Fourth) on total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) at order level. * Significant at $\alpha = 0.05$.

		S		H′	
Method	Sampling events	t	P_{perm}	t	P_{perm}
Beating	First vs Second sampling	2.642	0.010*	1.800	0.020*
	First vs Third sampling	1.410	0.070	1.106	0.340
	First vs Fourth sampling	2.163	0.010*	2.074	0.010*
	Second vs Third sampling	1.145	0.210	0.660	0.800
	Second vs Fourth sampling	0.742	0.780	0.767	0.670
	Third vs Fourth sampling	0.896	0.520	0.992	0.400
Mist-blowing	First vs Second sampling	2.495	0.010*	2.066	0.010*
	First vs Third sampling	4.086	0.010*	3.543	0.010*
	First vs Fourth sampling	2.331	0.010*	2.197	0.010*
	Second vs Third sampling	1.879	0.010*	1.832	0.020*
	Second vs Fourth sampling	1.130	0.200	1.124	0.230
	Third vs Fourth sampling	2.038	0.030*	1.838	0.020*

Table 4.9. Results of PERMANOVA to test the effect of sampling methods (beating and mist-blowing) and sampling events (First, Second, Third and Fourth) on total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) at family level. * Significant at $\alpha = 0.05$.

Variable	Source	df	SS	MS	F	P_{perm}
S	Method	1	190.424	190.424	4.012	0.129
	Sampling event	3	295.382	98.461	6.776	0.001*
	Method*Sampling event	3	142.382	47.461	3.267	0.001*
	Residual	280	4068.889	14.532		
	Total	287	4697.076			
H′	Method	1	11.223	11.223	2.628	0.192
	Sampling event	3	19.991	6.664	4.930	0.001*
	Method*Sampling event	3	12.812	4.271	3.160	0.002*
	Residual	280	378.465	1.352		
	Total	287	422.491			
J′	Method	1	1.679	1.679	1.341	0.285
	Sampling event	3	3.485	1.162	1.987	0.016*
	Method*Sampling event	3	3.756	1.252	2.142	0.012*
	Residual	280	163.655	0.585		
	Total	287	172.574			
d	Method	1	12.425	12.425	2.179	0.216
	Sampling event	3	20.490	6.830	2.677	0.003*
	Method*Sampling event	3	17.110	5.703	2.235	0.010*
	Residual	280	714.509	2.552		
	Total	287	764.534			

Table 4.10. Results of PERMANOVA t-tests to test the effect of sampling methods (beating and mist-blowing) and sampling events (First, Second, Third and Fourth) on total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) at family level. * Significant at $\alpha = 0.05$.

	S		H′		J′		d	
Groups	t	P_{Perm}	t	P_{perm}	t	P_{perm}	t	P_{perm}
First vs Second sampling	3.984	0.010*	3.193	0.010*	1.617	0.010*	2.369	0.010*
First vs Third sampling	3.774	0.010*	3.155	0.010*	1.763	0.060	2.254	0.010*
First vs Fourth sampling	2.929	0.010*	2.634	0.010*	1.678	0.050	1.680	0.050
Second vs Third sampling	0.712	0.770	0.778	0.670	1.069	0.220	0.632	0.840
Second vs Fourth sampling	1.047	0.420	0.758	0.760	0.828	0.670	0.947	0.520
Third vs Fourth sampling	1.106	0.280	0.752	0.650	0.876	0.560	0.739	0.750

Table 4.11. Results of PERMANOVA t-tests to test the effect of sampling methods (beating and mist-blowing) and sampling events (First, Second, Third and Fourth) on total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) at family level. * Significant at α = 0.05.

		S		H′		J′		d	
Method	Sampling events	t	P_{perm}	t	P_{perm}	t	P_{perm}	t	P_{perm}
Beating	First vs Second sampling	2.550	0.010*	1.872	0.010*	0.995	0.480	1.285	0.130
	First vs Third sampling	1.081	0.350	0.715	0.730	0.658	0.810	0.685	0.830
	First vs Fourth sampling	1.806	0.010*	1.596	0.030*	1.090	0.320	0.972	0.530
	Second vs Third sampling	1.441	0.100	1.230	0.180	1.093	0.260	1.028	0.340
	Second vs Fourth sampling	0.957	0.520	0.920	0.520	0.844	0.580	0.934	0.450
	Third vs Fourth sampling	0.852	0.560	1.014	0.380	1.254	0.210	0.868	0.560
Mist-blowing	First vs Second sampling	3.155	0.010*	2.795	0.010*	1.502	0.040*	2.225	0.010*
	First vs Third sampling	4.479	0.010*	4.188	0.010*	2.634	0.010*	3.173	0.010*
	First vs Fourth sampling	2.552	0.010*	2.478	0.010*	1.699	0.020*	1.892	0.010*
	Second vs Third sampling	1.506	0.100	1.669	0.050	1.848	0.010*	1.192	0.290
	Second vs Fourth sampling	1.142	0.230	1.192	0.260	1.515	0.040*	1.255	0.190
	Third vs Fourth sampling	2.163	0.030*	2.054	0.030*	1.831	0.010*	1.688	0.030*

Table 4.12. Results of PERMANOVA to test the effect of sampling methods (beating and mist-blowing) and sampling events (First, Second, Third and Fourth) on the total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) at morphospecies level. * Significant at $\alpha = 0.05$.

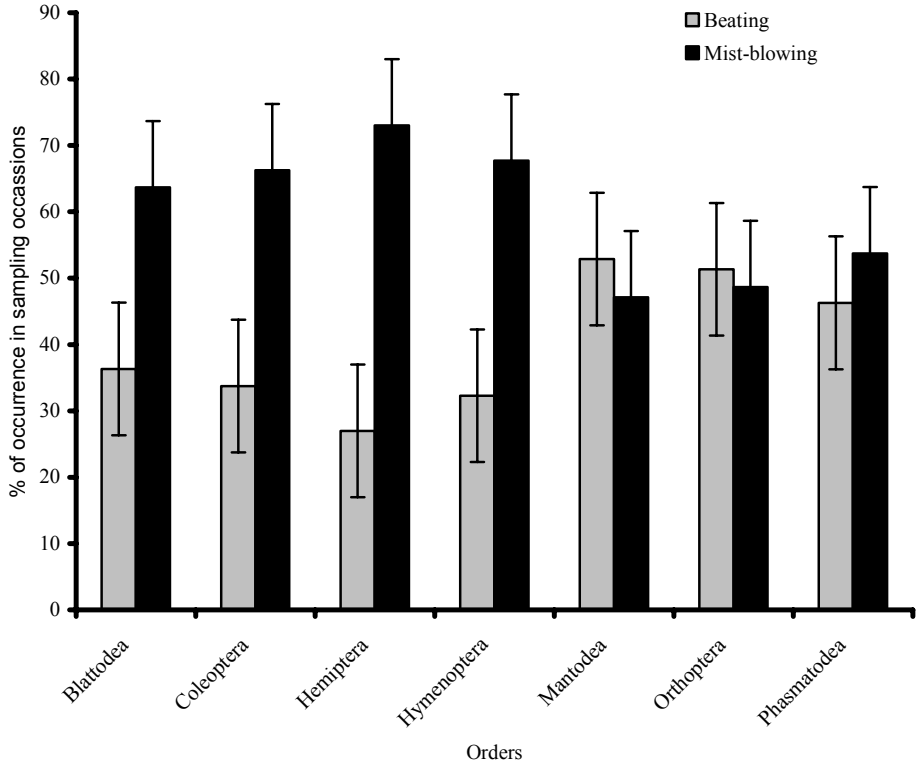
Variable	Source	df	SS	MS	F	P_{perm}
S	Method	1	222.226	222.226	4.216	0.119
	Sampling event	3	342.441	114.147	6.096	0.001*
	Method*Sampling event	3	158.122	52.707	2.815	0.003*
	Residual	280	5242.861	18.725		
	Total	287	5965.649			
H′	Method	1	11.741	11.741	2.884	0.161
	Sampling event	3	19.819	6.606	4.382	0.001*
	Method*Sampling event	3	12.214	4.071	2.701	0.005*
	Residual	280	422.096	1.508		
	Total	287	465.870			
J′	Method	1	2.020	2.020	1.936	0.204
	Sampling event	3	2.664	0.888	1.537	0.096
	Method*Sampling event	3	3.130	1.043	1.806	0.040*
	Residual	280	161.761	0.578		
	Total	287	169.576			
d	Method	1	15.122	15.122	2.539	0.192
	Sampling event	3	21.559	7.186	2.355	0.005*
	Method*Sampling event	3	17.870	5.957	1.952	0.022*
	Residual	280	854.289	3.051		
	Total	287	908.839			

Table 4.13. Results of PERMANOVA t-tests to test the effect of sampling methods (beating and mist-blowing) and sampling events (First, Second, Third and Fourth) on total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) at morphospecies level. * Significant at $\alpha = 0.05$.

	S		H′		D	
Sampling events	t	P_{perm}	t	P_{perm}	t	P_{perm}
First vs Second sampling	3.435	0.010*	2.7450	0.010*	1.891	0.020*
First vs Third sampling	3.750	0.010*	3.167	0.010*	2.305	0.010*
First vs Fourth sampling	2.693	0.010*	2.377	0.010*	1.496	0.090
Second vs Third sampling	1.127	0.280	0.970	0.390	0.942	0.430
Second vs Fourth sampling	0.875	0.590	0.588	0.910	0.720	0.830
Third vs Fourth sampling	1.306	0.150	0.952	0.420	0.972	0.390

Table 4.14. Results of PERMANOVA t-tests to test the effect of sampling methods (beating and mist-blowing) and sampling events (First, Second, Third and Fourth) on total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) at morphospecies level. * Significant at $\alpha = 0.05$.

		S		H′		J′		d	
Method	Sampling events	t	P_{perm}	t	P_{perm}	t	P_{perm}	t	P_{perm}
Beating	First vs Second sampling	2.061	0.010*	1.462	0.100	0.904	0.560	0.910	0.570
	First vs Third sampling	1.116	0.300	0.720	0.750	0.693	0.800	0.585	0.890
	First vs Fourth sampling	1.588	0.050	1.376	0.150	1.001	0.430	0.884	0.630
	Second vs Third sampling	0.952	0.390	0.785	0.530	0.844	0.590	0.469	0.950
	Second vs Fourth sampling	0.745	0.740	0.716	0.780	0.754	0.700	0.687	0.780
	Third vs Fourth sampling	0.758	0.730	0.810	0.660	1.053	0.330	0.690	0.800
Mist-blowing	First vs Second sampling	2.835	0.010*	2.593	0.010*	1.302	0.110	1.969	0.010*
	First vs Third sampling	4.309	0.010*	4.117	0.010*	2.478	0.010*	3.102	0.010*
	First vs Fourth sampling	2.449	0.010*	2.324	0.010*	1.368	0.090	1.797	0.010*
	Second vs Third sampling	1.812	0.020*	1.852	0.020*	1.738	0.020*	1.561	0.060
	Second vs Fourth sampling	1.306	0.100	1.284	0.130	1.366	0.090	1.359	0.110
	Third vs Fourth sampling	2.051	0.020*	2.001	0.030*	1.839	0.010*	1.602	0.030*



Figur

e 4.1. The percentage occurrence of the seven insect orders collected by the two methods during the whole duration of the study.

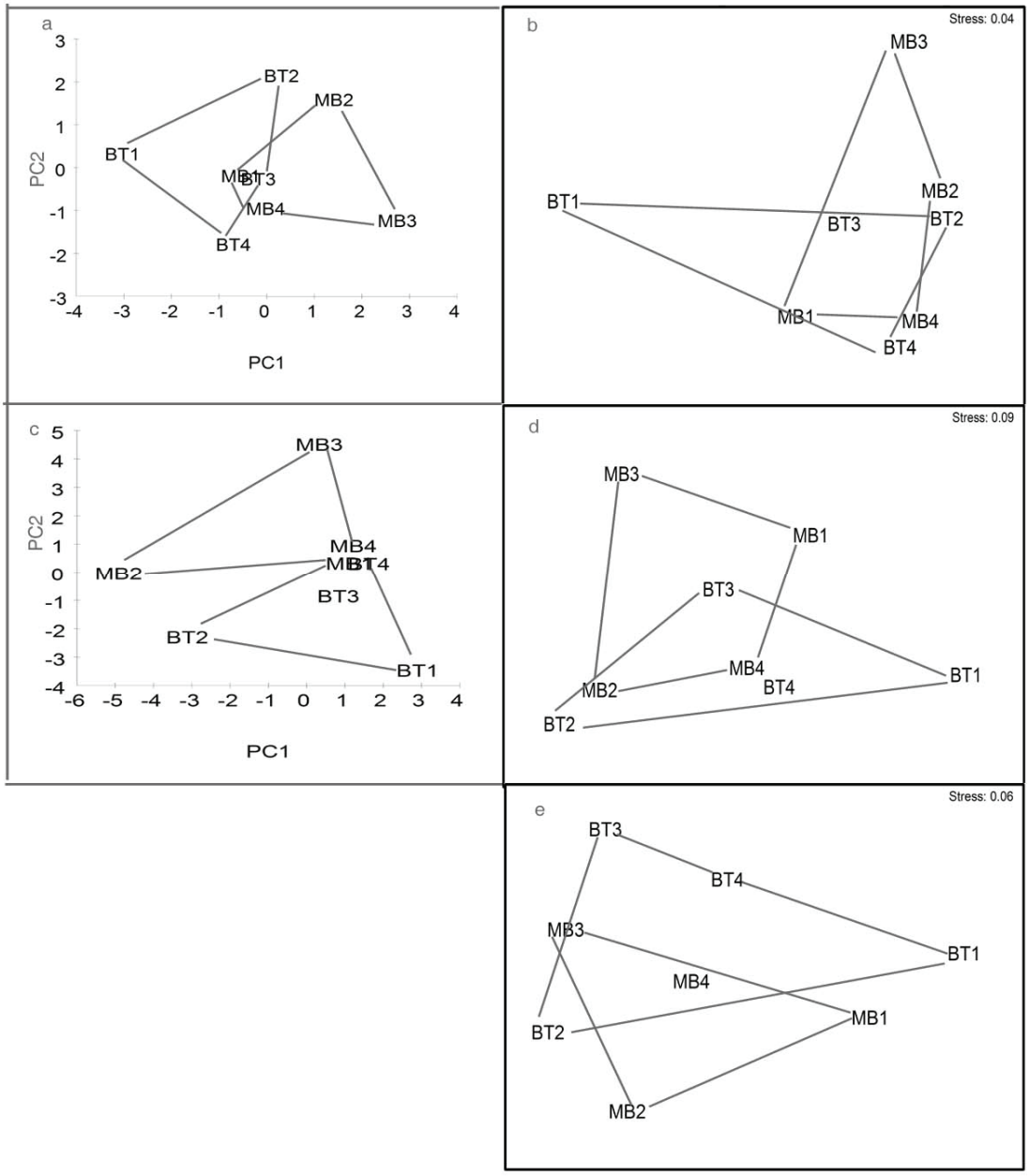


Figure 4.2. Ordinations of log-transformed abundances of insects collected using beating and mist-blowing (BT = beating; MB = mist-blowing) to test the effect of sampling methods on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. Digits represent the sampling sessions.

CHAPTER 5: COMMUNITY STRUCTURE AND COMPOSITION

Introduction

An ecological community is defined as an assemblage of interacting species and the various interrelationships which bind them and their responses to the environment (Whittaker, 1975; Kikkawa and Andersen, 1986; Howe and Westley, 1988; Putman, 1994). The species composition of any community is determined by two basic considerations: what species are available for inclusion within the community, and what species are selected from that pool of candidates (Putman, 1994). The effect of invasion history on the composition of the resultant community (Putman, 1994) is also important in defining community structure. Miller *et al*. (2002) showed that invasion can be affected by migration, predation and resource availability. In the case of Mpala Research Centre it would have been better if history was available on which of the four ant species colonised this ecosystem first, or whether more than one species was present at the same time. Between the ants and *S. drepanolobium*, which was the first to colonise this ecosystem? Were other arthropods present before ants coevolved a mutualistic association with *S. drepanolobium*?

Community structure is affected by various factors such as competition, predation and mutualism among others (Yanoviak, 2001; Smith, 2006). Competition is the negative effects which one organism has upon another by consuming, or controlling access to, a resource that is limited in availability (May, 1976; Haering and Fox, 1987; Keddy, 1989; Speight *et al*., 1999). Intraspecific competition occurs between members of the same species, whereas interspecific competition takes place between members of different species (Whittaker, 1975; Speight *et al*., 1999). Competition plays an important role in determining species composition, abundance and species associations within communities (Price, 1975; Howe and Westley, 1988; Putman, 1994; Abrams, 1996; Molles, 2005). Speight *et al*. (1999) stipulated that abiotic forces, natural enemies, and mutualism will interact with competition to determine the variation in insect populations and communities that we observe in space and time. Surveys of published field experiments on interspecific competition show that many taxa compete in a variety of communities (Karban, 1986; Morin, 1999). Janzen (1973) pointed out that species of root-feeder, leaf-chewer, stem-

borer, etc might still compete for shared host plants because they are linked by the common resource budget of the plant. Studies carried out in the Chihuahuan Desert demonstrated how interspecific competition affects community structure: removal of kangaroo rats (*Dipodomys*) resulted in numbers of other seed-eating rodents more than doubling (Brown *et al*., 2001). Experiments have also shown that taxonomically disparate species, such as granivorous rodents and ants can compete strongly when they exploit a shared resource (Morin, 1999). Ecologists are, however, divided in their views concerning the apparent significance of competition in structuring natural communities (May, 1976). Some have argued that interspecific competition is not essential in structuring communities of herbivorous insects (Price, 1975; Lawton and Strong, 1981; Kikkawa, and Andersen, 1986).

In the Central Amazon, Fonseca (1999) showed that ant colony number and distribution was determined by the local availability and distribution of ant plants. At Mpala Research Centre, four ant species compete for *S. drepanolobium* trees. The two dominant species (*C. sjostedti* and *C. mimosae*) usually occupy bigger trees, while subordinate species (*C. nigriceps* and *T. penzigi*) occupy smaller trees (Palmer *et al*., 2000). Price (1975) stated that if populations increase until they reach the carrying capacity of the environment, the resource in shortest supply becomes the limiting factor. In the case of ants at Mpala Research Centre, competition is mainly for nesting sites on *S. drepanolobium* trees, which are a limiting resource (Palmer *et al*., 2000).

Predation and parasitism also affect community structure. Predators affect community composition in diverse ways. They may reduce competition intensity and hence facilitate coexistence (May, 1976). Some might feed selectively on competitively superior species that would otherwise exclude weaker competitors (Morin, 1999). This enhances the number of prey species that can coexist by reducing interspecific competition among surviving prey. Predators can also drastically affect species composition without changing species richness, by creating communities dominated by species that have particularly effective antipredator strategies (Morin, 1999). The successful biological control of introduced pests by deliberate introductions of predators provides fundamental evidence for predation's significance in regulating populations and structuring communities (Speight *et al*., 1999).

Herbivory, especially by vertebrates, has been considered as a disturbance that may increase plant diversity by reducing competitive dominants and allowing rarer species to coexist (Rambo and Faeth, 1999). However, recent evidence suggests that vertebrate herbivory does not always increase plant diversity and occasionally may decrease it (Rambo and Faeth, 1999). If herbivory by vertebrates alters plant diversity and availability of resources, then associated changes in diversity and abundances of other herbivores, such as invertebrates, are also expected (Siemann *et al*., 1998). Livestock grazing alters species composition of communities, causes decline in density and biomass of individual species and reduces species richness (Fleischner, 1994). Rambo and Faeth (1999) while working in Mogollon Rim in Arizona noted that insect species richness was not different between grazed and ungrazed plant communities, although insect abundance increased between four and ten fold in ungrazed vegetation. A five year study by O'Neill *et al*. (2003) in Montana, USA did not show any significant effect of livestock grazing on grasshopper abundances.

Another factor which affects community structure is mutualism. Many higher plants are involved in a facultative mutualism with arthropods and vertebrates that pollinate their flowers and disperse their seeds (Morin, 1999). The plant-pollinator mutualism is vital to the successful reproduction of many flowering plants and their pollinators (Morin, 1999). Some mutualisms involve defending of one mutualist by another and include a variety of guarding behaviours, such as the protection of domicile plants by the ants that inhabit them (Gorb and Gorb, 1999; Brouat *et al*., 2000, 2001; Gerardo *et al*., 2004; Bruna *et al.,* 2005). Some ant-plant associations involve special morphological adaptations of seeds that promote their dispersal into favourable germination sites by ants (Beattie, 1985).

Ants in the canopy of rainforest form mosaic territories of different species, which has differential effects on the insect fauna (Kikkawa and Andersen, 1986). Ant-hemipteran mutualism (Fischer *et al*., 2002) for example can affect community structure in several ways. The ants protect the hemipterans by keeping away would-be predators; however, some predators may break the barrier and prey on the hemipterans. Alternatively, high abundance of ants on the trees may also attract predators which prey on ants; these predators might also be followed by their predators. Mutualisms can therefore affect community structure in different ways. However, the

importance of mutualisms and commensalisms for most aspects of community structure and function remains very poorly understood (Morin, 1999). Other factors that might affect community structure and composition include host plant size, structural diversity, host density and neighbour effects, habitat topography, migration and climate changes (Ross, 1994; Armbruster *et al*., 2002; Reyes-López *et al.*, 2003; Schowalter and Zhang, 2005).

Studies on phytophagous insect community on *Ficus burtt-davyi* Hutch in the Eastern Cape, South Africa showed that species richness was mainly affected by architectural complexity of the tree and to some extent by ant occurrence (Ross, 1994). Krüger and McGavin (1998) working in Mkomazi Game Reserve, Tanzania, showed that ant biomass was significantly correlated with biomass share of the phytophagous sapsucker guild of insect samples collected from six *Acacia* species. They concluded that ants may play an important role on *Acacia* species even when there was no obvious symbiotic association.

In spite of the diverse literature of plant species that form mutualistic associations with ants, only four exploiting parasites have been described (Raine *et al*., 2004). One of these parasites, *C. nigriceps*, was shown to castrate *S. drepanolobium* trees (Young *et al*., 1997; Stanton *et al*., 1999). Competitively inferior *T. penzigi* ants, though not parasites, destroy foliar nectaries of *S. drepanolobium*, reducing the probability of their being replaced by more aggressive ants that require higher rates of resource supply and are more effective mutualists of the plant (Young *et al*., 1997; Palmer *et al*., 2002). These two ant species occur on the study area and it would be important to see what kind of insect community they support. The other ant species on the study area are *C. sjostedti* and *C. mimosae*. *Crematogaster sjostedti* is the most dominant among the four ant species; it generally nests on hollowed-out cavities within the tree's twigs and stems and tends scale insects. The most common ant in the study area and also the most aggressive in protecting the trees against herbivory is *C. mimosae*, which also tends scale insects. Other defensive mechanisms against herbivory by *S. drepanolobium* include long and sharp thorns (Young and Okello, 1998) and accumulation of tannins on its leaves (Wood and Young, 2002).

Plants rarely interact with a single mutualistic or antagonistic species (Strauss and Irwin, 2004). Rather, sessile plants must integrate interactions across a suite of different mutualists and

antagonists, usually simultaneously (Strauss and Irwin, 2004). These visitors are taxonomically diverse, use many different parts of a plant, and usually vary in their impacts on plant fitness. Based on this argument and having described the various factors that affect the community structure and composition, and given that the four ants behave differently and modify the tree canopies differently, the current study was undertaken to determine the effect of the four acacia-ants on insect community inhabiting canopies of *S. drepanolobium*. The tree constitutes more than 99% of the woody vegetation of the black cotton soil ecosystem of Laikipia, Kenya (Young *et al*., 1997). Knowledge on the abundance and diversity of canopy arthropods on *S. drepanolobium* will provide an insight to understanding the complex interactions that may exist between these insect community and the four acacia-ants.

Objectives

The objectives of these studies were:

i) To establish a checklist of the insect species that coexists with the four acacia-ants on *S. drepanolobium*

ii) To determine the effect of block location (North, Central and South), grazing patterns, acacia-ants and ant-hemipteran mutualism on community structure and composition of canopy insects

iii) To determine the effect of block location, various grazing systems, acacia-ants and ant-hemipteran mutualism on diversity, richness index and evenness index of canopy insects

Hypotheses

1. Few arthropods were to be found on *S. drepanolobium* canopies since the tree was defended by symbiotic ants.

All insect samples would be identified to recognizable taxonomic units. The tree is defended by symbiotic ants, thorns and tannins. It was therefore hypothesized that a small number of taxonomic units would be found coexisting with acacia-ants on canopies of *S. drepanolobium.*

2. The location of the blocks (North, Central and South) had an effect on canopy insects.

Blocks were widely spaced with the furthest plots approximately 5 kilometres apart. The location of the blocks was therefore expected to have an impact on the canopy insects. Community pattern was therefore supposed to reflect on block location.

3. Insect community structure was affected by grazing patterns.

All insect species were collected from canopies of *S. drepanolobium*. Grazing patterns were expected to affect the community structure. It was therefore hypothesized that insect communities would cluster according to the grazing patterns.

4. The four acacia-ants support different invertebrate communities in all the three treatments.

The four ant species modify the canopies differently. They also differ in aggressiveness, with *T. penzigi* being the least aggressive. The canopy arthropod communities were therefore expected to be ant-specific. Community pattern was therefore expected to reflect the effect of the four ant species.

5. Ant-hemipteran mutualism had an effect on the canopy insect community.

There are two guilds of ants on canopies of *S. drepanolobium*. One guild tends scale insects (coccids) while the other does not. Ant-hemipteran mutualism was expected to have an effect on insect community. Therefore, community pattern was expected to show the effects of these two guilds.

6. The insect community structure and composition varied between blocks (North, Central and South), grazing patterns, ant species and ant-hemipteran mutualism.

a) The insect community structure and composition varied between the blocks (North, Central and South).

Blocks were widely spaced. The location of the blocks was therefore expected to have an impact on the canopy insects. It was hypothesized that insect communities in different blocks would be

different and that total number of taxa, the Shannon-Wiener diversity index, Margalef's richness index and Pielou's evenness index would be significantly different between the plots.

b) The grazing patterns have an effect on canopy insect community.

All insect species were collected from plots which were under different grazing pressure. Grazing patterns were expected to affect the community structure. The grazing patterns were expected to have an effect on canopy insects. Browsing pressure was highest on experimental plots exposed to cows and all wild herbivores compared to control plots. Therefore, it was hypothesized that total number of taxa, the Shannon-Wiener diversity index, Pielou's evenness index and Margalef's richness index would be significantly different in the three different treatments.

c) The four ant species modify the canopies differently and behave differently, so they would affect the insect community differently.

The four ant species modify the canopies differently. They also differ in aggressiveness with *C. mimosae* being the most aggressive. The canopy arthropods were therefore expected to be ant-specific. It was therefore hypothesized that total number of taxa, the Shannon-Wiener diversity index, Margalef's richness index and Pielou's evenness index would be significantly different between the four ant species.

d) The variation due to ant-hemipteran mutualism was expected to affect the insect community differently.

Two ant species at the study area tend scale insects while the other two do not. Ant-hemipteran mutualism was expected to have an effect on insect community. Therefore, it was hypothesized that total number of taxa, the Shannon-Wiener diversity index, Margalef's richness index and Pielou's evenness index would be significantly different between the two guilds of ant species.

Methods and Analysis

The number of taxa collected depends largely on which trapping method is used (Bartlett, 1997; personal observation). To improve on catches, both mist-blowing and beating or jarring methods were used to sample canopy arthropods of *S. drepanolobium*. Using a hand-pumped knap-sack sprayer each tree was sprayed for 30-40 seconds and all arthropod falling on the ground were

collected using four light blue sheets (each $1m^2$) placed under the tree. Five trees occupied by each of the four ant species were sampled, making a total of 20 trees during each sampling session. A tree was beaten twenty times using a wooden pole and arthropod samples falling on the ground were collected using four light blue sheets (each 1 m^2) placed under the tree. In total four sampling sessions using the two methods were carried out, and a total of 720 trees were sampled using each method. Details of these methods can be found in Chapter Two. Two species were identified in each of the genera *Camponotus* (Hymenoptera: Formicidae) and *Clonaria* (Phasmida: Diapheromeridae). But samples were earlier wrongly identified and placed together; therefore it was not possible to record abundance data for each of the two species separately for the two genera and were recorded as *Camponotus* sp. and *Clonaria* sp. respectively.

Data analysis

Community structure analysis was performed using non-metric multidimensional scaling (MDS) and principal component analysis (PCA) using the software program PRIMER. For more details see Chapter Four. At species level only MDS was used to describe the community structure, since PCA cannot handle more than 30 variables effectively (Clarke and Warwick, 1994). Principal scores generated by PCA at order and family levels were subjected to PERMANOVA to establish whether the insect communities were different. However, interaction effect between sampling event and (block location, ant species and ant-hemipteran mutualism) was not tested, because whenever two factors were considered together it resulted in one replicate for the second factor and PERMANOVA program do not test factors when there is one replicate. The original data set of individual insect species collected from the canopy of each tree using the two sampling methods was also run through the DIVERSE module of the PRIMER program to generate diversity indices. For more details see Chapter Four.

Results

Community Structure

The current study involved collecting canopy insects of *S. drepanolobium* which has symbiotic association with four ant species at Mpala Research Centre. A total of 117 morphospecies

belonging to 25 families and seven orders were identified. 84 species were sampled from trees inhabited by *C. sjostedti*, while 66 species were collected from trees colonized by *T. penzigi* (Table 5.2). Trees occupied by *C. nigriceps* had the highest percentages of individuals for the orders Blattodea and Hemiptera, 49.83% and 47.39% respectively. From the combined samples for the four ant species, 57.69% of Hymenoptera and 30.29% of Coleoptera came from trees occupied by *C. sjostedti* (Table 5.1).

Out of 25 insect families recorded at the study site, 20 associated with all four ant species. However, members of the family Polyphagidae were not found on trees occupied by *C. mimosae* and *C. nigriceps*, while one individual of the family Meenoplidae was collected only from a tree inhabited by *C. sjostedti* (Table 5.2). Members of the families Coccinellidae and Bostrichidae were missing on trees occupied by *C. nigriceps* and *T. penzigi* respectively (Table 5.2).

Effects of block location on insect community structure

Beating samples

At the order level 64.4% of the variation was captured by the first two axes of the PCA (Table 5.3). Examination of the Eigenvectors showed that the first axis emphasized the abundances of most orders but mainly those with lower abundances (Table 5.3). The second axis represented a gradient between Coleoptera, Hymenoptera, Hemiptera and Phasmatodea with little influence from Mantodea, Blattodea and Orthoptera (Table 5.3). These two dimensions revealed that the three blocks (North, Central and South) were slightly different from one another in that their convex hulls overlapped (Figure 5.1a). The differences seemed to be consistent with the sampling events, with samples collected during the same period being closer to each other compared to those collected from different blocks (Figure 5.1a). The scores for second and third sampling sessions were higher on the two axes than those of the first and fourth sampling sessions (Figure 5.1a). PERMANOVA results showed that there was a significant difference between sampling events (Table 5.6). However, pairwise comparison did not reveal any significant differences between sampling events (Table 5.7). A two-dimensional MDS ordination obtained using the same data was similar to that obtained using PCA, which had revealed a pattern on sampling events but not on block locations (Figure 5.1b). The stress value of 0.09 was good and therefore justified this interpretation.

At the family level the first two axes of the PCA explained 47.7% of the total variation. Assessment of the Eigenvectors revealed that the first axis was mainly affected by Acrididae, Diapheromeridae, Tenebrionidae, Cerambycidae, Curculionidae and Mantidae with minimal influence from the other families (Table 5.4). The second axis represented a gradient between (Pentatomidae + Miridae + Formicidae + Blattidae) and Pamphagidae with little effect from the other families (Table 5.4). The two dimensions again showed that the blocks were only slightly different with their convex hulls overlapping (Figure 5.1c). But a similar pattern of clustering which reflected sampling events observed at order level was evident. There was a significant difference between sampling events (Table 5.6). But pairwise comparisons did not reveal any significant differences between the sampling events (Table 5.7). However, a two-dimensional MDS configuration generated using the same data was slightly different from that obtained using PCA (Figure 5.1d). A stress of 0.13 was not good enough to justify further interpretation.

At the species level a two-dimensional MDS configuration was very similar to that obtained at order level (Figure 5.1e). Again a stress value of 0.18 was not good enough to justify further interpretation. Grouping pattern was still on sampling events but not on block locations (Figure 5.1e). This implied that sampling events had more influence on insect communities than the block locations. But one aspect was clear after examining all the ordination maps, that all blocks were positioned separately from each other, which implies the insect communities in these blocks might be slightly different between blocks.

Mist-blowing

At the ordinal level 55.2% of the total variation was captured by the first two axes of the PCA (Table 5.3). An examination of the Eigenvectors revealed that the first axis highlighted abundances of most orders except Orthoptera and Hemiptera (Table 5.3). The second axis was mainly influenced by Orthoptera, Blattodea and Mantodea (Table 5.3). These two dimensions show that there was no difference between blocks and also the convex hulls overlapped (Figure 5.2a). However, the only pattern observed was due to sampling periods and not blocks location (Figure 5.2a). PERMANOVA results revealed that there was a significant difference between sampling events (Table 5.6). However, pairwise comparisons did not show any significant differences between the sampling events (Table 5.7). Scores for samples collected during the

fourth sampling period were higher on the two axes compared to those collected on other sampling sessions. A two-dimensional MDS configuration was slightly different from that obtained using PCA (Figure 5.2b). However, there was still a pattern reflecting sampling events and not block locations (Figure 5.2b). The stress value was 0.08 which was good enough for this interpretation.

At the family level the first two axes of the PCA explained 43.3% of the total variation (Table 5.5). The first axis was a gradient between (Cerambycidae + Gryllacrididae + Mantidae) and Cleridae with substantial influence from the other families; the second axis was influenced mainly by Curculionidae, Miridae and Chrysomelidae with considerable influence from the other families (Table 5.5). An ordination map generated using the two principal components showed that blocks were not different with convex hulls overlapping (Figure 5.2c). However, there was a pattern portraying sampling events but not on block locations (Figure 5.2c). It appears as sampling events had a greater effect on community structure than the block locations. This was apparent for samples collected during the first, second and third sampling sessions (Figure 5.2c). PERMANOVA results showed that there was a significant difference between sampling sessions (Table 5.6). Pairwise comparisons did not reveal any significant differences between sampling events (Table 5.7). PERMANOVA results showed that there was no significances difference between block locations at order and family levels (Table 5.6). The low stress value of 0.09 of a two-dimensional MDS ordination of the same data justified further interpretation. The convex hulls of the three blocks overlapped and samples from the same sampling events were consistently placed next to one another except samples collected from the south block during the fourth sampling session (Figure 5.2d).

At the species level a two-dimensional MDS map had convex hulls from the three blocks overlapping but samples from the same sampling events were consistently placed next to each other with the exception of samples collected during the fourth sampling session (Figure 5.2e). The same trend was observed at the order level. The different blocks did not cluster together but were positioned separately in all the ordination maps, which meant insect communities on these blocks might be slightly different from each other but the current method might have failed to detect the source of difference.

Effects of grazing treatments on insect community structure

Beating samples

At the ordinal level 49.9% of the total variation was explained by the first two axes of the PCA (Table 5.8). Examination of the Eigenvectors showed that the first axis emphasized the abundances of most orders with the exception of Orthoptera and Hymenoptera (Table 5.8). The second axis was a gradient between (Phasmatodea + Mantodea) and Hymenoptera with minimal influence from the other orders. Grazing patterns were not very different from each other with convex hulls for different grazing systems overlapping; but there was a tendency of samples collected during the same sampling event to lie next to one another although there was no consistency (Figure 5.3a). PERMANOVA carried out using principal scores showed that there was a significant difference between grazing systems and sampling events (Table 5.11). However, pairwise comparisons did not reveal any significant differences between grazing systems (Table 5.12). Pairwise comparisons revealed that there was a significant difference between all the four sampling events (Table 5.13). There was no interaction effect between treatment and sampling event (Table 5.11). A two-dimensional MDS ordination did not reveal any pattern with convex hulls for the different treatments overlapping (Figure 5.3b). The stress value of 0.2 was high, which meant that the data points may have been arbitrary placed on the configuration.

Further analyses were carried out at the familial level. The first two axes of the PCA captured 30.5% of the total variation. Examination of the Eigenvectors showed that the first axis was a gradient between (Diapheromeridae + Gryllidae) and (Acrididae + Tenebrionidae) with little impact from the other families; the second axis was a gradient between (Miridae + Formicidae + Blattidae + Pentatomidae) and Pamphagidae (Table 5.9). These two dimensions revealed that there were some differences between treatments although convex hulls overlapped (Figure 5.3c). Further analysis revealed that there was a significant difference between treatments and sampling events (Table 5.11). However, pairwise comparisons did not show any significant differences between treatments (Table 5.12). PERMANOVA results showed that there was a significant difference between the sampling events except for the third and fourth sampling sessions (Table 5.13). Also a two-dimensional MDS configuration did not reveal any pattern with convex hulls overlapping (Figure 5.3d). Samples collected during the same session occurred next to each other

but not consistently (Figure 5.3d). The stress value of 0.21 was high and therefore there was no need for further interpretation (Clarke and Warwick, 1994).

At the species level a two-dimensional MDS ordination did not reveal any particular pattern portraying grazing systems (Figure 5.3e). Ordination maps generated at order, family and species levels did not show any specific patterns reflecting the different grazing systems, therefore samples collected from the different treatments might not be different from each other.

Mist-blowing

At the ordinal level 54.8% of the total variation was explained by the first two axes of the PCA (Table 5.8). Evaluation of the Eigenvectors showed that the first axis highlighted abundances of most orders except for Orthoptera and Hymenoptera; the second axis was a gradient between Hymenoptera and (Mantodea + Phasmatodea) with the rest of the orders contributing little influence (Table 5.8). A two-dimensional PCA ordination showed that grazing systems were not distinct with convex hulls overlapping (Figure 5.4a). However, samples did not cluster according to grazing patterns but samples' nearest neighbours were from different treatments but collected during the same sampling event (Figure 5.4a). There was a pattern which reflected sampling events although the clustering was not consistent (Figure 5.4a). Results of PERMANOVA on principal scores showed that there was a significant difference between sampling events (Table 5.11). Pairwise comparisons revealed that all the four sampling events were significantly different (Table 5.13). A stress value of 0.15 of a two-dimensional MDS ordination of the same data did not justify further interpretation (Figure 5.4b). The convex hulls for the different grazing systems overlapped (Figure 5.4b).

At the family level the first two axes of the PCA captured 29.5% of the total variation (Table 5.10). Evaluation of the Eigenvectors showed that the first axis was a gradient between (Tenebrionidae + Mantidae) and (Miridae + Carabidae + Cleridae + Anthicidae) with little influence from the other families (Table 5.10). The second axis was mainly affected by Curculionidae, Chrysomelidae, Cerambycidae and Diapheromeridae (Table 5.10). The two dimensions showed that grazing systems were not different from each other with convex hulls for the different grazing patterns overlapping (Figure 5.4c). Samples did not cluster on grazing

systems. However, three clusters reflecting sampling events were observed (Figure 5.4c). Samples collected during the first and fourth sampling sessions formed two distinct groups while those collected on the second and third sampling sessions formed another group (Figure 5.4c). Results of PERMANOVA showed that sampling events were significantly different (Table 5.11). Pairwise comparisons showed that all the four sampling events were significantly different from each other (Table 5.13). A two-dimensional MDS ordination of the same data revealed the three clusters as observed on PCA configuration, but there was no consistency (Figure 5.4d). The stress value of 0.2 was large and therefore there was no need for further interpretation. PERMANOVA results show that there was no significant effect by the different grazing patterns on insect communities at order and family levels (Table 5.11).

At the species level the convex hulls for the different grazing systems overlapped showing that grazing patterns were not completely different from each other (Figure 5.4e). A two-dimensional MDS ordination did not reflect any clustering portraying grazing systems (Figure 5.4e). But a pattern reflecting sampling events was observed, all samples collected during the first sampling session separated out from the rest of the samples (Figure 5.4e). A stress of 0.21 was big and there was no need for further interpretation. These ordination maps generated at three taxonomic levels shows that convex hulls from different grazing systems overlap and therefore, the insect communities on these grazing systems may not be different from each other.

Effects of acacia-ants on insect community structure

Beating samples

At the ordinal level 59.0% of the total variation was explained by the first two axes of the PCA (Table 5.14). An assessment of the Eigenvectors showed that the first axis emphasized abundances of most orders except for Mantodea; the second axis was a gradient between Phasmatodea and (Hymenoptera + Blattodea) with little influence from the other orders (Table 5.14). These two dimensions show that *C. sjostedti* coexist with a different insect community from the other ant species, the same with *T. penzigi* since their convex hulls barely overlap with any other group (Figure 5.5a). However, convex hulls for *C. mimosae* and *C. nigriceps* overlaps which means insect communities coexisting with these two ant species may not be different (Figure 5.5a). A pattern of clustering reflecting the effect of ant species was observed for *C.*

sjostedti and *T. penzigi* (Figure 5.5a). The scores for samples collected during second sampling session for *T. penzigi* and *C. sjostedti* were higher on axis two compared to those collected during the other sampling sessions (Figure 5.5a). After subjecting principal scores to PERMANOVA, ant species and sampling sessions were found to be significantly different (Table 5.17). Pairwise comparisons showed that *C. sjostedti* was significantly different from *C. nigriceps* and *T. penzigi* (Table 5.18); it also revealed that the first sampling session was significantly different from the third and fourth sampling sessions (Table 5.19). A two-dimensional MDS configuration further confirmed PCA results that showed *C. sjostedti* coexisted with a different insect community compared with the other ant species (Figure 5.5b). The convex hulls of *C. sjostedti* did not overlap with those of the other ant species (Figure 5.5b). However, there were some variations on samples collected from trees colonized by *T. penzigi*, samples collected during the first sampling session isolated from those collected during the second, third and fourth sampling sessions (Figure 5.5b). Convex hulls for *C. mimosae* and *C. nigriceps* overlapped in a similar way as in PCA (Figure 5.5b).

At the familial level the first two axes of PCA explained only 37.0% of the total variation (Table 5.15). The first axis was a gradient between Diapheromeridae and (Tenebrionidae + Anthicidae) with little influence from the other families; the second axis was a gradient between Gryllacrididae and (Acrididae + Mantidae + Polyphagidae) with minimal influence from the other families (Table 5.15). Convex hulls for *T. penzigi* barely overlap with those of *C. sjostedti* (Figure 5.5c) but not with those of *C. nigriceps* and *C. mimosae*. But also convex hulls for *C. nigriceps* and *C. mimosae* barely overlap (Figure 5.5c). Principal component scores generated by PCA were later subjected to PERMANOVA. Results show that there was a significant effect by the ant species and sampling events on insect communities (Table 5.17). Pairwise comparisons showed that there was a significant difference between insect communities coexisting with *C. sjostedti* and those coexisting with *C. nigriceps* and *T. penzigi* (Table 5.18). The first sampling session was significantly different from the fourth sampling session (Table 5.19). A two-dimensional MDS configuration was similar to that of PCA. Convex hulls for *C. sjostedti* barely overlapped with those of *T. penzigi* (Figure 5.5d). However, convex hulls for *C. mimosae* and *C. nigriceps* overlapped (Figure 5.5d). The stress value was 0.18.

At the species level, two clusters formed with one group consisting of *C. sjostedti* and *T. penzigi* and their convex hulls overlapped, while the other group consisted of *C. mimosae* and *C. nigriceps* and also their convex hulls overlapped (Figure 5.5e). However, there was no overlap between the two groups (Figure 5.5e).

Mist-blowing

At the ordinal level 64.8% of the total variation was explained by the first two axes of the PCA (Table 5.14). An examination of the Eigenvectors showed that the first axis emphasized abundances of most orders except for Blattodea and Coleoptera (Table 5.14). The second axis was a gradient between Blattodea and (Orthoptera + Coleoptera + Mantodea) with slight influence from Hemiptera, Hymenoptera and Phasmatodea (Table 5.14). A two-dimensional PCA configuration showed that acacia-ants were slightly different from each other (Figure 5.6a). Convex hulls for *C. nigriceps* did not overlap with those of *T. penzigi* and *C. sjostedti* but they overlapped with those of *C. mimosae*. But convex hulls for *T. penzigi*, *C. sjostedti* and *C. mimosae* overlapped (Figure 5.6a). Scores for samples collected during the first sampling session were low on both axes compared to those collected during the second, third and fourth sampling sessions (Figure 5.6c). When principal scores were subjected to PERMANOVA, results showed that there was a significant difference between ant species and sampling events (Table 5.17). Pairwise comparisons revealed that *C. sjostedti* was significantly different from *C. nigriceps* (Table 5.18). Further analysis showed that the first sampling session was significantly different from the third sampling session (Table 5.19). When the same data set was used to generate a two-dimensional MDS ordination, convex hulls for the different ant species barely overlapped (Figure 5.6b).

At the family level the first two axes of the PCA explained 40.6% of the total variation (Table 5.16). The first axis was mainly affected by Acrididae, Diapheromeridae and Mantidae, while the second axis was affected by Chrysomelidae, Curculionidae, Scarabaeidae and Staphylinidae (Table 5.16). These two dimensions showed that ant species supported different insect communities. Convex hulls for *C. nigriceps* did not overlap with those of *C. sjostedti* and *T. penzigi*, but they overlapped with those of *C. mimosae* (Figure 5.6c). Convex hulls for *T. penzigi*, *C. mimosae* and *C. sjostedti* barely overlapped (Figure 5.6c). PERMANOVA test carried out

using principal scores showed that ant species and sampling events were significantly different (Table 5.17). Pairwise comparisons revealed that *C. sjostedti* was significantly different from *C. nigriceps* and *T. penzigi* (Table 5.18). Similar results were observed at order level. Further pairwise comparisons showed that the first sampling session was significantly different from the fourth sampling session (Table 5.19). A two-dimensional MDS configuration with a stress value of 0.15 showed convex hulls overlapping in a similar manner as in PCA (Figure 5.6d).

At the species level a two-dimensional MDS ordination reflected a pattern, with two distinct groups, one consisting of *T. penzigi* and *C. sjostedti* and the other composed of *C. mimosae* and *C. nigriceps* (Figure 5.6e). Convex hulls of *C. sjostedti* overlapped with those of *T. penzigi* only, while convex hulls for *C. mimosae* and *C. nigriceps* overlapped (Figure 5.6e).

Effects of ant-hemipteran mutualism on insect community structure

Beating samples

At the ordinal level 63.6% of the total variation was explained by the first two axes of the PCA (Table 5.20). Assessment of the Eigenvectors showed that the first axis highlighted abundances of most orders except Orthoptera; second axis was mainly a gradient between Hemiptera, Orthoptera and Phasmatodea with little influence from the other orders (Table 5.20). A two-dimensional PCA ordination did not reveal any pattern reflecting ant-hemipteran mutualism (Figure 5.7a). However, there was a pattern which reflected sampling events, which meant sampling events had more effect than ant-hemipteran mutualism (Figure 5.7a). But in all cases samples collected from trees which had ant-hemipteran mutualism had a lower score on axis two (Figure 5.7a). Principal scores generated by PCA were subjected to PERMANOVA. Results did not show any significant difference between the hemipteran-tending ants and non-tending ants, however, there was a significant difference between sampling events (Table 5.23). Pairwise comparisons did not reveal any significant differences between the sampling events (Table 5.24). A two-dimensional MDS plot of the same data was slightly different from that obtained using PCA but the pattern reflecting sampling events was evident (Figure 5.7b). Convex hulls for hemipteran-tending ants and non-tending ants overlapped, which indicates that the two insect communities are not completely different (Figure 5.7b).

At the family level the first two axes of the PCA explained 51.8% of the total variation (Table 5.21). The first axis was a gradient between (Tenebrionidae + Anthicidae) and Curculionidae + Diapheromeridae), but the other families had substantial influence (Table 5.21). The second axis was a gradient between (Pentatomidae + Blattidae) and (Pamphagidae + Mantidae) with little impact from the other families (Table 5.21). The two dimensions show that the hemipteran-tending ants and non-tending ants were not distinct with convex hulls overlapping (Figure 5.7c). But there was a pattern which reflected the sampling events; samples collected during the same period were always found neighbouring each other (Figure 5.7c). PERMANOVA results showed that there was a significant difference between sampling events (Table 5.23). But pairwise comparisons did not reveal any significant differences between the sampling sessions (Table 5.24). However, there was no significant difference between hemipteran-tending ants and non-tending ants when principal component scores were subjected to PERMANOVA (Table 5.23). A stress value of 0.08 for a two-dimensional MDS configuration supported further interpretation. This ordination showed that hemipteran-tending ants and non-tending ants were not distinct because their convex hulls overlapped (Figure 5.7d).

At the species level a two-dimensional MDS ordination showed convex hulls of hemipteran-tending ants and non-tending ants overlapping (Figure 5.7e). But a pattern observed at order level which reflected sampling events was evident, with samples collected on the same sessions consistently found neighbouring each other (Figure 5.7e). This pattern showed that sampling events had an effect on insect communities.

Mist-blowing samples

At the order level the first two axes of the PCA captured 67.7% of the total variation (Table 5.20). Further examination of Eigenvectors showed that the first axis emphasized the abundances of most orders except for Coleoptera and Orthoptera (Table 5.20). The second axis was a gradient between (Orthoptera + Blattodea) and (Phasmatodea + Hemiptera) with little influence from Mantodea, Hymenoptera and Coleoptera (Table 5.20). The two-dimensional PCA ordination revealed that convex hulls for hemipteran-tending ants and non-tending ants barely overlapped (Figure 5.8a). But close examination revealed that there was a tendency of samples separating either towards hemipteran-tending ants or non-tending ants (Figure 5.8a). However, there was no

clear pattern either based on hemipteran-tending ants and non-tending ants or sampling events (Figure 5.8a). When principal scores were subjected to PERMANOVA, results did not reveal any significant difference between hemipteran-tending ants and non-tending ants (Table 5.23). However, there was a significant difference between sampling events (Table 5.23). Pairwise comparisons did not show any significant differences between the sampling sessions (Table 5.24). A stress value of 0.07 of a two-dimensional MDS configuration allowed further interpretation. The convex hulls of hemipteran-tending ants and non-tending ants overlapped but slightly different from those observed using PCA (Figure 5.8b).

At the family level the first two axes of the PCA explained 51.3% of the total variation (Table 5.22). Examination of the Eigenvectors revealed that the first axis mainly highlighted families with low abundances except for Anthicidae (Table 5.22). The second axis was a gradient between Diapheromeridae and (Coccinellidae + Formicidae), but the other families also had significant influence (Table 5.22). These two dimensions show that hemipteran-tending ants and non-tending ants are slightly different with convex hulls barely overlapping (Figure 5.8c). A close examination reveals a pattern of samples separating out based on hemipteran-tending ants and non-tending ants (Figure 5.8c). PERMANOVA results revealed that there was a significant difference between sampling events (Table 5.23). But pairwise comparisons failed to detect any significant differences between the sampling sessions (Table 5.24). A two-dimensional MDS ordination showed that the convex hulls for hemipteran-tending ants and non-tending ants overlapped, which meant ant-hemipteran mutualism had no effect on the insect communities (Figure 5.8d).

At the species level a two-dimensional MDS map had convex hulls for hemipteran-tending ants and non-tending ants overlapping (Figure 5.8e). However, a pattern reflecting sampling sessions was still evident with samples collected during the same sampling session being near each other but not consistently (Figure 5.8e).

Diversity indices

Analysis at order level

Results of PERMANOVA showed that there was a significant effect between ant species and also an interaction effect between ant species x treatments on total number of taxa, (Table 5.25). Further analysis on pairwise comparisons between ant species revealed a significant difference between the total number of taxa in insect communities found on trees inhabited by *C. sjostedti* x *C. nigriceps*, *C. sjostedti* x *T. penzigi*, and *C. mimosae* x *T. penzigi* (Table 5.26). However, there were no significant effects on treatments or locations on total number of taxa (Table 5.25). Further analysis of the interaction effect between treatments x ant species revealed a significant difference between total number of taxa in insect communities on trees colonized by *C. sjostedti* x *T. penzigi*, *C. mimosae* x *T. penzigi* and *C. nigriceps* x *T. penzigi* on plots which only cows were allowed to graze (Table 5.27). However, there were no significant differences between the total number of taxa in insect communities on trees colonized by *C. sjostedti* x *C. mimosae*, *C. sjostedti* x *C. nigriceps* and *C. mimosae* x *C. nigriceps* in plots where only cows were allowed to graze (Table 5.27). On plots where all herbivores including cows were allowed to feed, pairwise comparisons revealed that there was a significant difference between the total number of taxa on trees occupied by *C. sjostedti* and those colonized by *C. mimosae*, *C. nigriceps* and *T. penzigi* but there were no significant differences between the total number of taxa on trees inhabited by the four ant species at treatment '0' (Table 5.27).

PERMANOVA test performed on Pielou's evenness index showed that there was a significant difference between trees inhabited by the different ant species (Table 5.28). But there were no significant differences between locations or treatments (Table 5.28). There were also no interaction effects between locations, treatments and ant species (Table 5.28). Further analysis revealed that evenness indices of trees colonized by *C. sjostedti* x *C. nigriceps*, and *C. sjostedti* x *T. penzigi* were significantly different (Table 5.29). However, there were no significant differences on evenness index between trees colonized by the other ant species (Table 5.29).

Results of PERMANOVA revealed that there was a significant effect between ant species and there was an interaction effect between treatments x ant species on the Shannon-Wiener diversity index (Table 5.30). Pairwise comparisons on ant species showed that there was a significant

difference on the Shannon-Wiener diversity index between trees inhabited by *C. sjostedti* x *C. nigriceps*, *C. sjostedti* x *T. penzigi* and *C. mimosae* x *T. penzigi* (Table 5.31). Further analysis of the interaction effect between treatments x ant species revealed that the Shannon-Wiener diversity index of trees found in plots which only cows were allowed to graze and colonized by *C. sjostedti* x *T. penzigi* and *C. nigriceps* x *T. penzigi* were significantly different (Table 5.32). In plots where all herbivores including cows were allowed to feed, trees occupied by *C. sjostedti* x *C. nigriceps*, and *C. sjostedti* x *T. penzigi* had diversity indices that were significantly different (Table 5.32). But in plots where all herbivores and cows were not allowed only trees colonized by *C. nigriceps* x *T. penzigi* had the Shannon-Wiener diversity index that was significantly different (Table 5.32).

PERMANOVA test performed on Margalef's richness index revealed that there was a significant effect between ant species (Table 5.33). However, there were no significant differences between locations or treatments. There were also no interaction effects between locations, treatments and ant species (Table 5.33). Pairwise comparisons between ant species revealed that there was a significant difference in Margalef's richness index between trees colonized by *C. sjostedti* x *T. penzigi* (Table 5.34).

Analysis at family level

When total number of taxa (S) was subjected to PERMANOVA, results showed that there was a significant effect between ant species and an interaction effect between treatments and ant species (Table 5.35). Further analysis on ant species using pairwise comparisons revealed that total number of taxa on insect communities on trees colonized by *C. sjostedti* x *C. nigriceps* and *C. sjostedti* x *T. penzigi*, and *C. mimosae* x *T. penzigi* were significantly different (Table 5.36). Pairwise comparisons to test the interaction effect revealed that plots on which only cows were allowed to graze, total number of taxa in insect communities on trees colonized by *C. sjostedti* x *T. penzigi*, *C. mimosae* x *T. penzigi* and *C. nigriceps* x *T. penzigi* were significantly different (Table 5.37). In plots where all herbivores and cows were allowed to feed, results showed that there was a significant difference between the total number of taxa in insect communities on trees colonized by *C. sjostedti* x *C. mimosae*, *C. sjostedti* x *C. nigriceps*, and *C. sjostedti* x *T. penzigi* (Table 5.37). However, at plots where all herbivores including cows were not allowed, there was

no significant difference between the total number of taxa in insect communities found on trees inhabited by different ant species (Table 5.37).

PERMANOVA results also revealed that there was a significant effect between ant species and an interaction effect between treatments x ant species on Pielou's evenness index (Table 5.38). However, there was no interaction effect between locations and ant species as well as between locations and treatments (Table 5.38). Pairwise comparisons between ant species revealed that evenness indices in insect communities on trees inhabited by *C. sjostedti* x *T. penzigi* were significantly different (Table 5.39). Further analysis on the interaction effect between treatments and ant species showed that trees colonized by *C. sjostedti* x *T. penzigi* and *C. mimosae* x *T. penzigi* had evenness indices that were significantly different on plots which only cows were allowed to graze (Table 5.40). However, there was no significant difference in evenness indices between insect communities found on trees inhabited by the four ant species at treatments 'E' and '0' (Table 5.40).

When the Shannon-Wiener diversity index was subjected to PERMANOVA, results revealed that there was a significant effect between ant species and there was an interaction effect between treatments and ant species (Table 5.41). However, there was no significant effect between locations or treatments (Table 5.41). Pairwise comparisons between ant species revealed that diversity indices of insect communities on trees inhabited by *C. sjostedti* x *C. nigriceps*, *C. sjostedti* x *T. penzigi*, and *C. mimosae* x *T. penzigi* were significantly different (Table 5.42). Further analysis on the interaction effect revealed that diversity indices of insect communities on trees colonized by *C. sjostedti* x *T. penzigi*, *C. mimosae* x *T. penzigi* and *C. nigriceps* x *T. penzigi* were significantly different on plots where only cows were allowed to graze (Table 5.43). In plots where all herbivores including cows were allowed to feed insect communities on trees inhabited by *C. sjostedti* x *C. nigriceps* and *C. sjostedti* x *T. penzigi* had diversity indices that were significantly different (Table 5.43).

Results of PERMANOVA showed that there was a significant effect between ant species and also an interaction effect between treatments and ant species on Margalef's richness index (Table 5.44). There was no significant effect on interaction between locations and treatments and also

between locations and ant species on Margalef's richness index (Table 5.44). Pairwise comparisons between ant species revealed that richness indices of insect communities on trees colonized by *C. sjostedti* x *T. penzigi* were significantly different (Table 5.45). Further analysis of the interaction effect using pairwise comparisons revealed that richness indices of insect communities on trees inhabited by *C. sjostedti* x *T. penzigi*, *C. mimosae* x *T. penzigi* and *C. nigriceps* x *T. penzigi* were significantly different in plots where only cows were allowed to graze (Table 5.46). In plots where all herbivores including cows were present, insect communities on trees colonized by *C. sjostedti* x *C. nigriceps* had richness indices that were significantly different (Table 5.46). At treatment '0' there was no significant difference between richness indices in insect communities on trees occupied by the four ant species (Table 5.46).

Analysis at morphospecies level

Results of PERMANOVA revealed that there was a significant effect between ant species and there was an interaction effect between treatments and ant species on total number of taxa (Table 5.47). But there were no interaction effects between locations and treatments and between locations and ant species (Table 5.47). Pairwise comparisons between ant species showed that total number of taxa in insect communities on trees colonized by *C. sjostedti* x *C. nigriceps*, *C. sjostedti* x *T. penzigi* and *C. mimosae* x *T. penzigi* were significantly different (Table 5.48). Further pairwise comparisons to test interaction effect revealed that in plots where only cows were allowed to graze, insect communities on trees inhabited by *C. sjostedti* x *T. penzigi*, *C. mimosae* x *T. nigriceps* and *C. nigriceps* x *T. penzigi* had total number of taxa that were significantly different (Table 5.49). There was also a significant difference between the total number of taxa in insect communities on trees inhabited by *C. sjostedti* and (*C. mimosae*, *C. nigriceps* and *T. penzigi*) in plots where all herbivores and cows were allowed to feed (Table 5.49).

When PERMANOVA test was carried out on Pielou's evenness index, results did not reveal any significant difference between locations, treatments and ant species (Table 5.50). There was also no interaction effect between locations, treatments and ant species (Table 5.50).

PERMANOVA results revealed a significant effect between ant species and an interaction effect between treatments and ant species on the Shannon-Wiener diversity index (Table 5.51). Pairwise comparisons showed a significant difference in the Shannon-Wiener diversity index in insect communities between trees colonized by *C. sjostedti* x *C. nigriceps*, *C. sjostedti* x *T. penzigi* and *C. mimosae* x *T. penzigi* (Table 5.52). There was no significant difference between ant species on plots where all herbivores and cows were not allowed (Table 5.53). However, there was a significant difference in the Shannon-Wiener diversity index in insect communities between trees occupied by *C. sjostedti* x *T. penzigi*, *C. mimosae* x *T. penzigi* and *C. nigriceps* x *T. penzigi* in plots which only cows were allowed to graze (Table 5.53). There was also a significant difference in the Shannon-Wiener diversity index between trees colonized by *C. sjostedti* x *C. nigriceps* and *C. sjostedti* x *T. penzigi* in plots where all herbivores and cows were allowed to feed (Table 5.53).

PERMANOVA results also showed that there was an interaction effect between treatments and ant species on Margalef's richness index (Table 5.54). Pairwise comparisons further revealed that trees colonized by *C. sjostedti* x *T. penzigi*, *C. mimosae* x *T. penzigi* and *C. nigriceps* x *T. penzigi* had richness indices that were significantly different on plots which only cows were allowed to graze (Table 5.55). There was no significant difference between ant species on trees in plots which all herbivores and cows were allowed to feed and in plots where all herbivores and cows were not allowed (Table 5.55).

Ant-hemipteran mutualism

Data sets of canopy insects collected using beating and mist-blowing were analyzed to test the effect of ant-hemipteran mutualism on the insect community.

Analysis at order level

Results of PERMANOVA showed that there was a significant effect between the two ant guilds and also there was an interaction effect between treatments and ant guilds on total number of taxa (Table 5.56). Further analysis on the interaction effects revealed that the total number of taxa in insect communities on trees colonized by the two guilds were significantly different in plots where only cows were allowed to graze and also in plots which all herbivores and cows were allowed to feed (Table 5.57). Results also showed that there was a significant effect between

guilds on Pielou's evenness index (Table 5.58) and the Shannon-Wiener diversity index (Table 5.59). There was no interaction effect between locations, treatments and ant guilds on Pielou's evenness index (Table 5.58) and the Shannon-Wiener diversity index (Table 5.59). Similar results were obtained for Margalef's richness index (Table 5.60).

Analysis at family level

PERMANOVA results showed that there was a significant effect between guilds and an interaction effect between treatments and guilds on total number of taxa (Table 5.61). However, there was no interaction effect between locations and treatments (Table 5.61). Pairwise comparisons revealed that there was a significant difference on total number of taxa in insect communities on trees inhabited by the two guilds in treatments 'C' and 'E' (Table 5.62).

PERMANOVA results showed that there was a significant effect between guilds on Pielou's evenness index (Table 5.63), the Shannon-Wiener diversity index (Table 5.64) and Margalef's richness index (Table 5.65). In all the above cases there were no interaction effects between locations, treatments and guilds (Tables 5.63-5.65).

Analysis at morphospecies level

Results of PERMANOVA showed that there was a significant effect between guilds and an interaction effect between treatments and guilds on total number of taxa (Table 5.66). Further analysis using pairwise comparisons showed that there was a significant difference on total number of taxa in insect communities on trees colonized by the two guilds on plots where only cows were allowed to graze and in plots where all herbivores and cows were allowed to feed (Table 5.67).

There was a significant effect between guilds on Pielou's evenness index (Table 5.68), the Shannon-Wiener diversity index (Table 5.69) and Margalef's richness index (Table 5.70) after indices were subjected to PERMANOVA.

Discussion

The present study assessed the effects of the KLEE blocks and their immediate environments, grazing patterns, sampling events and four symbiotic ants on insect communities colonizing *S. drepanolobium* at Mpala Research Centre. Overall it was found that block locations had minimal effects while sampling events and symbiotic ants had significant effects on insect communities inhabiting canopies of *S. drepanolobium*.

Hypothesis 1: A small number of insect species was expected to be found coexisting with acacia-ants on canopies of *S. drepanolobium*.

A checklist of insect species coexisting with the four acacia-ants on canopies of *S. drepanolobium* was compiled. Previous studies have shown that the diversity of canopy arthropods is greatly influenced by sampling methods (Basset, 2001). More details can be found in Chapter Four. Fogging is the most popular method for collecting canopy arthropods (Basset, 2001), but the application of different insecticides may produce different results (Erwin, 1995). Other details can be found in Chapter Four. Although mist-blowing and beating/jarring methods were used together to improve the insect catches, the two techniques missed some insects. Although scale insects are found on these trees and were seen during sampling none of these methods collected any sample. Butterflies were also sighted perching on the trees and again these methods did not collect any of them.

However, the two methods combined managed to collect 117 morphospecies. This number is large considering the tree have several defensive mechanisms against herbivory. The black cotton ecosystem is also species poor. However, this is a small number compared to a mean of 616 arthropod species per tree species recorded by Stork (1991) from a forest canopy at Brunei, Borneo. In Mkomazi, Tanzania a total of 492 morphospecies were identified from samples collected from canopies of 31 trees belonging to six *Acacia* species (Krüger and McGavin, 1997).

Hypothesis 2: Block locations and sampling methods had an affect on insect community structure.

When insect samples collected by beating at order level were subjected to PCA, convex hulls for different blocks overlapped, which meant blocks were not distinct from each other. However, sampling events were found to have a significant effect on insect communities. Samples collected during the same sessions were mostly found next to each other. A similar pattern was obtained when the same data set was subjected to MDS. Samples at order level collected using mist-blowing were also subjected to PCA, again convex hulls for the different blocks overlapped, implying that blocks were not different from each other. Further analysis using MDS showed convex hulls for the different blocks overlapping. But the two dimensional PCA and MDS ordinations reflected an inconsistent pattern of samples collected during the same sessions occurring next to each other. This meant that sampling events had a more significant effect on insect communities than block locations. However, in all cases samples from different blocks did not cluster into one group, which would be mean that block location had some effect on insect communities. Similar patterns were observed for beating and mist-blowing samples at both family and species level when two-dimensional PCA and MDS configurations were generated using data at family and species level. These observations therefore show that block locations did not have a major effect on insect communities but sampling events played a major role. The effect of sampling events was also noted when comparing methods (Chapter Four). This was later confirmed when principal scores were subjected to PERMANOVA: there was no significant effect on block locations but sampling events were significantly different. Results were consistent at order, family and species levels.

Hypothesis 3: Grazing patterns and sampling methods affect insect community structure.

When data sets collected by beating were subjected to PCA and MDS, the two-dimensional ordination maps generated did not reveal any pattern on different grazing patterns, and convex hulls for the various grazing patterns overlapped. However, there was a consistent pattern which reflected the sampling events. Samples collected during the same sampling event were found neighbouring each other. When principal component scores were subjected to PERMANOVA, there was a significant difference between treatments and sampling sessions. At the order level all sampling events were significantly different, while at family level sampling events were

significantly different except between the third and fourth sampling events. This implied that both treatments and sampling sessions had an effect on insect communities. At species level the plot of two-dimensional MDS was similar to those obtained at order and family levels.

When data sets collected by mist-blowing were subjected to PCA and MDS, the ordination results were similar to those generated from beating samples. However, there was no significant difference between treatments at order and family levels. But there was a significant difference between sampling events, and pairwise comparisons revealed that all the sampling events were significantly different from each other at order and family levels. A two-dimensional MDS plot generated using insect abundance data at species level was similar to those produced at order and family levels.

Hypothesis 4: Ant species and sampling methods affect insect community structure.

The current study showed that ant species had a significant effect on the associated insect communities. At the order level when samples collected using beating were subjected to PCA, convex hulls for insect samples collected from trees colonized by *T. penzigi* and *C. sjostedti* barely overlapped with samples collected from trees inhabited by *C. mimosae* and *C. nigriceps*. But when the same data was subjected to MDS, convex hulls of samples collected from trees occupied by *C. sjostedti* did not overlap with those collected from the other ant species. This showed that *C. sjostedti* supported a different insect community from the other ant species. The community had a higher total number of taxa that were evenly distributed. This pattern was reflected at both family and species levels. However, when samples collected by mist-blowing were subjected to PCA and MDS, convex hulls for samples collected from trees colonized by the four ant species overlapped at order, family and species levels. However, a pattern was observed whereby *C. sjostedti* and *T. penzigi* tended to form one group, while *C. nigriceps* and *C. mimosae* forming another group. These observations revealed that sampling method had some effect on the insect community. PERMANOVA results on principal scores for beating and mist-blowing at order and family levels were significant for ant species and sampling events. This confirmed that ant species and sampling events had significant effect on insect communities.

Hypothesis 5: Ant-hemipteran mutualism and sampling methods affect insect community structure.

Two-dimensional PCA and MDS configuration generated using abundances of orders collected by beating did not show any pattern reflecting ant-hemipteran mutualism. However, a pattern was observed representing sampling events. At the family level a two-dimensional MDS ordination reflected a pattern on ant-hemipteran mutualism. The convex hulls of samples collected from trees with ants tending scale insects did not overlap with those samples collected from trees with ants not tending scale insects. At the species level, the MDS configuration was similar to that generated at order level. When samples collected by mist-blowing at order level were subjected to PCA and MDS, the two-dimensional ordinations had convex hulls overlapping for samples collected from hemipteran-tending ants and non-tending ants. There was no pattern reflecting ant-hemipteran mutualism, but there was a pattern portraying sampling events. Similar patterns were observed at family and species levels. However, when principal scores were subjected to PERMANOVA, there was a significant difference between the two guilds. Therefore, ant-hemipteran mutualism had a significant effect on insect communities.

Hypothesis 6a: The insect community structure and composition varied between the blocks (North, Central and South).

During the current study the community structure was analyzed at three levels, namely order, family and morphospecies. The results of PERMANOVA showed that there was no significant difference between the three blocks on total number of taxa, Pielou's evenness index, the Shannon-Wiener diversity index and Margalef's richness index for order (Tables 5.25, 5.28, 5.30, 5.33), family (Tables, 5.35, 5.38, 5.41, 5.44) and species (Tables 5.47, 5.50, 5.51, 5.54) levels. The insect communities inhabiting the three blocks were not different.

Hypothesis 6b: The grazing patterns have an effect on the canopy insect community.

Previous study on the study area had shown that removing herbivores lead to reduction in spine length of *S. drepanolobium* (Young and OKello, 1998) as the plant relaxed in investing in defence mechanisms. Huntzinger *et al*. (2004) while working at KLEE site showed that extrafloral nectaries production declined by 25% in plots where all herbivores were excluded for seven years. This translates to less reward for ants and therefore ants have to look for alternative

food sources to supplement their diet. This would translate to reduced intensity in defending their plants. This would hence result in many insect species gaining access to the canopies to feed and live there. However, the results of PERMANOVA showed that grazing patterns had no significant effect on total number of taxa, Pielou's evenness index, the Shannon-Wiener diversity index and Margalef's richness index at order (Tables 5.25, 5.28, 5.30, 5.33), family (Tables 5.35, 5.38, 5.41, 5.44) and species (Tables 5.47, 5.50, 5.51, 5.54) levels. But there was an interaction effect between grazing patterns and ant species. At the order level the effect was on total number of taxa and the Shannon-Wiener diversity index. At the family level it was on all four diversity indices, while at species level it was on total number of taxa, the Shannon-Wiener diversity index and Margalef's richness index. González-Megías *et al*. (2003) found that arthropods were more abundant and diverse in grazed than in ungrazed plots, and ungulates also affected species composition. A study carried out at montane grassland in Central Argentina showed that insect abundance, richness, diversity and biomass had minimum values in the most intensely grazed habitat (Cagnolo *et al*., 2002). Species richness of nectar seeking butterflies and bumble bees were shown to be negatively correlated with grazing intensity as reflected by grass height in south-central Sweden (Söderström *et al.* 2001). Another study showed that red deer grazing reduced abundance of lepidopterous larvae, *Formica rufa*, Coleoptera, Araneae, Diptera and Plecoptera in native pinewoods in the Scottish Highland (Baines *et al*., 1994). Other studies have also shown that grazing affects invertebrates (Dennis *et al*., 1997; Gómez and Gonzalez-Megías, 2002).

Hypothesis 6c: The four ant species modify the canopies differently and behave differently, so they would affect the insect community differently.

PERMANOVA results showed that ant species had a significant effect on total number of taxa, the Shannon-Wiener diversity index, Margalef's richness index and Pielou's evenness index at order (Tables 5.25, 5.28, 5.30, 5.33) and family (Tables 5.35, 5.38, 5.41, 5.44) levels. While at the species levels ant species had a significant effect on total number of taxa and the Shannon-Wiener diversity index (Tables 5.47, 5.51). Pairwise comparisons revealed that there was a significant difference on total number of taxa and the Shannon-Wiener diversity index at the three taxonomic levels between *C. sjostedti* x *C. nigriceps*, *C. sjostedti* x *T. penzigi* and *C. mimosae* x *T. penzigi*. Further analysis showed that there was a significant difference between *C.*

sjostedti x *T. penzigi* for Margalef's richness index at order and family levels. Results also showed that there was a significant difference between *C. sjostedti* x *C. nigriceps* and *C. sjostedti* x *T. penzigi* at order level and *C. sjostedti* x *T. penzigi* at family level for Pielou's evenness index. These results were in agreement with the hypothesis that different ant species would affect the insect community differently. These findings show that ant species play a major role in structuring the insect community in this ecosystem, and as suggested in the introductory chapter that one or more of the ant species may be keystone species in this savannah ecosystem.

At all times there are vacant niches on plants that colonization by new species of insects appears to have effectively stopped (Kikkawa and Andersen, 1986). If this theory holds it implies that there are still vacant niches on canopies of *S. drepanolobium* occurring on black cotton soils. Therefore, the variations observed in species composition occurring in trees inhabited by the different ant species were not due to lack of vacant niches but as a result of canopy modification by these ants. Insect samples were collected from the same locality and consequently the pool of insects that were invading the canopy was the same. Ants were shown to deter insect herbivores visiting plants (Skinner and Whittaker, 1981; Del-Claro *et al*., 1996; Gaume *et al*., 1997, 1998, 2005; Oliveira *et al*., 1999; Heil *et al*., 2001; Izzo and Vasconcelos, 2005), but the deterring capacity differs since some herbivores possess mechanisms to overcome ant predation and still feed on the plant despite the presence of ants (Eubanks *et al*., 1997; Vasconcelos and Casimiro, 1997; Ruhren, 2003), in addition the size, abundance and aggressiveness of the ants can affect their protective abilities (Rocha and Bergallo, 1992; Itioka *et al*., 2000; Bruna *et al*., 2004).

Previous study had shown that ants reduce the abundance of different arthropod groups such as Blattodea, Coleoptera, and Hemiptera (Mody and Linsenmair, 2004). However, they also found that some insect orders that mainly consisted of herbivores such as Lepidoptera, Orthoptera, Thysanoptera and Hemiptera were not affected. Gibb (2003) also indicated that predation by *Iridomyrmex purpureus* did not have a significant effect on other epigaeic arthropod communities. Selman (1988) and Jolivet (1991) showed that chrysomelids possessed different adaptations which allowed them to coexist with ants. Experiments carried out by Oliveira and Freitas (2004) on an ant-plant-butterfly system in cerrado habitats in Brazil showed that ant-plant mutualisms are important in structuring the community of canopy arthropods. *Pheidole*

megacephala was also shown to affect both terrestrial and arboreal invertebrate community in Howard Springs in Australia (Hoffmann and Andersen, 1999). In Cote d'Ivoire different ant species were shown to affect the composition of the arthropod community differently (Mody and Linsenmair, 2004). This study by Mody and Linsenmair (2004) shows that, apart from plant-intrinsic factors such as morphology or chemistry, plant-extrinsic factors, such as the distribution of plant-attracted ants, can govern the composition of arthropod communities on individual plants. This factor should increase heterogeneity of arthropod communities on conspecific plants the more ant-plant interactions there are. Therefore, ant diversity should be considered as one factor enhancing biodiversity of arthropod community on plant-arthropod interactions. Results obtained from the current studies are in agreement to those reported by Mody and Linsenmair (2004).

Hypothesis 6d: The variation due to ant-hemipteran mutualisms was expected to affect the insect community differently.

Most symbiotic association between ants and myrmecophytes involve a third partner, usually sap-sucking hemipteran tended by ants (Ito and Higashi, 1991; Davidson and McKey, 1993; Engel *et al*., 2001). Hemipterans benefit by having exclusive access to the host's sap in sheltered sites protected by ants from predation (Gaume *et al*., 1998). The association between honeydew-producing hemipterans and ants occurs on many plants and is generally considered mutualistic (Dansa and Rocha, 1992; but see Buckley, 1987; Hölldobler and Wilson, 1990). These interactions between plants, sap-feeding Hemiptera, and ants can affect each of the participants in a variety of ways (Buckley, 1987). These interactions can also be affected by other organisms such as other herbivorous insects, predators and parasites of the Hemiptera (Buckley, 1987). The association between ants and Membracidae was shown to reduce herbivory on *Didymopanax vinosum* (Araliaceae) in Brazilian cerrado (Dansa and Rocha, 1992). Suzuki *et al*. (2004) whilst working in Mt. Rokko, Kobe City, western Japan showed that the presence of *Lasius japonicus* and *Tetramorium tsushimae* on *Vicia angustifolia* L. (Leguminosae) reduced the number of larvae of the weevil *Hypera craccivora* (Curculionidae). *Iridomyrmex* spp. were also shown to reduce spider predation on *Ipoides melaleucae* (Eurymelidae) on saplings of *Eucalyptus camaldulensis* and *Melaleuca viridflora* in tropical north-western Australia (Buckley, 1990). However, work by Buckley (1983) showed that association of sap-sucking membracid treehopper

Sextius virescens and the ant *Iridomyrmex* sp. caused a negative effect to *Acacia decurrens* by causing a decline on growth and seed set. The cost to the tree of maintaining ants may be greater when ants associate with coccids (Gaume *et al*., 1998). At the study site *C. sjostedti* and *C. mimosae* associate with coccids. Although there is no evidence on whether ants tending coccids cost *S. drepanolobium* more compared to those that do not tend coccids, the current study investigated the effect of hemipterans on insect community coexisting with the four ant species.

PERMANOVA results at order (Tables 5.56, 5.58, 5.59, 5.60), family (Tables 5.61, 5.63, 5.64, 5.65) and species (5.66, 5.68, 5.69, 5.70) levels showed that ant-hemipteran mutualism had a significant effect on the insect community coexisting with these four acacia-ants on canopies of *S. drepanolobium*. In fact, the predatory/aggressive behaviour of ants near food sources affects the performance of other insect herbivores (Fagundes *et al*., 2005). Wimp and Whitham, (2001) showed that ant-hemipteran mutualism affects arthropod community, presence of ants and aphids on cottonwood resulted in 57% reduction in species richness. In addition, the mere presence of hemipterans feeding on the host plant can alter plant quality, producing an indirect negative effect on other herbivores (Fagundes *et al*., 2005).

Conclusions

The current study has shown that ant species defending *Acacia* species against herbivory still allow a large number of insect species to occupy the tree canopy. This study recorded more than 100 insect species that coexist with four acacia-ants on canopies of *S. drepanolobium* at Mpala Research Centre. These included herbivores, omnivores and predators. Therefore, a number of questions regarding this ant-acacia mutualism can be asked.

i) How did these insect species manage to break the ant defence barrier, assuming that during the evolution of ant–acacia mutualism these insect species were excluded from the canopies? Or was there no barrier?

ii) How many insect species colonized the canopies during the evolution of ant-acacia mutualism and what percentage managed to adapt and coexist with this ant species?

iii) Were the predators (praying mantises, spiders and lizards; personal observations) occupying *S. drepanolobium* canopies currently, attracted by the presence of prey on these canopies, or by the ant species or *S. drepanolobium* to feed on those herbivores

inhabiting canopies and competing with ants and tree for resources? If by *S. drepanolobium* or ants, are they therefore acting as a defensive mechanism?

iv) How do all these guilds (herbivores, omnivores and predators) interact with ants?

v) Are these insect species competing with both the ants and the tree for resources?

To answer these questions requires more research. However, this study has clearly demonstrated that mutualism is not a straight case of two or a few species benefiting from each other, but a complex system involving many organisms interacting at various levels and intensities. Insect herbivores in this case may affect the survival of *S. drepanolobium* and therefore indirectly reduce the habitat for ants. However, the presence of predators, parasites and diseases controls the populations for these herbivores. Future researchers ought to consider symbiotic mutualisms on a wider scope with a view to establishing all players involved and their roles for specific mutualisms.

Table 5.1. Relative frequencies (expressed as percentages) of individuals belonging to the various orders occurring on canopies of *S. drepanolobium* trees occupied by four acacia-ants. The expected value was 25% in all cases if the distribution were random.

	C. sjostedti	*C. mimosae*	*C. nigriceps*	*T. penzigi*
Blattodea	28.64	14.99	49.82	6.54
Coleoptera	30.29	19.90	20.15	29.66
Hemiptera	8.99	17.62	47.39	26.00
Hymenoptera	57.69	22.05	6.59	13.67
Mantodea	32.21	15.87	13.46	38.46
Orthoptera	33.19	17.04	17.82	31.94
Phasmatodea	6.99	21.83	42.36	28.82

Table 5.2. The checklist of the various species found associating with the four acacia-ants on canopies of *S. drepanolobium*. Showing orders, families and accumulative number of individuals collected for each insect species. They were collected using beating and mist-blowing.

Species	Order	Family	*C. sjostedti*	*C. mimosae*	*C. nigriceps*	*T. penzigi*
Acrididae sp. 1	Orthoptera	Acrididae	53	6	5	37
Acrididae sp. 2	Orthoptera	Acrididae	135	23	16	116
Acrididae sp. 3	Orthoptera	Acrididae	27	6	2	27
Acrididae sp. 4	Orthoptera	Acrididae	14	31	17	17
Acrididae sp. 5	Orthoptera	Acrididae	42	5	2	47
Acrididae sp. 8	Orthoptera	Acrididae	0	1	0	0
Acrididae sp. 9	Orthoptera	Acrididae	1	0	0	0
Acrididae sp. 10	Orthoptera	Acrididae	1	0	0	0
Acrididae sp. 11	Orthoptera	Acrididae	5	1	0	11
Acrididae sp. 12	Orthoptera	Acrididae	5	0	0	8
Acrididae sp. 14	Orthoptera	Acrididae	11	1	1	22
Acrididae sp. 15	Orthoptera	Acrididae	2	2	1	1
Acrididae sp. 16	Orthoptera	Acrididae	12	0	0	11
Acrididae sp. 17	Orthoptera	Acrididae	1	0	0	0
Acrididae sp. 19	Orthoptera	Acrididae	0	2	1	0
Acrididae sp. 20	Orthoptera	Acrididae	1	1	0	0
Acrididae sp. 21	Orthoptera	Acrididae	0	0	0	1
Acrididae sp. 23	Orthoptera	Acrididae	0	0	1	0

Species	Order	Family	*C. sjostedti*	*C. mimosae*	*C. nigriceps*	*T. penzigi*
Acrididae sp. 24	Orthoptera	Acrididae	1	0	0	0
Acrididae sp. 26	Orthoptera	Acrididae	0	0	1	0
Acrididae sp. 27	Orthoptera	Acrididae	1	0	0	0
Acrididae sp. 28	Orthoptera	Acrididae	2	0	0	2
Acrididae sp. 30	Orthoptera	Acrididae	0	1	0	0
Acrididae sp. 31	Orthoptera	Acrididae	0	1	0	0
Ectatoderus sp. A	Orthoptera	Gryllidae	308	239	283	303
Gryllodes sp. A	Orthoptera	Gryllidae	4	2	2	0
Gryllacris sp. A	Orthoptera	Gryllacrididae	1	1	1	4
Pamphagidae sp. 1	Orthoptera	Pamphagidae	0	0	5	1
Pamphagidae sp. 2	Orthoptera	Pamphagidae	0	0	1	0
Pamphagidae sp. 3	Orthoptera	Pamphagidae	3	2	2	2
Pamphagidae sp. 4	Orthoptera	Pamphagidae	1	0	0	2
Agrilus sp. A	Coleoptera	Buprestidae	3	3	0	0
Agrilus sp. B	Coleoptera	Buprestidae	0	6	3	1
Agrilus sp. D	Coleoptera	Buprestidae	1	0	0	0
Agrilus sp. G	Coleoptera	Buprestidae	1	0	0	0
Buprestid sp. 1	Coleoptera	Buprestidae	18	6	3	16
Buprestid sp. 2	Coleoptera	Buprestidae	1	5	0	0
Hoplistura sp. A	Coleoptera	Buprestidae	21	45	18	34
Chrysobothris sp. A	Coleoptera	Buprestidae	1	2	1	4

Species	Order	Family	*C. sjostedti*	*C. mimosae*	*C. nigriceps*	*T. penzigi*
Sjoestedtius sp. A	Coleoptera	Buprestidae	2	0	0	0
Sjoestedtius sp. B	Coleoptera	Buprestidae	0	1	0	0
Sjoestedtius sp. C	Coleoptera	Buprestidae	3	20	3	0
Chrysomelidae sp. 1	Coleoptera	Chrysomelidae	0	0	0	1
Chrysomelidae sp. 3	Coleoptera	Chrysomelidae	0	0	1	1
Chrysomelidae sp. 4	Coleoptera	Chrysomelidae	1	13	19	2
Chrysomelidae sp. 5	Coleoptera	Chrysomelidae	1	0	1	0
Chrysomelidae sp. 6	Coleoptera	Chrysomelidae	1	2	1	1
Cryptocephalus sp. A	Coleoptera	Chrysomelidae	1	0	0	0
Cryptocephalus sp. B	Coleoptera	Chrysomelidae	1	0	0	0
Dorcathispa sp. A	Coleoptera	Chrysomelidae	0	0	0	1
Hispa sp. A	Coleoptera	Chrysomelidae	2	0	1	5
Lema sp. A	Coleoptera	Chrysomelidae	2	0	2	1
Megalognatha sp. A	Coleoptera	Chrysomelidae	0	1	1	2
Monolepta sp. A	Coleoptera	Chrysomelidae	5	11	41	8
Monolepta sp. B	Coleoptera	Chrysomelidae	18	0	0	16
Monolepta sp. C	Coleoptera	Chrysomelidae	0	0	1	2
Monolepta sp. D	Coleoptera	Chrysomelidae	2	0	0	0
Systates sp. A	Coleoptera	Curculionidae	11	13	1	3
Curculionidae sp. 1	Coleoptera	Curculionidae	2	1	7	8
Curculionidae sp. 2	Coleoptera	Curculionidae	3	1	2	0

Species	Order	Family	*C. sjostedti*	*C. mimosae*	*C. nigriceps*	*T. penzigi*
Curculionidae sp. 4	Coleoptera	Curculionidae	2	1	1	0
Curculionidae sp. 5	Coleoptera	Curculionidae	1	3	0	0
Curculionidae sp. 6	Coleoptera	Curculionidae	0	0	0	2
Curculionidae sp. 7	Coleoptera	Curculionidae	1	0	0	0
Curculionidae sp. 8	Coleoptera	Curculionidae	0	0	0	1
Curculionidae sp. 9	Coleoptera	Curculionidae	0	0	1	0
Myllocerus sp. A	Coleoptera	Curculionidae	612	463	315	860
Neosphrigodes sp. A	Coleoptera	Curculionidae	7	0	0	12
Philonthus sp. A	Coleoptera	Staphylinidae	0	0	1	0
Bruchid sp. 1	Coleoptera	Bruchidae	0	4	10	0
Bruchid sp. 2	Coleoptera	Bruchidae	1	0	0	0
Bruchid sp. 3	Coleoptera	Bruchidae	0	0	0	2
Bruchid sp. 4	Coleoptera	Bruchidae	0	0	0	2
Anthicidae sp. A	Coleoptera	Anthicidae	411	116	265	70
Anthicidae sp. D	Coleoptera	Anthicidae	1	0	0	0
Aphodius sp. A	Coleoptera	Scarabaeidae	0	0	1	0
Arsinoe sp. A	Coleoptera	Carabidae	0	0	1	0
Carabidae sp. 1	Coleoptera	Carabidae	43	20	9	9
Carabidae sp. 2	Coleoptera	Carabidae	0	0	5	0
Carabidae sp. 3	Coleoptera	Carabidae	2	0	0	1
Scymnus sp. A	Coleoptera	Coccinellidae	2	1	0	0

Species	Order	Family	*C. sjostedti*	*C. mimosae*	*C. nigriceps*	*T. penzigi*
Micraspis sp. A	Coleoptera	Coccinellidae	1	2	0	1
Bostrichidae sp. 1	Coleoptera	Bostrichidae	3	10	1	0
Cleridae sp. 1	Coleoptera	Cleridae	96	98	116	202
Enaretta sp. A	Coleoptera	Cerambycidae	0	17	8	0
Lagria sp. A	Coleoptera	Tenebrionidae	26	11	16	20
Cilnia sp. A	Mantodea	Mantidae	14	0	3	9
Galepsus sp. A	Mantodea	Mantidae	1	8	7	5
Miomantis sp. A	Mantodea	Mantidae	9	5	1	15
Parasphendale sp. A	Mantodea	Mantidae	31	13	13	45
Popa sp. A	Mantodea	Mantidae	5	4	2	1
Mantidae sp. F	Mantodea	Mantidae	1	0	1	0
Mantidae sp. G	Mantodea	Mantidae	1	0	0	0
Mantidae sp. H	Mantodea	Mantidae	1	0	0	0
Mantidae sp. J	Mantodea	Mantidae	2	2	0	2
Mantidae sp. K	Mantodea	Mantidae	1	0	0	0
Mantidae sp. L	Mantodea	Mantidae	0	0	0	1
Mantidae sp. P	Mantodea	Mantidae	0	1	0	0
Miridae sp. 1	Hemiptera	Miridae	17	118	353	107
Miridae sp. 2	Hemiptera	Miridae	56	15	3	72
Miridae sp. 3	Hemiptera	Miridae	2	5	13	25
Hemiptera sp. 5	Hemiptera		4	0	0	2

Species	Order	Family	*C. sjostedti*	*C. mimosae*	*C. nigriceps*	*T. penzigi*
Hemiptera sp. 11	Hemiptera		3	0	0	3
Pentatomidae sp. 1	Hemiptera	Pentatomidae	1	7	8	0
Aeliomorpha? *simulans*	Hemiptera	Pentatomidae	1	1	2	1
Aeliomorpha senegalensis	Hemiptera	Pentatomidae	1	1	1	2
Anygrus ochreatus	Hemiptera	Meenoplidae	1	0	0	0
Clonaria sp.	Phasmatodea	Diapheromeridae	17	50	97	66
Derocalymma sp. A	Blattodea	Polyphagidae	7	0	0	3
Cyrtotria sp. A	Blattodea	Blattidae	32	0	3	2
Periplaneta sp. 1	Blattodea	Blattidae	366	212	704	91
Camponotus sp.	Hymenoptera	Formicidae	713	264	77	164
Pheidole crassinoda	Hymenoptera	Formicidae	0	0	2	0
Polyrhachis viscosa	Hymenoptera	Formicidae	4	6	2	0
Technomyrmex sp. A	Hymenoptera	Formicidae	0	0	0	9

Table 5.3. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect orders abundance data collected using beating and mist-blowing to test the effect of block location on insect communities.

	beating					mist-blowing				
Variable	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5
Blattodea	**0.508**	-0.164	0.202	0.428	-0.622	**-0.438**	**0.418**	0.044	0.426	0.066
Coleoptera	-0.084	**0.577**	-0.237	0.583	-0.110	**-0.452**	-0.060	-0.177	-0.464	-0.566
Hemiptera	**0.432**	**0.467**	-0.056	-0.298	-0.120	**-0.590**	0.199	-0.092	-0.078	-0.051
Hymenoptera	**0.390**	**0.477**	0.196	-0.065	0.467	0.084	0.179	-0.738	-0.396	0.467
Mantodea	**-0.481**	0.204	0.368	0.408	0.130	**0.342**	**0.340**	0.345	-0.519	-0.275
Orthoptera	0.140	-0.102	0.802	0.040	0.148	0.185	**0.796**	-0.006	0.079	-0.063
Phasmatodea	**-0.381**	**0.377**	0.289	-0.464	-0.574	**-0.312**	0.015	0.543	-0.406	0.611
Eigenvalues	2.48	2.02	1.36	0.55	0.35	2.60	1.27	1.18	1.02	0.58
% Variation	35.5	28.9	19.4	7.9	4.9	37.1	18.1	16.9	14.6	8.2
Cum.% Variation	35.5	64.4	83.8	91.6	96.6	37.1	55.2	72.1	86.7	94.9

Table 5.4. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect families' abundance data collected using beating to test the effect of block location on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	**0.349**	0.023	0.191	-0.006	0.072
Anthicidae	0.142	-0.028	-0.035	0.492	0.315
Diapheromeridae	**-0.348**	-0.084	-0.199	0.011	-0.068
Blattidae	0.225	**0.317**	0.008	-0.053	-0.225
Buprestidae	0.027	-0.235	0.264	0.221	-0.369
Carabidae	0.215	0.051	-0.382	0.240	-0.168
Chrysomelidae	-0.136	-0.013	-0.459	0.243	-0.068
Cleridae	0.154	0.167	0.133	0.348	-0.257
Curculionidae	**-0.302**	0.158	0.037	0.139	0.135
Formicidae	-0.094	**0.393**	0.025	0.067	0.332
Gryllidae	-0.226	0.232	0.133	-0.188	-0.280
Mantidae	-0.269	-0.179	0.100	0.158	0.134
Miridae	-0.034	**0.372**	-0.150	0.147	0.275
Polyphagidae	0.089	-0.024	0.385	0.162	-0.143
Tenebrionidae	**0.332**	-0.152	-0.166	-0.051	0.067
Bostrichidae	0.265	-0.126	0.083	0.225	0.183
Bruchidae	0.050	-0.193	-0.097	-0.330	0.036
Cerambycidae	**-0.324**	0.100	0.122	0.257	-0.098
Coccinellidae	0.198	0.268	0.080	0.071	-0.047
Gryllacrididae	0.089	-0.133	-0.442	0.066	-0.231
Pamphagidae	0.012	**-0.343**	0.121	-0.034	0.407
Pentatomidae	0.172	**0.326**	-0.060	-0.312	0.121
Eigenvalues	5.88	4.62	3.17	2.76	1.67
% Variation	26.7	21.0	14.4	12.5	7.6
Cum. % Variation	27.7	47.7	62.1	74.7	82.3

Table 5.5. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect families' abundance data collected using mist-blowing to test the effect of block location on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	0.057	0.147	-0.288	0.212	0.312
Anthicidae	-0.275	-0.162	0.196	-0.207	-0.027
Diapheromeridae	0.113	-0.271	0.171	0.375	0.042
Blattidae	-0.213	-0.188	-0.255	0.310	0.162
Buprestidae	0.123	-0.175	-0.166	-0.285	0.074
Chrysomelidae	0.122	**-0.321**	-0.076	-0.174	-0.267
Cleridae	-0.289	-0.110	0.013	-0.095	0.274
Curculionidae	0.047	**-0.387**	-0.173	-0.070	-0.169
Formicidae	-0.021	-0.013	-0.051	-0.077	-0.573
Gryllidae	0.161	-0.003	-0.382	0.041	-0.232
Mantidae	**0.303**	0.125	-0.025	0.148	-0.094
Miridae	-0.174	**-0.362**	-0.154	0.096	-0.003
Bostrichidae	-0.182	0.061	-0.256	-0.234	-0.043
Bruchidae	-0.271	-0.046	-0.123	0.210	-0.406
Carabidae	-0.174	-0.192	-0.340	0.159	0.108
Cerambycidae	**0.356**	-0.162	0.047	0.006	-0.024
Coccinellidae	0.045	0.237	-0.171	0.351	-0.202
Gryllacrididae	**0.319**	0.013	0.004	-0.090	-0.084
Meenoplidae	-0.071	0.210	0.321	0.104	-0.155
Pamphagidae	0.179	-0.189	0.113	0.299	0.028
Pentatomidae	-0.123	-0.127	0.291	0.388	-0.108
Scarabaeidae	0.245	-0.259	0.095	-0.021	0.119
Staphylinidae	0.245	-0.259	0.095	-0.021	0.119
Tenebrionidae	0.244	0.213	-0.320	0.064	0.106
Eigenvalues	5.60	4.78	3.64	2.47	2.24
% Variation	23.3	19.9	15.2	10.3	9.3
Cum. % Variation	23.3	43.3	58.4	68.7	78.0

Table 5.6. Results of PERMANOVA carried out on principal scores generated using order- and family-level data collected using beating and mist-blowing to test the effect of block location and sampling event. * Significant at $\alpha = 0.05$.

		beating					mist-blowing				
Taxa	Source	df	SS	MS	F	P_{perm}	df	SS	MS	F	P_{perm}
Order	Location	2	8.089	4.045	0.549	0.881	2	9.254	4.627	0.653	0.796
	Residual	9	66.276	7.364			9	63.805	7.089		
	Total	11	74.365				11	73.060			
	Sampling event	3	44.724	14.908	4.024	0.002*	3	42.436	14.145	3.695	0.002*
	Residual	8	29.641	3.705			8	30.624	3.828		
	Total	11	74.365				11	73.060			
Family	Location	2	32.167	16.084	0.867	0.615	2	39.263	19.632	1.060	0.433
	Residual	9	166.914				9	166.754	18.528		
	Total	11	199.081				11	206.017			
	Sampling event	3	117.415	39.138	3.834	0.002*	3	115.158	38.386	3.380	0.002*
	Residual	8	81.666	10.208			8	90.859	11.357		
	Total	11	199.081				11	206.017			

Table 5.7. Results of PERMANOVA t-tests performed using principal scores generated using order- and family-level data collected using beating and mist-blowing to test the effect of block location and sampling events on insect communities. * Significant at $\alpha = 0.05$.

		beating		mist-blowing	
Taxa	Sampling events	t	P_{perm}	t	P_{perm}
Order	First vs Second sampling	2.514	0.090	1.484	0.090
	First vs third sampling	2.304	0.140	2.745	0.140
	First vs fourth sampling	2.106	0.150	1.529	0.150
	Second vs third sampling	1.673	0.100	2.277	0.100
	Second vs fourth sampling	2.046	0.050	1.520	0.050
	Third vs fourth sampling	1.582	0.120	2.274	0.120
Family	First vs Second sampling	2.693	0.090	1.817	0.090
	First vs third sampling	1.796	0.140	2.147	0.140
	First vs fourth sampling	1.852	0.150	1.437	0.150
	Second vs third sampling	2.180	0.100	2.768	0.100
	Second vs fourth sampling	2.059	0.050	1.539	0.050
	Third vs fourth sampling	1.302	0.160	1.921	0.120

Table 5.8. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect orders abundance data collected using beating and mist-blowing to test the effect of treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded) on insect communities.

	beating					mist-blowing				
Variable	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5
Blattodea	**0.412**	-0.281	0.455	0.286	0.220	**0.399**	-0.015	-0.485	-0.496	0.536
Coleoptera	0.240	**0.492**	-0.395	0.187	-0.510	**0.517**	0.235	0.024	0.509	-0.188
Hemiptera	**0.580**	0.191	-0.102	0.053	0.462	**0.614**	0.049	0.041	0.037	-0.042
Hymenoptera	**0.496**	**0.357**	0.074	-0.259	-0.017	-0.090	**0.613**	-0.252	0.408	0.376
Mantodea	**-0.352**	**0.523**	0.078	-0.396	0.520	-0.186	**-0.545**	-0.222	0.552	0.446
Orthoptera	0.065	0.156	0.699	-0.369	-0.451	-0.073	-0.078	-0.801	0.052	-0.578
Phasmatodea	-0.250	**0.466**	0.355	0.721	0.061	**0.385**	**-0.514**	0.087	0.144	-0.043
Eigenvalues	1.89	1.61	1.42	0.61	0.53	2.20	1.63	1.24	0.75	0.54
% Variation	27.0	23.0	20.3	8.7	7.6	31.5	23.3	17.7	10.7	7.7
Cum. % Variation	27.0	49.9	70.3	79.0	86.6	31.5	54.8	72.4	83.2	90.8

Table 5.9. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect families' abundance data collected using beating to test the effect of treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded) on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	**-0.327**	0.048	-0.050	0.140	-0.224
Anthicidae	-0.215	0.060	0.473	0.131	-0.008
Diapheromeridae	**0.377**	-0.129	-0.047	0.098	0.116
Blattidae	-0.112	**0.347**	-0.287	0.133	0.195
Bostrichidae	-0.265	-0.139	0.106	0.436	0.067
Bruchidae	-0.116	-0.191	0.063	-0.448	-0.298
Buprestidae	-0.053	-0.125	0.063	0.396	-0.179
Carabidae	-0.245	0.089	0.416	-0.123	0.199
Cerambycidae	0.276	0.154	0.200	0.122	-0.179
Chrysomelidae	0.128	0.038	0.353	0.110	0.292
Cleridae	-0.200	0.262	0.101	0.216	-0.289
Coccinellidae	-0.190	0.253	-0.179	-0.091	-0.073
Curculionidae	0.291	0.244	0.186	-0.066	-0.192
Formicidae	0.061	**0.340**	0.129	-0.072	-0.114
Gryllacrididae	0.053	-0.072	0.036	-0.033	0.455
Gryllidae	**0.323**	0.170	-0.193	0.135	-0.167
Mantidae	0.194	-0.128	0.252	-0.076	-0.188
Miridae	-0.018	**0.386**	0.282	-0.232	0.062
Pamphagidae	-0.069	**-0.305**	0.072	-0.142	-0.403
Pentatomidae	-0.146	**0.304**	-0.196	-0.297	0.022
Polyphagidae	-0.141	0.153	-0.110	0.244	-0.134
Tenebrionidae	**-0.311**	-0.190	-0.041	-0.186	0.151
Eigenvalues	3.61	3.09	2.32	1.80	1.73
% Variation	16.4	14.0	10.6	8.2	7.9
Cum. % Variation	16.4	30.5	41.0	49.2	57.0

Table 5.10. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect families' abundance data collected using mist-blowing to test the effect of treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded) on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	0.076	0.069	0.442	0.105	0.211
Anthicidae	**-0.335**	-0.189	-0.112	-0.140	-0.033
Diapheromeridae	-0.074	**0.390**	-0.064	0.301	0.173
Blattidae	-0.202	0.109	0.338	0.022	0.011
Bostrichidae	-0.076	-0.171	0.141	-0.263	-0.135
Bruchidae	-0.251	0.045	0.263	0.128	-0.018
Buprestidae	0.070	0.177	-0.076	-0.038	-0.238
Carabidae	**-0.303**	0.058	0.332	-0.097	0.215
Cerambycidae	0.074	**0.401**	-0.162	0.125	0.009
Chrysomelidae	-0.142	**0.310**	-0.134	-0.225	-0.283
Cleridae	**-0.323**	-0.154	0.022	-0.050	0.180
Coccinellidae	0.207	0.031	0.129	0.106	-0.081
Curculionidae	-0.273	**0.349**	-0.032	-0.120	-0.294
Formicidae	-0.046	-0.137	0.027	-0.201	-0.397
Gryllacrididae	0.081	0.083	-0.011	-0.444	0.142
Gryllidae	0.116	0.244	0.405	-0.182	-0.263
Mantidae	**0.314**	0.226	0.043	0.044	0.040
Meenoplidae	0.058	-0.195	-0.158	-0.039	-0.043
Miridae	**-0.382**	0.207	0.063	0.019	-0.026
Pamphagidae	-0.007	0.161	-0.112	-0.249	0.484
Pentatomidae	-0.196	-0.053	0.017	0.394	0.032
Scarabaeidae	0.009	0.152	-0.182	0.249	-0.162
Staphylinidae	-0.012	0.237	-0.216	-0.346	0.291
Tenebrionidae	**0.338**	0.028	0.344	-0.124	0.012
Eigenvalues	3.95	3.14	2.26	2.06	1.86
% Variation	16.4	13.1	9.4	8.6	7.7
Cum. % Variation	16.4	29.5	38.9	47.5	55.2

Table 5.11. Results of PERMANOVA carried out using principal scores generated using order- and family-level data collected using beating and mist-blowing to test the effect of treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded) and sampling events on insect communities. * Significant at $\alpha = 0.05$.

		beating					mist-blowing				
Taxa	Source	df	SS	MS	F	P_{perm}	df	SS	MS	F	P_{perm}
Order	Treatment	2	12.290	6.145	2.885	0.019*	2	10.635	5.317	2.084	0.095
	Sampling event	3	70.949	23.650	4.891	0.001*	3	83.675	27.892	5.929	0.001*
	Treatment*Sampling event	6	12.779	2.130	0.441	0.996	6	15.309	2.552	0.542	0.967
	Residual	24	116.038	4.835			24	112.906	4.704		
	Total	35	212.056				35	222.524			
Family	Treatment	2	28.619	14.310	2.429	0.044*	2	16.885	8.443	1.557	0.178
	Sampling event	3	163.844	54.615	6.201	0.001*	3	184.874	61.625	6.437	0.001*
	Treatment* Sampling event	6	35.350	5.892	0.669	0.898	6	32.529	5.421	0.566	0.974
	Residual	24	211.392	8.808			24	229.756	9.573		
	Total	35	439.205				35	464.043			

Table 5.12. Results of PERMANOVA t-tests performed using principal scores generated using order- and family-level data collected using beating to test the effect of treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded) and sampling events on insect communities. * Significant at $\alpha = 0.05$.

Taxa	Treatment	t	P_{perm}
Order	C*E	0.922	0.630
	C*0	0.926	0.550
	E*0	0.601	0.720
Family	C*E	0.932	0.620
	C*0	0.769	0.680
	E*0	0.728	0.630

Table 5.13. Results of PERMANOVA t-tests performed using principal scores generated using order- and family-level data collected using beating and mist-blowing to test the effect of treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded) and sampling events on insect communities. * Significant at $\alpha = 0.05$.

		beating		mist-blowing	
Taxa	Sampling session	t	P_{perm}	t	P_{perm}
Order	First vs second sampling	2.605	0.010*	1.909	0.010*
	First vs third sampling	2.103	0.010*	3.429	0.010*
	First fourth sampling	2.620	0.010*	2.292	0.010*
	Second vs third sampling	1.836	0.030*	2.219	0.010*
	Second vs fourth sampling	2.570	0.010*	1.994	0.010*
	Third vs fourth sampling	2.026	0.010*	3.344	0.010*
Family	First vs second sampling	4.026	0.010*	2.743	0.010*
	First vs third sampling	2.121	0.010*	3.314	0.010*
	First vs fourth sampling	2.478	0.010*	2.516	0.010*
	Second vs third sampling	2.511	0.010*	2.745	0.010*
	Second vs fourth sampling	2.625	0.010*	2.055	0.010*
	Third vs fourth sampling	1.489	0.070	2.880	0.010*

Table 5.14. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect orders abundance data collected using beating and mist-blowing to test the effect of ant species (*C. sjostedti*, *C. mimosae*, *C. nigriceps* and *T. penzigi*) on insect communities.

	beating					mist-blowing				
Variable	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5
Blattodea	**0.380**	**-0.478**	0.042	-0.278	-0.460	0.245	**-0.380**	0.563	-0.678	0.111
Coleoptera	**-0.545**	0.056	-0.098	0.387	-0.554	0.226	**0.656**	0.231	-0.139	-0.536
Hemiptera	-0.265	-0.052	0.859	0.010	0.291	**0.433**	0.297	0.346	0.257	0.302
Hymenoptera	-0.244	**-0.590**	0.148	0.308	-0.194	**-0.424**	-0.071	0.479	0.152	-0.497
Mantodea	**-0.542**	0.194	-0.281	-0.297	0.097	**-0.393**	**0.336**	-0.306	-0.631	0.032
Orthoptera	**-0.350**	-0.282	0.002	-0.735	-0.055	**-0.357**	**0.442**	0.321	0.019	0.600
Phasmatodea	0.110	**0.548**	0.388	-0.223	-0.589	**0.490**	0.155	-0.289	-0.184	-0.043
Eigenvalues	2.20	1.92	1.06	0.96	0.48	3.11	1.42	1.12	0.53	0.47
% Variation	31.5	27.5	15.2	13.7	6.9	44.5	20.3	16.0	7.6	6.7
Cum. % Variation	31.5	59.0	74.1	87.9	94.7	44.5	64.8	80.8	88.4	95.2

Table 5.15. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect families' abundance data collected using beating to test the effect of ant species (*C. sjostedti*, *C. mimosae*, *C. nigriceps* and *T. penzigi*) on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	-0.166	**0.384**	-0.134	-0.102	-0.025
Anthicidae	**-0.417**	0.039	0.166	0.049	0.013
Diapheromeridae	**0.310**	-0.249	-0.090	-0.238	0.000
Blattidae	-0.083	-0.170	0.329	0.281	-0.140
Bostrichidae	-0.014	-0.144	-0.425	0.331	0.038
Bruchidae	-0.061	-0.199	0.070	-0.326	-0.293
Buprestidae	0.118	0.143	-0.450	0.093	0.178
Carabidae	-0.281	0.086	0.124	0.235	0.149
Cerambycidae	0.266	-0.063	0.034	0.066	0.398
Chrysomelidae	0.125	-0.197	0.068	0.050	0.161
Cleridae	0.054	0.297	-0.064	-0.303	-0.309
Coccinellidae	0.106	-0.034	-0.164	0.264	-0.110
Curculionidae	0.291	0.201	0.217	-0.064	0.214
Formicidae	-0.028	0.258	0.360	0.308	0.029
Gryllacrididae	-0.177	**-0.313**	0.037	-0.367	-0.024
Gryllidae	0.201	0.279	0.221	0.026	-0.102
Mantidae	0.032	**0.327**	-0.176	-0.213	0.092
Miridae	0.257	0.096	0.263	-0.048	-0.212
Pamphagidae	-0.208	-0.197	0.186	-0.214	0.372
Pentatomidae	0.153	-0.054	-0.017	0.188	-0.481
Polyphagidae	-0.241	**0.313**	-0.031	-0.179	0.133
Tenebrionidae	**-0.387**	-0.026	-0.188	0.093	-0.219
Eigenvalues	4.47	3.68	2.82	2.37	1.91
% Variation	20.3	16.7	12.8	10.8	8.7
Cum. % Variation	20.3	37.0	49.9	60.6	69.3

Table 5.16. Eigenvectors and Eigenvalues of the correlation matrix generated by PCA from log-transformed insect families' abundance data collected by mist-blowing to test the effect of ant species (*C. sjostedti*, *C. mimosae*, *C. nigriceps* and *T. penzigi*) on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	**-0.352**	0.083	0.016	0.076	-0.198
Anthicidae	0.217	0.263	0.187	-0.134	0.020
Diapheromeridae	**0.329**	-0.189	-0.106	-0.030	-0.134
Blattidae	0.253	0.117	0.297	-0.137	0.196
Buprestidae	-0.144	-0.226	0.212	-0.011	-0.269
Carabidae	0.042	0.083	0.386	0.174	-0.046
Chrysomelidae	-0.009	**-0.422**	0.065	0.046	0.068
Cleridae	0.145	0.161	0.070	0.325	-0.330
Curculionidae	0.022	**-0.324**	0.117	0.324	-0.043
Formicidae	-0.289	0.097	0.203	-0.080	0.048
Gryllidae	-0.169	-0.240	0.315	0.169	0.102
Mantidae	**-0.317**	-0.120	-0.115	-0.111	0.076
Miridae	0.221	-0.149	0.223	0.316	-0.226
Bostrichidae	-0.072	0.126	0.290	0.010	0.299
Bruchidae	0.230	0.109	0.035	0.181	0.429
Cerambycidae	0.090	-0.266	-0.018	-0.277	0.259
Coccinellidae	-0.296	0.105	0.215	-0.121	0.056
Gryllacrididae	-0.211	-0.157	-0.296	0.210	0.180
Meenoplidae	-0.091	0.210	-0.069	-0.351	-0.270
Pamphagidae	0.012	-0.041	-0.388	0.219	0.228
Pentatomidae	0.288	0.083	-0.039	-0.073	0.151
Scarabaeidae	0.105	**-0.330**	0.106	-0.330	-0.050
Staphylinidae	0.105	**-0.330**	0.106	-0.330	-0.050
Tenebrionidae	-0.201	-0.012	0.216	0.066	0.340
Eigenvalues	5.52	4.23	3.25	2.63	1.83
% Variation	23.0	17.6	13.5	10.9	7.6
Cum. % Variation	23.0	40.6	54.2	65.1	72.7

Table 5.17. Results of PERMANOVA performed using principal scores generated using order- and family-level data collected using beating to determine the effect of acacia-ants (*C. sjostedti*, *C. mimosae*, *C. nigriceps* and *T. penzigi*) and sampling events on insect communities. * Significant at $\alpha = 0.05$.

		beating					mist-blowing				
Taxa	Source	df	SS	MS	F	P_{perm}	df	SS	MS	F	P_{perm}
Order	Ants species	3	45.321	15.107	3.347	0.001*	3	43.861	14.620	3.130	0.003*
	Residual	12	54.158	4.513			12	56.061	4.672		
	Total	15	99.479				15	99.921			
	Sampling event	3	39.902	13.301	2.679	0.003*	3	42.731	14.244	2.989	0.001*
	Residual	12	59.576	4.965			12	57.190	4.766		
	Total	15	99.479				15	99.921			
Family	Ant species	3	111.105	37.035	3.780	0.001*	3	89.590	29.863	2.081	0.012*
	Residual	12	117.585	9.799			12	172.181	14.349		
	Total	15	228.688				15	261.771			
	Sampling event	3	85.332	28.444	2.381	0.004*	3	116.902	38.967	3.228	0.001*
	Residual	12	143.356	11.946			12	144.870	12.073		
	Total	15	228.688				15	261.771			

Table 5.18. Results of PERMANOVA t-tests performed using principal scores generated using order- and family-level data collected using beating and mist-blowing to test the effect of acacia-ants (*C. sjostedti*, *C. mimosae*, *C. nigriceps* and *T. penzigi*) on insect communities. * Significant at $\alpha = 0.05$.

		beating		mist-blowing	
Taxa	Ant species	t	P_{perm}	t	P_{perm}
Order	*C. sjostedti*C. mimosae*	1.766	0.070	1.427	0.200
	*C. sjostedti*C. nigriceps*	2.102	0.040*	2.866	0.040*
	*C. sjostedti*T. penzigi*	1.923	0.030*	1.458	0.100
	*C. mimosae*C. nigriceps*	1.028	0.380	1.665	0.070
	*C. mimosae*T. penzigi*	1.654	0.070	1.089	0.290
	*C. nigriceps*T. penzigi*	2.159	0.050	2.081	0.050
Family	*C. sjostedti*C. mimosae*	2.121	0.070	1.033	0.650
	*C. sjostedti*C. nigriceps*	2.280	0.040*	1.703	0.040*
	*C. sjostedti*T. penzigi*	2.004	0.030*	1.503	0.030*
	*C. mimosae*C. nigriceps*	1.609	0.090	0.920	0.630
	*C. mimosae*T. penzigi*	1.766	0.050	1.291	0.120
	*C. nigriceps*T. penzigi*	1.941	0.050	1.889	0.050

Table 5.19. Results of PERMANOVA t-tests performed using principal component scores generated using order- and family-level data collected using beating and mist-blowing to test the effect of acacia-ants (*C. sjostedti*, *C. mimosae*, *C. nigriceps* and *T. penzigi*) and sampling events on insect communities. * Significant at $\alpha = 0.05$.

		beating		Mist-blowing	
Taxa	Sampling session	t	P_{perm}	t	P_{perm}
Order	First vs Second sampling	1.820	0.080	1.871	0.070
	First vs third sampling	1.733	0.040*	2.148	0.040*
	First vs fourth sampling	1.943	0.030*	1.543	0.140
	Second vs third sampling	1.247	0.260	1.350	0.250
	Second vs fourth sampling	1.732	0.090	1.551	0.080
	Third vs fourth sampling	1.377	0.180	1.820	0.060
Family	First vs Second sampling	2.158	0.070	1.829	0.070
	First vs third sampling	1.267	0.290	2.016	0.040*
	First vs fourth sampling	1.743	0.030*	1.737	0.030*
	Second vs third sampling	1.349	0.150	1.974	0.040*
	Second vs fourth sampling	1.674	0.110	1.414	0.130
	Third vs fourth sampling	0.831	0.700	1.858	0.060

Table 5.20. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect orders abundance data collected by beating to test the effect of hemipteran-tending ants (*C. sjostedti* and *C. mimosae*) and non-tending ants (*C. nigriceps* and *T. penzigi*) on insect communities.

	Beating					Mist-blowing				
Variable	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5
Blattodea	**-0.540**	0.212	0.306	-0.120	-0.175	**0.386**	**0.462**	0.295	0.235	0.454
Coleoptera	**0.478**	0.220	-0.403	-0.311	0.158	**0.310**	0.038	-0.589	-0.565	-0.093
Hemiptera	0.000	**0.576**	-0.199	0.555	-0.515	**0.480**	**0.317**	-0.138	-0.179	0.300
Hymenoptera	-0.272	0.260	-0.683	-0.227	0.082	**-0.449**	0.233	0.056	-0.534	0.231
Mantodea	**0.493**	0.084	0.243	-0.403	-0.602	**-0.311**	-0.128	-0.622	0.382	0.595
Orthoptera	-0.201	**0.560**	0.286	-0.500	0.181	-0.145	**0.675**	-0.350	0.340	-0.510
Phasmatodea	**0.352**	**0.431**	0.313	0.342	0.527	**0.453**	**-0.397**	-0.185	0.217	-0.166
Eigenvalues	2.63	1.82	1.34	0.78	0.38	3.35	1.39	1.20	0.80	0.21
% Variation	37.5	26.1	19.1	11.1	5.4	47.8	19.9	17.1	11.4	3.0
Cum. % Variation	37.5	63.6	82.7	93.8	99.2	47.8	67.7	84.8	96.2	99.2

Table 5.21. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect families abundance data collected by beating to test the effect of hemipteran-tending ants (*C. sjostedti* and *C. mimosae*) and non-tending ants (*C. nigriceps* and *T. penzigi*) on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	-0.292	-0.266	0.111	-0.012	0.021
Anthicidae	**-0.306**	0.097	-0.035	0.229	0.203
Diapheromeridae	**0.335**	0.046	0.203	-0.149	-0.050
Blattidae	-0.033	**-0.421**	-0.073	-0.164	0.075
Bostrichidae	-0.281	0.105	-0.236	-0.059	-0.088
Bruchidae	-0.039	-0.071	0.437	-0.087	0.056
Buprestidae	-0.035	0.259	-0.311	-0.254	0.031
Carabidae	-0.274	0.012	-0.089	0.280	0.380
Cerambycidae	0.233	0.134	-0.248	0.035	-0.029
Chrysomelidae	0.128	0.237	0.171	0.197	-0.080
Cleridae	0.176	-0.180	0.118	-0.391	0.238
Coccinellidae	-0.004	-0.274	-0.221	-0.191	-0.471
Curculionidae	**0.322**	0.110	-0.064	0.291	-0.030
Formicidae	0.043	-0.169	-0.281	0.383	-0.091
Gryllacrididae	-0.074	0.031	0.413	-0.109	-0.232
Gryllidae	0.266	-0.192	-0.218	-0.141	0.257
Mantidae	0.143	**0.301**	0.083	-0.133	0.462
Miridae	0.254	-0.166	0.104	0.294	0.124
Pamphagidae	-0.132	**0.326**	0.213	0.030	-0.123
Pentatomidae	0.003	**-0.363**	0.106	0.116	0.308
Polyphagidae	-0.159	0.188	-0.217	-0.366	0.199
Tenebrionidae	**-0.374**	-0.078	0.112	-0.004	0.030
Eigenvalues	6.43	4.97	4.39	2.93	1.30
% Variation	29.2	22.6	20.0	13.3	5.9
Cum. % Variation	29.2	51.8	71.8	85.1	91.0

Table 5.22. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect families abundance data collected by mist-blowing to test the effect of hemipteran-tending ants (*C. sjostedti* and *C. mimosae*) and non-tending ants (*C. nigriceps* and *T. penzigi*) on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	-0.177	0.259	0.181	-0.166	-0.265
Anthicidae	-0.278	-0.179	-0.099	0.107	0.309
Diapheromeridae	0.200	**-0.341**	0.017	-0.124	-0.080
Blattidae	-0.144	-0.214	0.320	0.001	-0.174
Bostrichidae	-0.138	0.224	0.154	0.087	-0.233
Bruchidae	-0.157	-0.089	0.224	0.442	0.086
Buprestidae	0.052	0.147	0.141	-0.269	0.490
Carabidae	-0.171	0.053	0.278	0.003	0.108
Cerambycidae	**0.309**	0.207	-0.105	0.120	0.110
Chrysomelidae	**0.328**	-0.019	0.211	0.011	-0.004
Cleridae	-0.220	-0.243	0.186	-0.122	-0.237
Coccinellidae	-0.102	**0.344**	0.058	-0.169	-0.202
Curculionidae	0.192	-0.076	0.319	0.032	0.315
Formicidae	-0.120	**0.312**	-0.091	0.191	0.267
Gryllacrididae	0.266	0.012	-0.060	0.380	0.103
Gryllidae	0.105	0.222	0.347	-0.063	0.145
Mantidae	0.236	0.252	-0.052	0.084	-0.199
Meenoplidae	-0.112	0.067	-0.365	-0.312	0.039
Miridae	-0.002	-0.227	0.364	-0.142	0.107
Pamphagidae	0.232	-0.193	-0.048	0.308	-0.259
Pentatomidae	-0.120	-0.232	-0.193	0.155	-0.003
Scarabaeidae	**0.334**	-0.065	0.019	-0.239	-0.080
Staphylinidae	**0.334**	-0.065	0.019	-0.239	-0.080
Tenebrionidae	0.037	0.254	0.218	0.265	-0.203
Eigenvalues	6.53	5.78	4.44	2.74	2.26
% Variation	27.2	24.1	18.5	11.4	9.4
Cum. % Variation	27.2	51.3	69.8	81.2	90.7

Table 5.23. Results of PERMANOVA carried out using principal scores generated using order- and family-level data collected using beating and mist-blowing to test the effect of hemipteran-tending ants (*C. sjostedti*, *C. mimosae*) and non-tending ants (*C. nigriceps* and *T. penzigi*) and sampling events on insect communities. * Significant at $\alpha = 0.05$.

		beating					mist-blowing				
Taxa	Source	df	SS	MS	F	P_{perm}	df	SS	MS	F	P_{perm}
Order	Guild	1	9.107	9.107	1.383	0.276	1	12.001	12.001	1.967	0.132
	Residual	6	39.508	6.585			6	36.609	6.101		
	Total	7	48.615				7	48.609			
	Sampling event	3	34.569	11.523	3.282	0.014*	3	32.073	10.691	2.586	0.024*
	Residual	4	14.046	3.511			4	16.536	4.134		
	Total	7	48.615				7	48.609			
Family	Guild	1	29.748	29.748	1.616	0.071	1	27.187	27.187	1.304	0.279
	Residual	6	110.455	18.409			6	125.107	20.851		
	Total	7	140.203				7	152.294			
	Sampling event	3	90.924	30.308	2.460	0.019*	3	97.980	32.660	2.405	0.014*
	Residual	4	49.279	12.320			4	54.315	13.579		
	Total	7	140.203				7	152.294			

Table 5.24. Results of PERMANOVA t-tests performed using principal scores generated using order- and family-level data collected using beating and mist-blowing to test the effect of hemipteran-tending ants (*C. sjostedti*, *C. mimosae*) and non-tending ants (*C. nigriceps* and *T. penzigi*) and sampling events on insect communities. * Significant at $\alpha = 0.05$.

		beating		mist-blowing	
Taxa	Sampling session	t	P_{perm}	t	P perm
Order	First vs Second sampling	1.882	0.290	1.479	0.290
	First vs third sampling	1.772	0.470	2.430	0.470
	First vs fourth sampling	2.252	0.260	1.668	0.260
	Second vs third sampling	1.417	0.330	1.414	0.330
	Second vs fourth sampling	1.960	0.270	1.251	0.720
	Third vs fourth sampling	1.608	0.340	1.703	0.340
Family	First vs Second sampling	1.748	0.290	1.272	0.290
	First vs third sampling	1.243	0.690	1.476	0.470
	First vs fourth sampling	1.566	0.260	1.510	0.260
	Second vs third sampling	1.623	0.330	1.740	0.330
	Second vs fourth sampling	1.833	0.270	1.476	0.270
	Third vs fourth sampling	1.393	0.340	2.173	0.340

Table 5.25. Results of PERMANOVA to test the effects of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on total number of taxa (S) at order level * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	13.764	6.882	0.723	0.593
Treatment	2	17.931	8.965	0.478	0.776
Ant species	3	91.264	30.421	4.134	0.001*
Location*treatment	4	35.924	8.981	1.599	0.129
Location*Ant species	6	57.153	9.526	1.295	0.149
Treatment*Ant species	6	112.486	18.748	2.548	0.001*
Location*treatment*Ant species	12	67.410	5.618	0.763	0.900
Residual	252	1854.250	7.358		
Total	287	2250.181			

Table 5.26. Results of PERMANOVA t-tests to test the effects of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on total number of taxa (S) at order level * Significant at $\alpha = 0.05$.

Ant species	t	P_{perm}
*C. sjostedti***C. mimosae*	1.327	0.140
*C. sjostedti***C. nigriceps*	2.275	0.010*
*C. sjostedti***T. penzigi*	3.222	0.010*
*C. mimosae***C. nigriceps*	1.041	0.380
*C. mimosae***T. penzigi*	1.983	0.020*
*C. nigriceps***T. penzigi*	1.249	0.160

Table 5.27. Results of PERMANOVA t-tests to test the effects of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on total number of taxa (S) at order level. * Significant at $\alpha = 0.05$.

Treatments	Ant species	t	P_{perm}
C	*C. sjostedti*C. mimosae*	0.936	0.490
	*C. sjostedti*C. nigriceps*	1.235	0.180
	*C. sjostedti*T. penzigi*	3.380	0.010*
	*C. mimosae*C. nigriceps*	0.511	0.900
	*C. mimosae*T. penzigi*	2.495	0.010*
	*C. nigriceps*T. penzigi*	2.241	0.020*
E	*C. sjostedti*C. mimosae*	1.849	0.010*
	*C. sjostedti*C. nigriceps*	3.484	0.010*
	*C. sjostedti*T. penzigi*	2.484	0.010*
	*C. mimosae*C. nigriceps*	1.507	0.110
	*C. mimosae*T. penzigi*	0.891	0.500
	*C. nigriceps*T. penzigi*	1.380	0.130
0	*C. sjostedti*C. mimosae*	0.548	0.860
	*C. sjostedti*C. nigriceps*	0.575	0.910
	*C. sjostedti*T. penzigi*	0.340	0.360
	*C. mimosae*C. nigriceps*	0.936	0.430
	*C. mimosae*T. penzigi*	0.992	0.390
	*C. nigriceps*T. penzigi*	1.474	0.080

Table 5.28. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on Pielou's evenness index (J') at order level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	1.773	0.887	1.872	0.118
Treatment	2	1.392	0.696	0.791	0.588
Ant species	3	4.684	1.561	2.595	0.005*
Location*Treatment	4	2.704	0.676	1.190	0.285
Location*Ant species	6	2.842	0.474	0.787	0.779
Treatment*Ant species	6	5.277	0.880	1.462	0.065
Location*Treatment*Ant species	12	6.815	0.568	0.944	0.565
Residual	252	151.581	0.602		
Total	287	177.068			

Table 5.29. Results of PERMANOVA t-tests to test the effects of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on Pielou's evenness index (J') at order level. * Significant at α = 0.05.

Ant species	t	P_{perm}
*C. sjostedti***C. mimosae*	0.930	0.500
*C. sjostedti***C. nigriceps*	1.896	0.020*
*C. sjostedti***T. penzigi*	2.331	0.010*
*C. mimosae***C. nigriceps*	1.051	0.330
*C. mimosae***T. penzigi*	1.671	0.060
*C. nigriceps***T. penzigi*	1.307	0.120

Table 5.30. Results of PERMANOVA to test the effects of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ant species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on the Shannon-Wiener diversity index (H') at order level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	2.262	1.131	1.139	0.378
Treatment	2	2.771	1.386	0.720	0.586
Ant species	3	10.926	3.642	3.768	0.001*
Location*Treatment	4	3.543	0.886	1.130	0.324
Location*Ant species	6	5.961	0.994	1.028	0.419
Treatment*Ant species	6	11.551	1.925	1.992	0.001*
Location*Treatment*Ant species	12	9.406	0.784	0.811	0.809
Residual	252	243.545	0.966		
Total	287	289.964			

Table 5.31. Results of PERMANOVA t-tests to test the effects of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on the Shannon-Wiener diversity index (H') at order level. * Significant at $\alpha = 0.05$.

Ant species	t	P_{perm}
*C. sjostedti*C. mimosae*	1.193	0.230
*C. sjostedti*C. nigriceps*	2.106	0.010*
*C. sjostedti*T. penzigi*	3.062	0.010*
*C. mimosae*C. nigriceps*	0.991	0.470
*C. mimosae*T. penzigi*	1.967	0.030*
*C. nigriceps*T. penzigi*	1.458	0.080

Table 5.32. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ant species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on the Shannon-Wiener diversity index (H') at order level. * Significant at $\alpha = 0.05$.

Treatments	Ant species	t	P_{perm}
C	*C. sjostedti*C. mimosae*	1.350	0.140
	*C. sjostedti*C. nigriceps*	1.435	0.080
	*C. sjostedti*T. penzigi*	3.388	0.010*
	*C. mimosae*C. nigriceps*	0.226	1.000
	*C. mimosae*T. penzigi*	1.896	0.030*
	*C. nigriceps*T. penzigi*	1.940	0.020*
E	*C. sjostedti*C. mimosae*	1.556	0.060
	*C. sjostedti*C. nigriceps*	2.836	0.010*
	*C. sjostedti*T. penzigi*	2.257	0.010*
	*C. mimosae*C. nigriceps*	1.520	0.080
	*C. mimosae*T. penzigi*	1.001	0.410
	*C. nigriceps*T. penzigi*	1.391	0.120
0	*C. sjostedti*C. mimosae*	0.446	0.980
	*C. sjostedti*C. nigriceps*	0.683	0.840
	*C. sjostedti*T. penzigi*	0.989	0.340
	*C. mimosae*C. nigriceps*	0.828	0.660
	*C. mimosae*T. penzigi*	1.281	0.160
	*C. nigriceps*T. penzigi*	1.615	0.010*

Table 5.33. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on Margalef's richness index (d) at order level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	4.085	2.042	1.374	0.240
Treatment	2	4.716	2.358	0.983	0.487
Ant species	3	8.682	2.894	1.695	0.047*
Location*Treatment	4	7.215	1.804	1.178	0.289
Location*Ant species	6	8.916	1.486	0.870	0.669
Treatment*Ant species	6	14.398	2.400	1.405	0.080
Location*Treatment*Ant species	12	18.367	1.531	0.896	0.672
Residual	252	430.304	1.708		
Total	287	496.683			

Table 5.34. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on Margalef's richness index (d) at order level. * Significant at $\alpha = 0.05$.

Ant species	t	P_{perm}
*C. sjostedti*C. mimosae*	0.846	0.670
*C. sjostedti*C. nigriceps*	1.438	0.120
*C. sjostedti*T. penzigi*	1.878	0.020*
*C. mimosae*C. nigriceps*	0.761	0.710
*C. mimosae*T. penzigi*	1.361	0.160
*C. nigriceps*T. penzigi*	1.179	0.270

Table 5.35. Results of PERMANOVA to test the effects of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on total number of taxa (S) at family level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	23.500	11.750	0.534	0.745
Treatment	2	40.792	20.396	0.520	0.732
Ant species	3	198.188	66.063	4.319	0.001*
Location*Treatment	4	67.417	16.854	1.334	0.260
Location*Ant species	6	132.083	22.014	1.439	0.079
Treatment*Ant species	6	235.458	39.243	2.566	0.001*
Location*Treatment*Ant species	12	151.583	12.632	0.826	0.783
Residual	252	3854.750	15.297		
Total	287	4703.771			

Table 5.36. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on total number of taxa (S) at family level. * Significant at $\alpha = 0.05$.

Ant species	t	P_{perm}
*C. sjostedti*C. mimosae*	1.533	0.050
*C. sjostedti*C. nigriceps*	2.305	0.010*
*C. sjostedti*T. penzigi*	3.254	0.010*
*C. mimosae*C. nigriceps*	1.173	0.270
*C. mimosae*T. penzigi*	2.016	0.020*
*C. nigriceps*T. penzigi*	1.163	0.300

Table 5.37. Results of PERMANOVA t-tests to test the effects of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on total number of taxa (S) at family level. * Significant at $\alpha = 0.05$.

Treatments	Ant species	t	P_{perm}
C	*C. sjostedti*C. mimosae*	0.760	0.770
	*C. sjostedti*C. nigriceps*	1.261	0.140
	*C. sjostedti*T. penzigi*	3.380	0.010*
	*C. mimosae*C. nigriceps*	0.934	0.460
	*C. mimosae*T. penzigi*	2.903	0.010*
	*C. nigriceps*T. penzigi*	2.279	0.010*
E	*C. sjostedti*C. mimosae*	1.831	0.010*
	*C. sjostedti*C. nigriceps*	3.189	0.010*
	*C. sjostedti*T. penzigi*	1.964	0.030*
	*C. mimosae*C. nigriceps*	1.369	0.110
	*C. mimosae*T. penzigi*	0.724	0.670
	*C. nigriceps*T. penzigi*	1.307	0.210
0	*C. sjostedti*C. mimosae*	0.941	0.460
	*C. sjostedti*C. nigriceps*	0.305	0.990
	*C. sjostedti*T. penzigi*	0.986	0.400
	*C. mimosae*C. nigriceps*	1.200	0.260
	*C. mimosae*T. penzigi*	1.049	0.380
	*C. nigriceps*T. penzigi*	1.209	0.260

Table 5.38. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on Pielou's evenness index (J') at family level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	1.831	0.915	1.887	0.097
Treatment	2	0.926	0.463	0.524	0.838
Ants species	3	3.205	1.068	1.820	0.045*
Location*Treatment	4	2.843	0.711	1.129	0.343
Location*Ant species	6	2.910	0.485	0.826	0.738
Treatment*Ant species	6	5.295	0.883	1.504	0.045*
Location*Treatment*Ant species	12	7.553	0.629	1.072	0.313
Residual	252	147.896	0.587		
Total	287	172.459			

Table 5.39. Results of PERMANOVA t-tests to test the effects of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on Pielou's evenness index (J') at family level. * Significant at $\alpha = 0.05$.

Ant species	t	P_{perm}
*C. sjostedti***C. mimosae*	0.540	0.920
*C. sjostedti***C. nigriceps*	1.539	0.080
*C. sjostedti***T. penzigi*	1.925	0.020*
*C. mimosae***C. nigriceps*	1.075	0.340
*C. mimosae***T. penzigi*	1.550	0.080
*C. nigriceps***T. penzigi*	0.971	0.450

Table 5.40. Results of PERMANOVA t-tests to test the effects of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on Pielou's evenness index (J') at family level. * Significant at α = 0.05.

Treatments	Ant species	t	P_{perm}
C	*C. sjostedti*C. mimosae*	1.038	0.480
	*C. sjostedti*C. nigriceps*	1.245	0.140
	*C. sjostedti*T. penzigi*	2.459	0.020*
	*C. mimosae*C. nigriceps*	0.508	0.960
	*C. mimosae*T. penzigi*	1.672	0.040*
	*C. nigriceps*T. penzigi*	1.400	0.120
E	*C. sjostedti*C. mimosae*	1.074	0.390
	*C. sjostedti*C. nigriceps*	1.632	0.060
	*C. sjostedti*T. penzigi*	1.640	0.050
	*C. mimosae*C. nigriceps*	1.451	0.110
	*C. mimosae*T. penzigi*	1.002	0.430
	*C. nigriceps*T. penzigi*	1.556	0.050
0	*C. sjostedti*C. mimosae*	0.287	1.000
	*C. sjostedti*C. nigriceps*	0.716	0.750
	*C. sjostedti*T. penzigi*	1.024	0.250
	*C. mimosae*C. nigriceps*	0.675	0.820
	*C. mimosae*T. penzigi*	0.990	0.430
	*C. nigriceps*T. penzigi*	1.313	0.170

Table 5.41. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on the Shannon-Wiener diversity index (H') at family level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	2.888	1.444	0.985	0.452
Treatment	2	2.927	1.464	0.483	0.792
Ant species	3	15.173	5.058	3.609	0.001*
Location*Treatment	4	5.558	1.390	1.069	0.386
Location*Ant species	6	8.801	1.467	1.047	0.399
Treatment*Ant species	6	18.170	3.028	2.161	0.003*
Location*Treatment*Ant species	12	15.600	1.300	0.928	0.580
Residual	252	353.200	1.402		
Total	287	422.317			

Table 5.42. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on the Shannon-Wiener diversity index (H') at family level. * Significant at $\alpha = 0.05$.

Ant species	t	P_{perm}
*C. sjostedti*C. mimosae*	1.113	0.270
*C. sjostedti*C. nigriceps*	2.103	0.010*
*C. sjostedti*T. penzigi*	3.003	0.010*
*C. mimosae*C. nigriceps*	1.142	0.310
*C. mimosae*T. penzigi*	1.985	0.020*
*C. nigriceps*T. penzigi*	1.145	0.320

Table 5.43. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on the Shannon-Wiener diversity index (J') at family level * Significant at $\alpha = 0.05$.

Treatments	Ant species	t	P_{perm}
C	*C. sjostedti*C. mimosae*	0.961	0.550
	*C. sjostedti*C. nigriceps*	1.430	0.070
	*C. sjostedti*T. penzigi*	3.406	0.010*
	*C. mimosae*C. nigriceps*	0.625	0.860
	*C. mimosae*T. penzigi*	2.609	0.010*
	*C. nigriceps*T. penzigi*	2.170	0.010*
E	*C. sjostedti*C. mimosae*	1.556	0.050
	*C. sjostedti*C. nigriceps*	2.725	0.010*
	*C. sjostedti*T. penzigi*	1.878	0.020*
	*C. mimosae*C. nigriceps*	1.515	0.070
	*C. mimosae*T. penzigi*	0.817	0.610
	*C. nigriceps*T. penzigi*	1.453	0.070
0	*C. sjostedti*C. mimosae*	0.587	0.830
	*C. sjostedti*C. nigriceps*	0.365	0.990
	*C. sjostedti*T. penzigi*	1.045	0.310
	*C. mimosae*C. nigriceps*	0.878	0.520
	*C. mimosae*T. penzigi*	1.014	0.400
	*C. nigriceps*T. penzigi*	1.337	0.140

Table 5.44. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on Margalef's richness index (d) at family level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	5.795	2.898	1.254	0.328
Treatment	2	4.674	2.337	0.489	0.849
Ant species	3	15.299	5.100	1.959	0.026*
Location*Treatment	4	10.112	2.528	0.998	0.468
Location*Ant species	6	13.869	2.312	0.888	0.627
Treatment*Ant species	6	28.652	4.775	1.834	0.004*
Location*Treatment*Ant species	12	30.387	2.532	0.973	0.507
Residual	252	656.020	2.603		
Total	287	764.809			

Table 5.45. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on Margalef's richness index (d) at family level. * Significant at $\alpha = 0.05$.

Ant species	t	P_{perm}
*C. sjostedti***C. mimosae*	0.899	0.530
*C. sjostedti***C. nigriceps*	1.499	0.110
*C. sjostedti***T. penzigi*	2.087	0.010*
*C. mimosae***C. nigriceps*	1.031	0.380
*C. mimosae***T. penzigi*	1.527	0.090
*C. nigriceps***T. penzigi*	0.910	0.560

Table 5.46. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on Margalef's richness index (d) at family level. * Significant at $\alpha = 0.05$.

Treatments	Ant species	t	P_{perm}
C	*C. sjostedti*C. mimosae*	0.822	0.700
	*C. sjostedti*C. nigriceps*	1.209	0.160
	*C. sjostedti*T. penzigi*	2.774	0.010*
	*C. mimosae*C. nigriceps*	0.608	0.850
	*C. mimosae*T. penzigi*	2.178	0.010*
	*C. nigriceps*T. penzigi*	1.776	0.030*
E	*C. sjostedti*C. mimosae*	1.388	0.080
	*C. sjostedti*C. nigriceps*	1.808	0.030*
	*C. sjostedti*T. penzigi*	1.458	0.090
	*C. mimosae*C. nigriceps*	1.122	0.270
	*C. mimosae*T. penzigi*	0.918	0.510
	*C. nigriceps*T. penzigi*	1.576	0.070
0	*C. sjostedti*C. mimosae*	1.023	0.300
	*C. sjostedti*C. nigriceps*	0.590	0.830
	*C. sjostedti*T. penzigi*	1.016	0.360
	*C. mimosae*C. nigriceps*	0.937	0.450
	*C. mimosae*T. penzigi*	1.022	0.390
	*C. nigriceps*T. penzigi*	1.118	0.300

Table 5.47. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on total number of taxa (S) at species level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	36.264	18.132	0.639	0.698
Treatment	2	40.785	20.392	0.446	0.788
Ants species	3	220.389	73.463	3.723	0.001*
Location*Treatment	4	78.194	19.549	1.325	0.253
Location*Ant species	6	170.153	28.359	1.437	0.076
Treatment*Ant species	6	274.465	45.744	2.318	0.002*
Location*Treatment*Ant species	12	177.056	14.755	0.748	0.906
Residual	252	4972.750	19.733		
Total	287	5970.056			

Table 5.48. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on total number of taxa (S) at species level. * Significant at α = 0.05.

Ant species	t	P perm
*C. sjostedti*C. mimosae*	1.552	0.070
*C. sjostedti*C. nigriceps*	2.167	0.010*
*C. sjostedti*T. penzigi*	3.014	0.010*
*C. mimosae*C. nigriceps*	1.090	0.360
*C. mimosae*T. penzigi*	1.837	0.030*
*C. nigriceps*T. penzigi*	1.108	0.340

Table 5.49. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on total number of taxa (S) at species level. * Significant at α = 0.05.

Treatments	Ant species	t	P_{perm}
C	*C. sjostedti*C. mimosae*	0.851	0.610
	*C. sjostedti*C. nigriceps*	1.176	0.210
	*C. sjostedti*T. penzigi*	3.185	0.010*
	*C. mimosae*C. nigriceps*	0.938	0.490
	*C. mimosae*T. penzigi*	2.608	0.010*
	*C. nigriceps*T. penzigi*	2.230	0.010*
E	*C. sjostedti*C. mimosae*	1.722	0.010*
	*C. sjostedti*C. nigriceps*	3.008	0.010*
	*C. sjostedti*T. penzigi*	1.997	0.020*
	*C. mimosae*C. nigriceps*	1.210	0.200
	*C. mimosae*T. penzigi*	0.859	0.500
	*C. nigriceps*T. penzigi*	1.125	0.320
0	*C. sjostedti*C. mimosae*	0.699	0.740
	*C. sjostedti*C. nigriceps*	0.472	0.960
	*C. sjostedti*T. penzigi*	1.045	0.370
	*C. mimosae*C. nigriceps*	1.087	0.330
	*C. mimosae*T. penzigi*	1.050	0.390
	*C. nigriceps*T. penzigi*	1.362	0.160

Table 5.50. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on Pielou's evenness index (J') at species level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	1.663	0.831	2.122	0.070
Treatment	2	1.018	0.509	0.645	0.725
Ant species	3	2.595	0.865	1.479	0.125
Location*Treatment	4	2.693	0.673	1.153	0.309
Location*Ants species	6	2.351	0.392	0.670	0.915
Treatment*Ant species	6	4.734	0.789	1.349	0.116
Location*Treatment*Ant species	12	7.005	0.584	0.998	0.449
Residual	252	147.385	0.585		
Total	287	169.443			

Table 5.51. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on the Shannon-Wiener diversity index (H') at species level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	3.410	1.705	1.034	0.424
Treatment	2	3.231	1.616	0.505	0.761
Ant species	3	14.680	4.893	3.134	0.001*
Location*Treatment	4	5.942	1.485	1.134	0.347
Location*Ant species	6	9.895	1.649	1.056	0.387
Treatment*Ant species	6	19.204	3.201	2.050	0.004*
Location*Treatment*Ants species	12	15.716	1.310	0.839	0.764
Residual	252	393.487	1.562		
Total	287	465.564			

Table 5.52. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on the Shannon-Wiener diversity index (H') at species level. * Significant at $\alpha = 0.05$.

Ant species	t	P_{perm}
*C. sjostedti***C. mimosae*	1.138	0.250
*C. sjostedti***C. nigriceps*	2.022	0.010*
*C. sjostedti***T. penzigi*	2.749	0.010*
*C. mimosae***C. nigriceps*	1.092	0.320
*C. mimosae***T. penzigi*	1.843	0.030*
*C. nigriceps***T. penzigi*	1.012	0.460

Table 5.53. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on the Shannon-Wiener diversity index (H') at species level. * Significant at α = 0.05.

Treatments	Ant species	t	P_{perm}
C	*C. sjostedti*C. mimosae*	0.895	0.610
	*C. sjostedti*C. nigriceps*	1.379	0.090
	*C. sjostedti*T. penzigi*	3.237	0.010*
	*C. mimosae*C. nigriceps*	0.625	0.860
	*C. mimosae*T. penzigi*	2.395	0.010*
	*C. nigriceps*T. penzigi*	2.058	0.020*
E	*C. sjostedti*C. mimosae*	1.516	0.060
	*C. sjostedti*C. nigriceps*	2.630	0.010*
	*C. sjostedti*T. penzigi*	1.857	0.020*
	*C. mimosae*C. nigriceps*	1.493	0.090
	*C. mimosae*T. penzigi*	0.956	0.420
	*C. nigriceps*T. penzigi*	1.328	0.150
0	*C. sjostedti*C. mimosae*	0.409	0.970
	*C. sjostedti*C. nigriceps*	0.498	0.960
	*C. sjostedti*T. penzigi*	0.991	0.370
	*C. mimosae*C. nigriceps*	0.731	0.700
	*C. mimosae*T. penzigi*	0.991	0.380
	*C. nigriceps*T. penzigi*	1.456	0.110

Table 5.54. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on Margalef's richness index (d) at species level. * Significant at $\alpha = 0.05$.

Location	df	SS	MS	F	P_{perm}
Location	2	8.154	4.077	1.374	0.275
Treatment	2	6.602	3.301	0.621	0.725
Ant species	3	15.320	5.107	1.635	0.074
Location*Treatment	4	12.418	3.104	1.242	0.284
Location*Ant species	6	17.807	2.968	0.950	0.526
Treatment*Ant species	6	31.915	5.319	1.703	0.016*
Location*Treatment*Ant species	12	30.005	2.500	0.801	0.839
Residual	252	787.179	3.124		
Total	287	909.399			

Table 5.55. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and ants species (*C. mimosae*, *C. nigriceps*, *C. sjostedti* and *T. penzigi*) on Margalef's richness index (d) at species level. * Significant at $\alpha = 0.05$.

Treatments	Ant species	t	P_{perm}
C	*C. sjostedti***C. mimosae*	0.839	0.650
	*C. sjostedti***C. nigriceps*	1.215	0.180
	*C. sjostedti***T. penzigi*	2.682	0.010*
	*C. mimosae***C. nigriceps*	0.609	0.860
	*C. mimosae***T. penzigi*	1.950	0.020*
	*C. nigriceps***T. penzigi*	1.702	0.030*
E	*C. sjostedti***C. mimosae*	1.326	0.160
	*C. sjostedti***C. nigriceps*	1.699	0.050
	*C. sjostedti***T. penzigi*	1.451	0.100
	*C. mimosae***C. nigriceps*	1.038	0.370
	*C. mimosae***T. penzigi*	1.045	0.300
	*C. nigriceps***T. penzigi*	1.330	0.170
0	*C. sjostedti***C. mimosae*	0.671	0.730
	*C. sjostedti***C. nigriceps*	0.520	0.960
	*C. sjostedti***T. penzigi*	0.921	0.460
	*C. mimosae***C. nigriceps*	0.680	0.740
	*C. mimosae***T. penzigi*	1.039	0.410
	*C. nigriceps***T. penzigi*	1.408	0.100

Table 5.56. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds (hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on total number of taxa (S) at order level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	13.764	6.882	0.945	0.590
Treatment	2	17.931	8.965	0.468	0.785
Guild	1	66.056	66.056	8.729	0.001*
Location*Treatment	4	35.924	8.981	1.764	0.180
Location*Guild	2	14.569	7.285	0.963	0.455
Treatment*Guild	2	38.319	19.160	2.532	0.011*
Location*Treatment*Guild	4	20.368	5.092	0.673	0.841
Residual	270	2043.250	7.568		
Total	287	2250.181			

Table 5.57. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds (hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on total number of taxa (S) at order level. * Significant at $\alpha = 0.05$.

Treatment	Guilds	t	P perm
C	Hemipteran-tending ants*non-tending ants	2.595	0.010*
E	Hemipteran-tending ants *non-tending ants	2.601	0.010*
0	Hemipteran-tending ants *non-tending ants	0.660	0.740

Table 5.58. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds (hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on Pielou's evenness index (J') at order level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	1.773	0.887	1.202	0.515
Treatment	2	1.392	0.696	1.327	0.357
Guild	1	3.188	3.188	5.282	0.001*
Location*Treatment	4	2.704	0.676	1.076	0.425
Location*Guild	2	1.475	0.738	1.222	0.276
Treatment*Guild	2	1.049	0.525	0.869	0.546
Location*Treatment*Guild	4	2.513	0.628	1.041	0.415
Residual	270	162.974	0.604		
Total	287	177.068			

Table 5.59. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds (hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on the Shannon-Wiener diversity index (H') at order level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	2.262	1.131	1.131	0.538
Treatment	2	2.771	1.386	0.850	0.535
Guild	1	7.461	7.461	7.575	0.001*
Location*Treatment	4	3.543	0.886	1.297	0.301
Location*Guild	2	2.000	1.000	1.015	0.434
Treatment*Guild	2	3.261	1.630	1.655	0.092
Location*Treatment*Guild	4	2.731	0.683	0.683	0.823
Residual	270	265.936	0.985		
Total	287	289.964			

Table 5.60. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds (hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on Margalef's richness index (d) at order level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	4.085	2.042	1.852	0.237
Treatment	2	4.716	2.358	1.603	0.306
Guild	1	5.165	5.165	3.006	0.012*
Location*Treatment	4	7.215	1.804	1.121	0.382
Location*Guild	2	2.206	1.103	0.642	0.776
Treatment*Guild	2	2.941	1.471	0.856	0.563
Location*Treatment*Guild	4	6.438	1.610	0.837	0.545
Residual	270	463.916	1.718		
Total	287	496.683			

Table 5.61. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds (hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on total number of taxa (S) at family level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	23.500	11.750	0.580	0.688
Treatment	2	40.792	20.396	0.497	0.754
Guild	1	140.285	140.285	8.898	0.001*
Location*Treatment	4	67.417	16.854	1.288	0.367
Location*Guild	2	40.528	20.264	1.285	0.262
Treatment*Guild	2	82.153	41.076	2.605	0.015*
Location*Treatment*Guild	4	52.347	13.087	0.830	0.655
Residual	270	4256.750	15.766		
Total	287	4703.771			

Table 5.62. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds (hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on total number of taxa (S) at family level. * Significant at $\alpha = 0.05$.

Treatment	Guilds	t	P perm
C	Hemipteran-tending ants *non-tending ants	2.871	0.010*
E	Hemipteran-tending ants *non-tending ants	2.146	0.010*
0	Hemipteran-tending ants *non-tending ants	0.816	0.680

Table 5.63. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds (hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on Pielou's evenness index (J') at family level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	1.831	0.915	1.583	0.240
Treatment	2	0.926	0.463	0.695	0.637
Guild	1	2.525	2.525	4.289	0.002*
Location*Treatment	4	2.843	0.711	0.985	0.488
Location*Guild	2	1.156	0.578	0.982	0.434
Treatment*Guild	2	1.332	0.666	1.131	0.348
Location*Treatment*Guild	4	2.886	0.722	1.225	0.238
Residual	270	158.961	0.589		
Total	287	172.459			

Table 5.64. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds (hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on the Shannon-Wiener diversity index (H') at family level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	2.888	1.444	0.865	0.688
Treatment	2	2.927	1.464	0.581	0.681
Guild	1	11.518	11.518	8.061	0.001*
Location*Treatment	4	5.558	1.390	1.056	0.463
Location*Guild	2	3.339	1.669	1.168	0.327
Treatment*Guild	2	5.039	2.519	1.763	0.089
Location*Treatment*Guild	4	5.265	1.316	0.921	0.557
Residual	270	385.782	1.429		
Total	287	422.317			

Table 5.65. Results of PERMANOVA to test the effects of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds (hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on Margalef's richness index (d) at family level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	5.795	2.898	1.016	0.622
Treatment	2	4.674	2.337	0.733	0.617
Guild	1	10.986	10.986	4.171	0.004*
Location*Treatment	4	10.112	2.528	1.002	0.500
Location*Guild	2	5.705	2.853	1.083	0.384
Treatment*Guild	2	6.378	3.189	1.211	0.274
Location*Treatment*Guild	4	10.097	2.524	0.959	0.534
Residual	270	711.060	2.634		
Total	287	764.809			

Table 5.66. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds (hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on total number of taxa (S) at species level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	36.264	18.132	0.782	0.688
Treatment	2	40.785	20.392	0.398	0.814
Guild	1	147.556	147.556	7.316	0.002*
Location*Treatment	4	78.194	19.549	1.078	0.457
Location*Guild	2	46.403	23.201	1.150	0.325
Treatment*Guild	2	102.590	51.295	2.543	0.017*
Location*Treatment*Guild	4	72.514	18.129	0.899	0.559
Residual	270	5445.750	20.169		
Total	287	5970.056			

Table 5.67. Results of PERMANOVA t-tests to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds (hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on total number of taxa (S) at species level. * Significant at $\alpha = 0.05$.

Treatment	Guilds	t	P perm
C	Hemipteran-tending ants*non-tending ants	2.622	0.010*
E	Hemipteran-tending ants*non-tending ants	2.112	0.010*
0	Hemipteran-tending ants*non-tending ants	0.843	0.640

Table 5.68. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds ((hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on Pielou's evenness index (J') at species level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	1.663	0.831	1.611	0.185
Treatment	2	1.018	0.509	0.749	0.579
Guild	1	1.967	1.967	3.384	0.007*
Location*Treatment	4	2.693	0.673	0.973	0.505
Location*Guild	2	1.032	0.516	0.888	0.544
Treatment*Guild	2	1.360	0.680	1.170	0.327
Location*Treatment*Guild	4	2.769	0.692	1.191	0.263
Residual	270	156.942	0.581		
Total	287	169.443			

Table 5.69. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds (hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on the Shannon-Wiener diversity index (H') at species level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	3.410	1.705	1.023	0.635
Treatment	2	3.231	1.616	0.549	0.709
Guild	1	10.994	10.994	6.953	0.001*
Location*Treatment	4	5.942	1.485	1.018	0.477
Location*Guild	2	3.334	1.667	1.054	0.402
Treatment*Guild	2	5.886	2.943	1.861	0.064
Location*Treatment*Guild	4	5.840	1.460	0.923	0.557
Residual	270	426.929	1.581		
Total	287	465.564			

Table 5.70. Results of PERMANOVA to test the effect of locations (North, Central and South), treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded), and guilds (hemipteran-tending ants (*C. mimosae* and *C. sjostedti*) and non-tending ants (*C. nigriceps* and *T. penzigi*)) on Margalef's richness (d) at species level. * Significant at $\alpha = 0.05$.

Source	df	SS	MS	F	P_{perm}
Location	2	8.154	4.077	1.256	0.330
Treatment	2	6.601	3.301	0.808	0.530
Guild	1	10.599	10.599	3.384	0.008*
Location*Treatment	4	12.418	3.104	1.109	0.399
Location*Guild	2	6.492	3.246	1.036	0.417
Treatment*Guild	2	8.173	4.087	1.305	0.240
Location*Treatment*Guild	4	11.202	2.801	0.894	0.603
Residual	270	845.759	3.132		
Total	287	909.399			

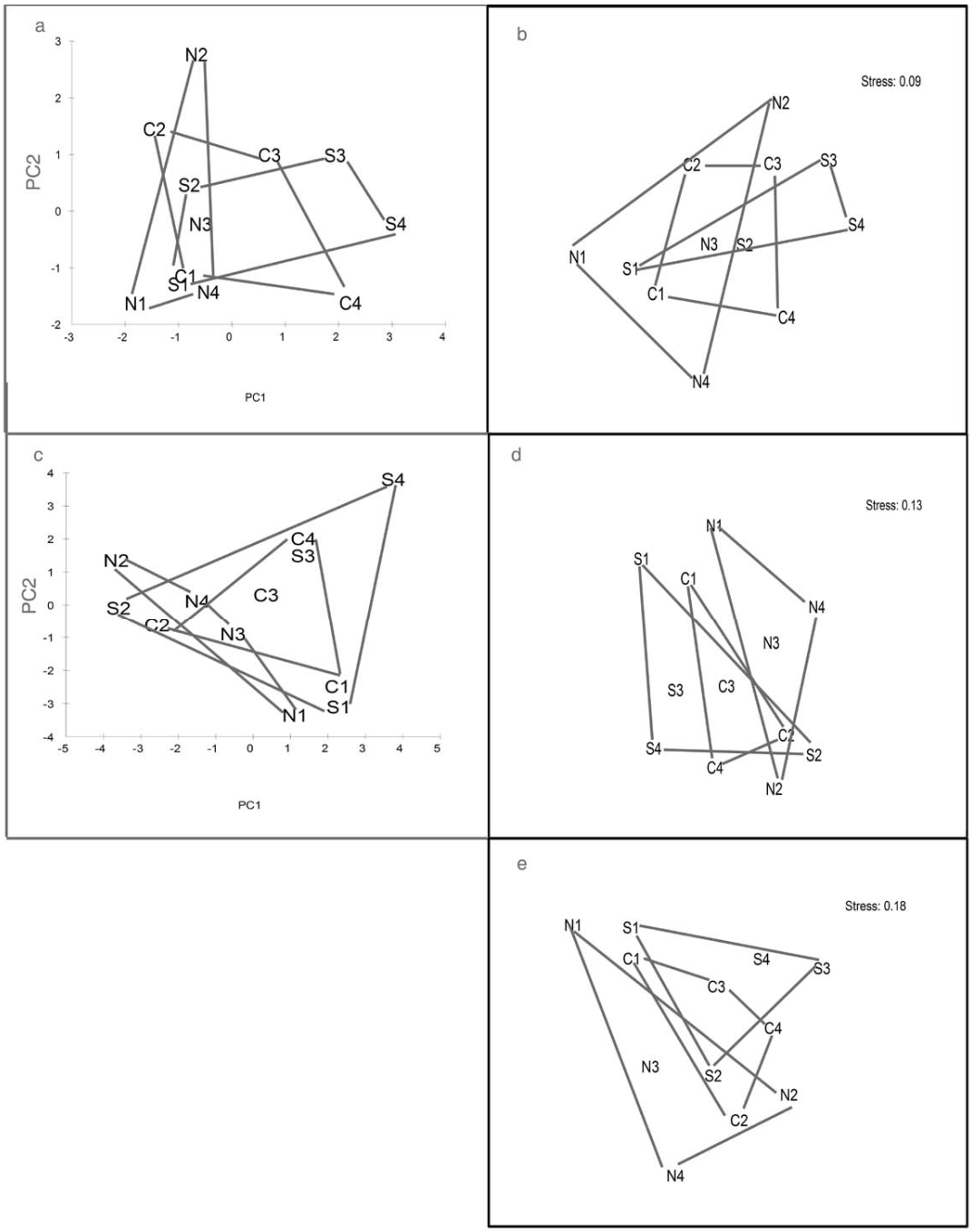


Figure 5.1. Ordinations of log-transformed abundances of insects collected using beating to test the effect of block location (N = north, C = central and S = south) on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. Digits represent the sampling sessions.

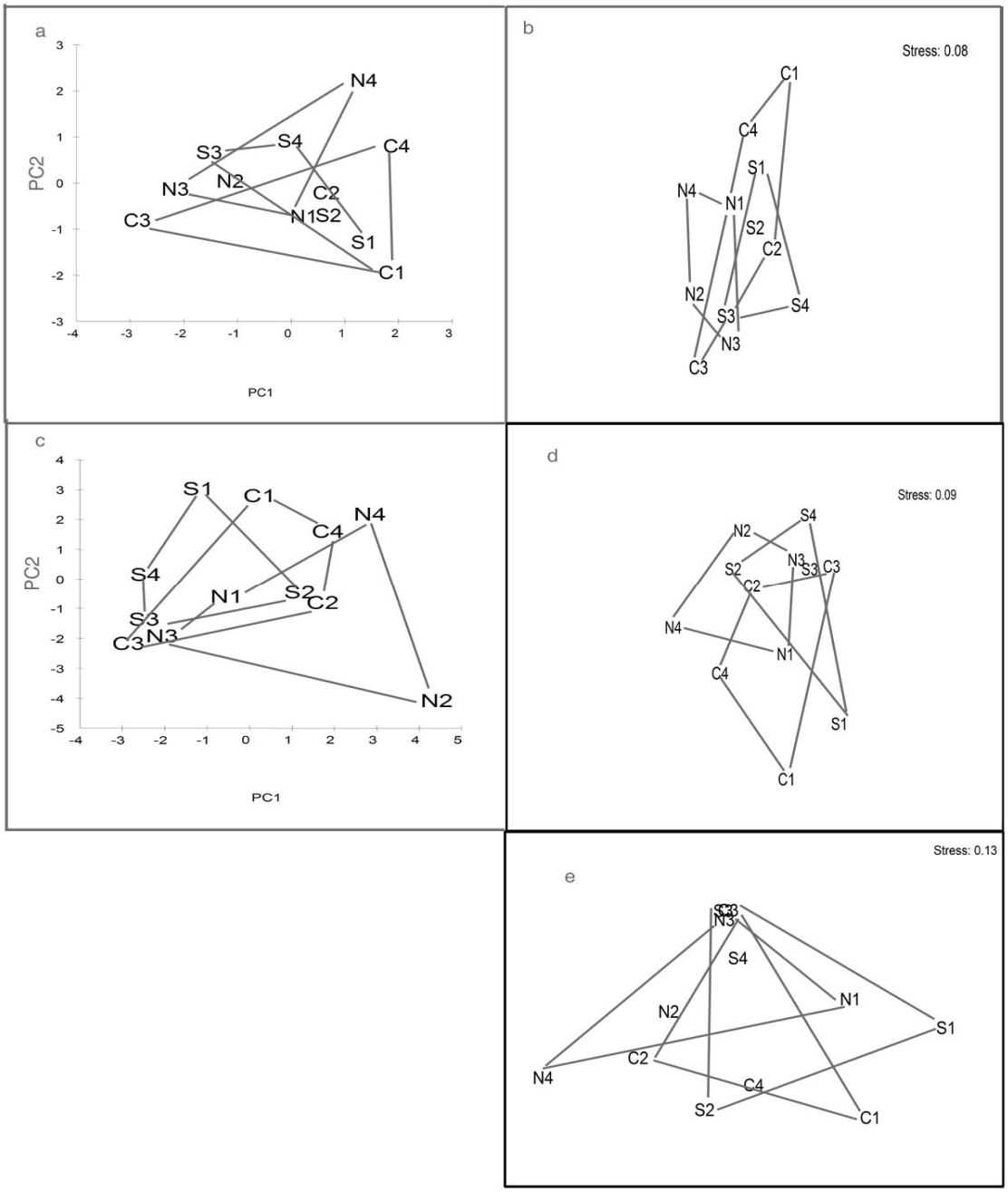


Figure 5.2. Ordinations of log-transformed abundances of insects collected using mist-blowing to test the effect of block location (N = north, C = central and S = south) on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. Digits represent the sampling sessions.

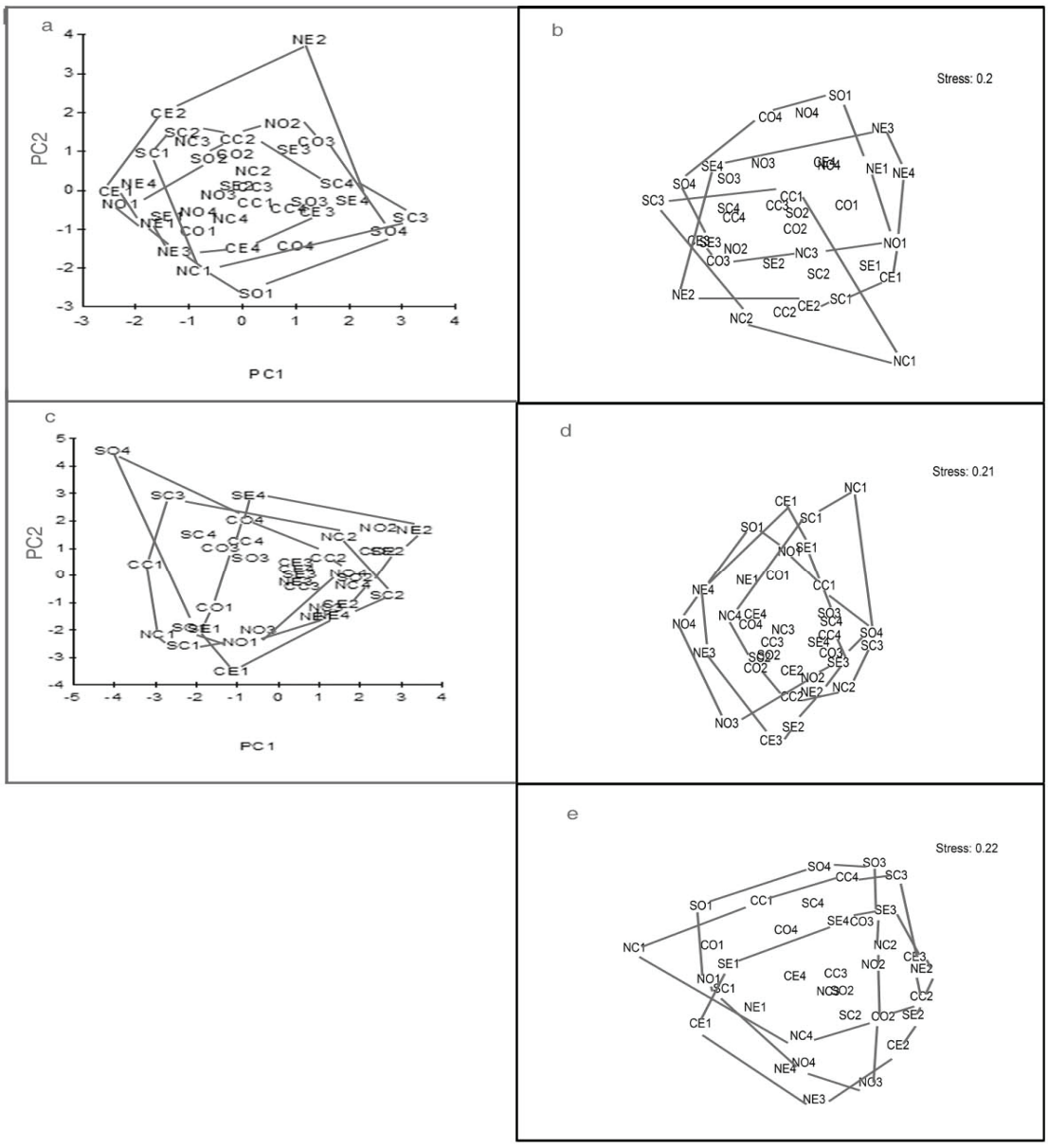


Figure 5.3. Ordinations of log-transformed abundances of insects collected using beating to establish the effect of treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded) on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. The first letters in all cases represent blocks (N = north, C = central and S = south) and the second letters represent treatments. The digits represent the sampling sessions.

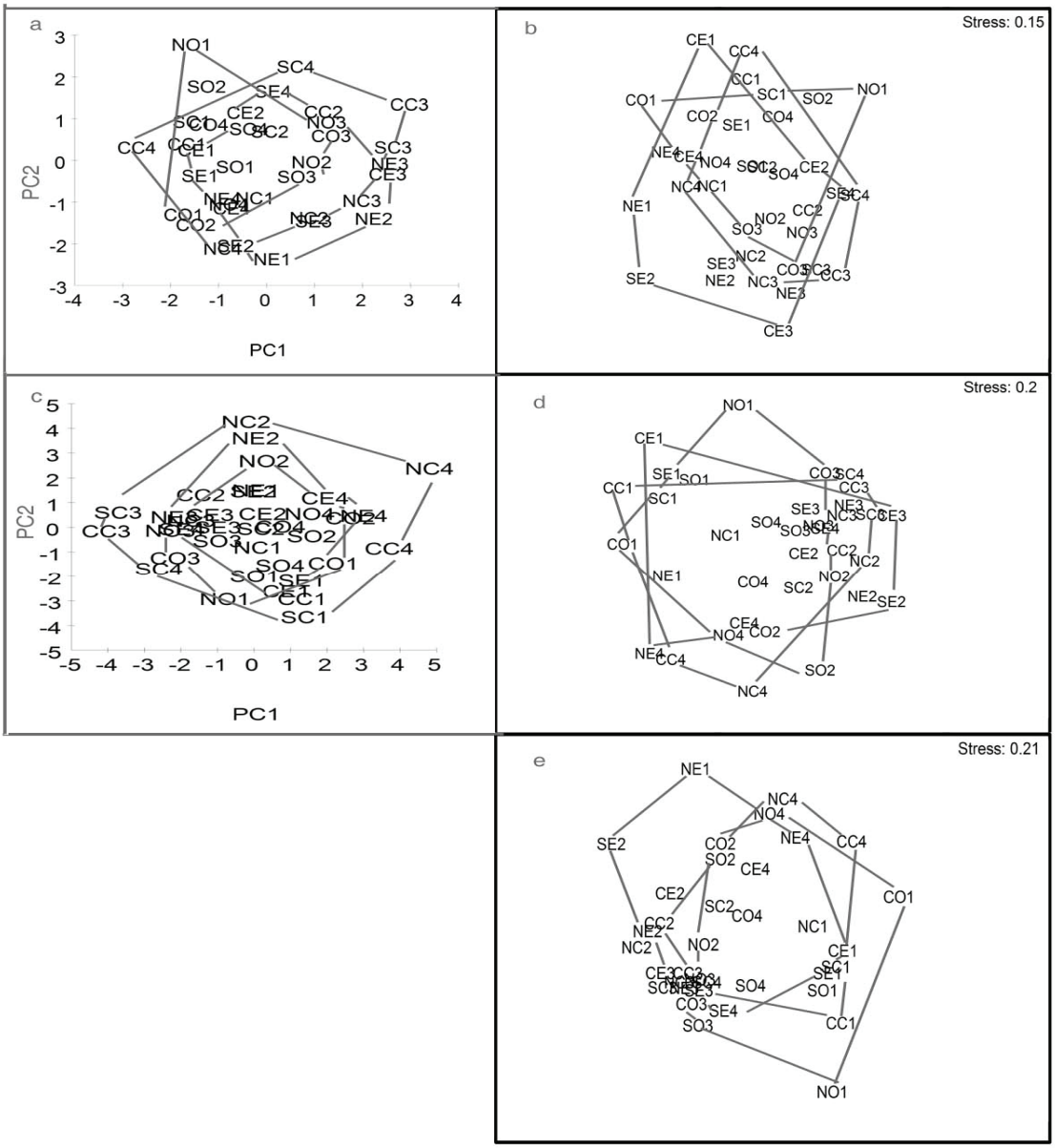


Figure 5.4. Ordinations of log-transformed abundances of insects collected using mist-blowing to establish the effect of treatments C (cattle present), E (all herbivores and cattle present) and 0 (control all herbivores and cattle excluded) on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. The first letters in all cases represent blocks (N = north, C = central and S = south) and the second letters represent treatments. The digits represent the sampling sessions.

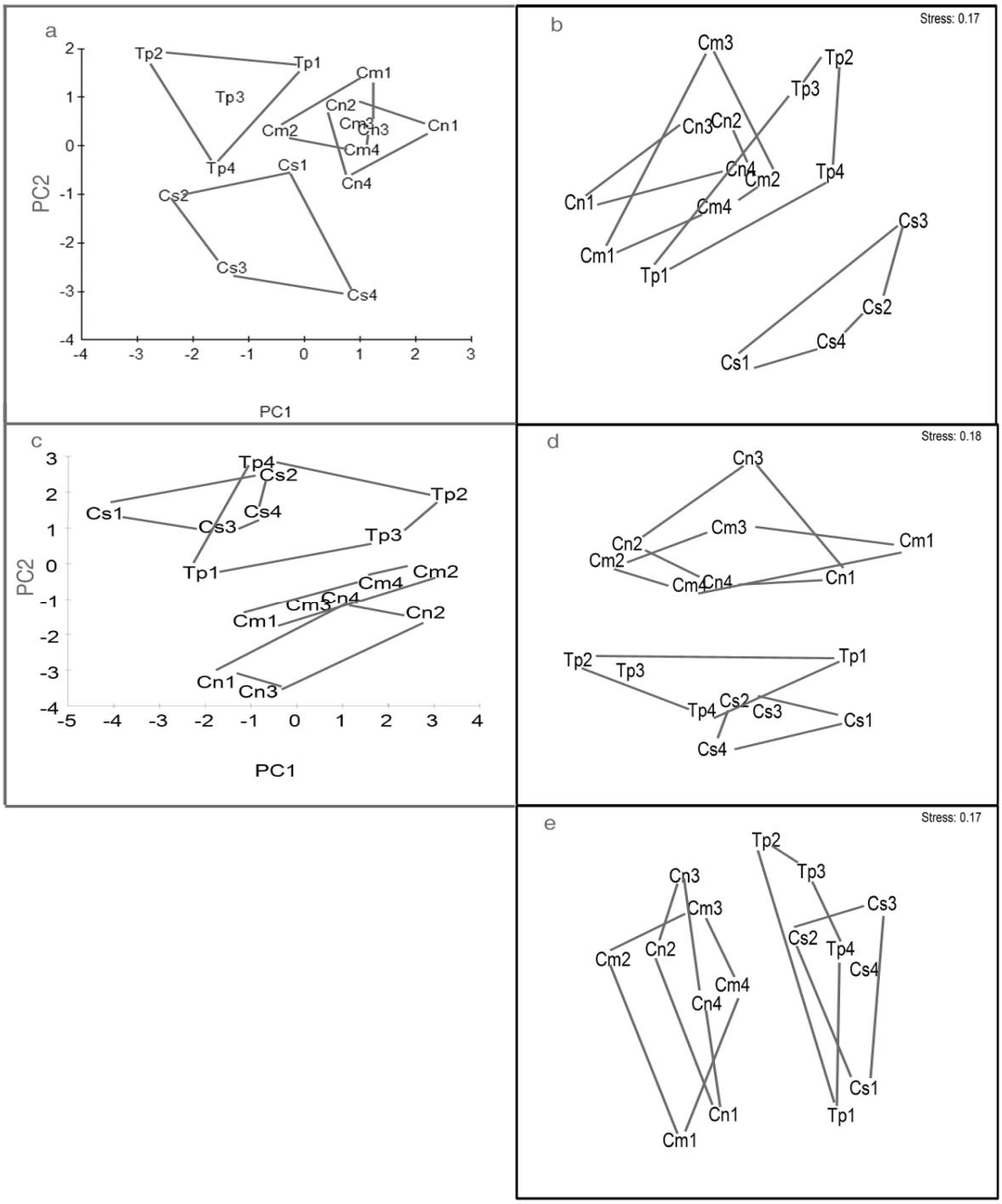


Figure 5.5. Ordinations of log-transformed abundances of insects collected using beating to establish the effect of acacia-ants (Cs- *C. sjostedti*, Cm - *C. mimosae*, Cn - *C. nigriceps* and Tp - *T. penzigi*) on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. Digits represent the sampling sessions.

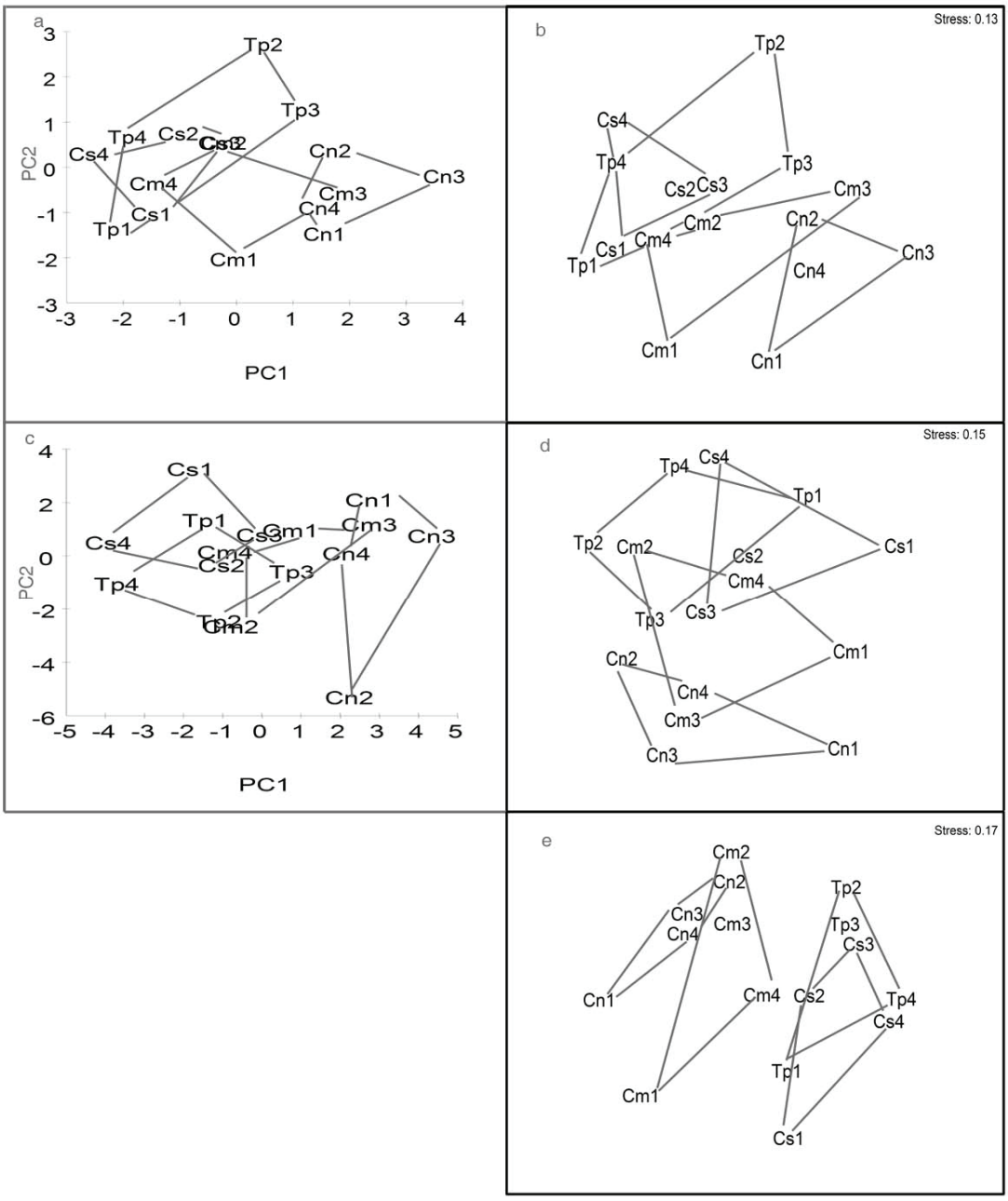


Figure 5.6. Ordinations of log-transformed abundances of insects collected using mist-blowing to establish the effect of acacia-ants (Cs- *C. sjostedti*, Cm - *C. mimosae*, Cn - *C. nigriceps* and Tp - *T. penzigi*) on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. Digits represent the sampling sessions.

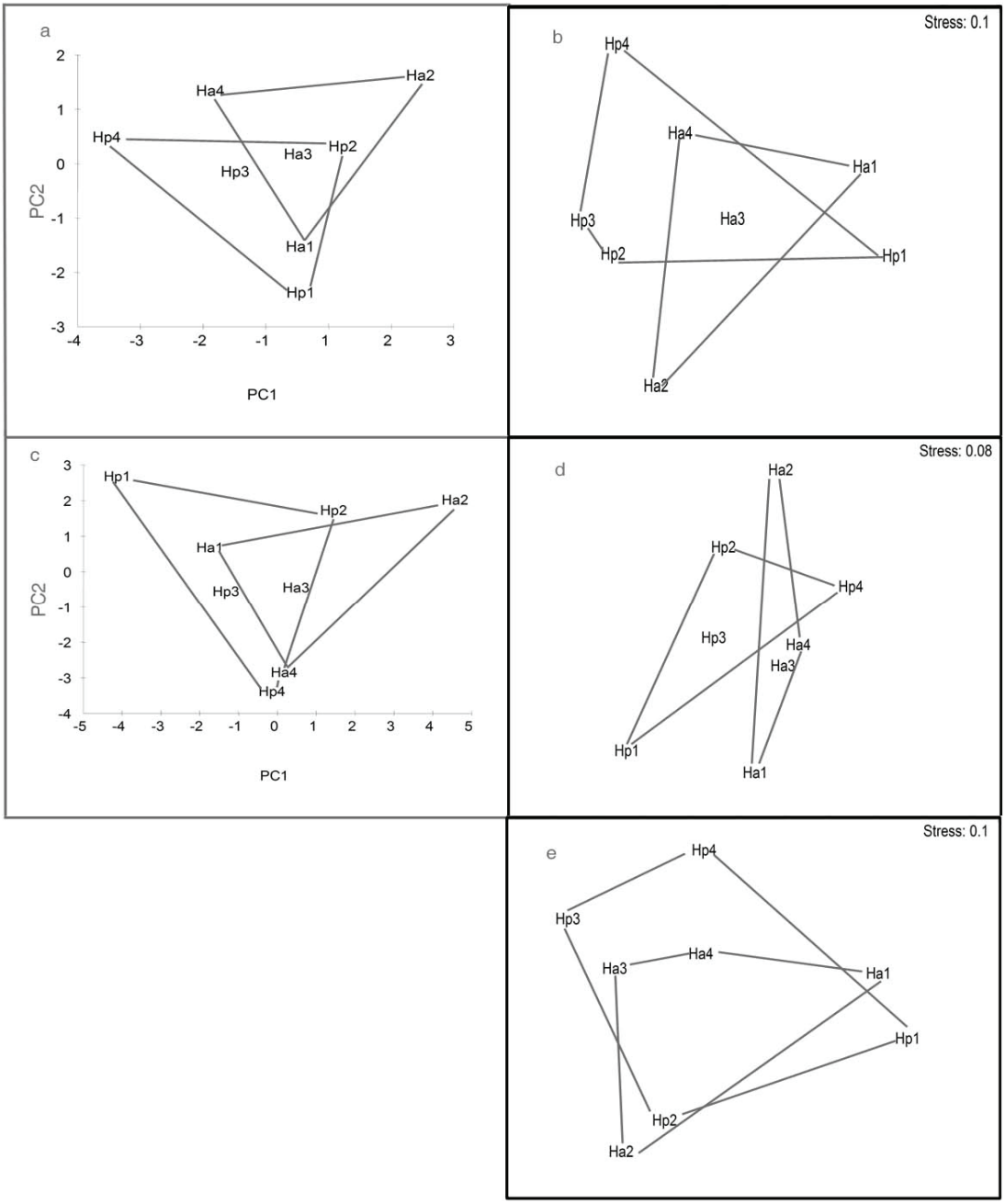


Figure 5.7. Ordinations of log-transformed abundances of insects collected using beating to establish the effect of hemipteran-tending ants (Hp - *C. sjostedti*, *C. mimosae*) and non-tending ants (Ha - *C. nigriceps* and *T. penzigi*) on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. Digits represent the sampling sessions.

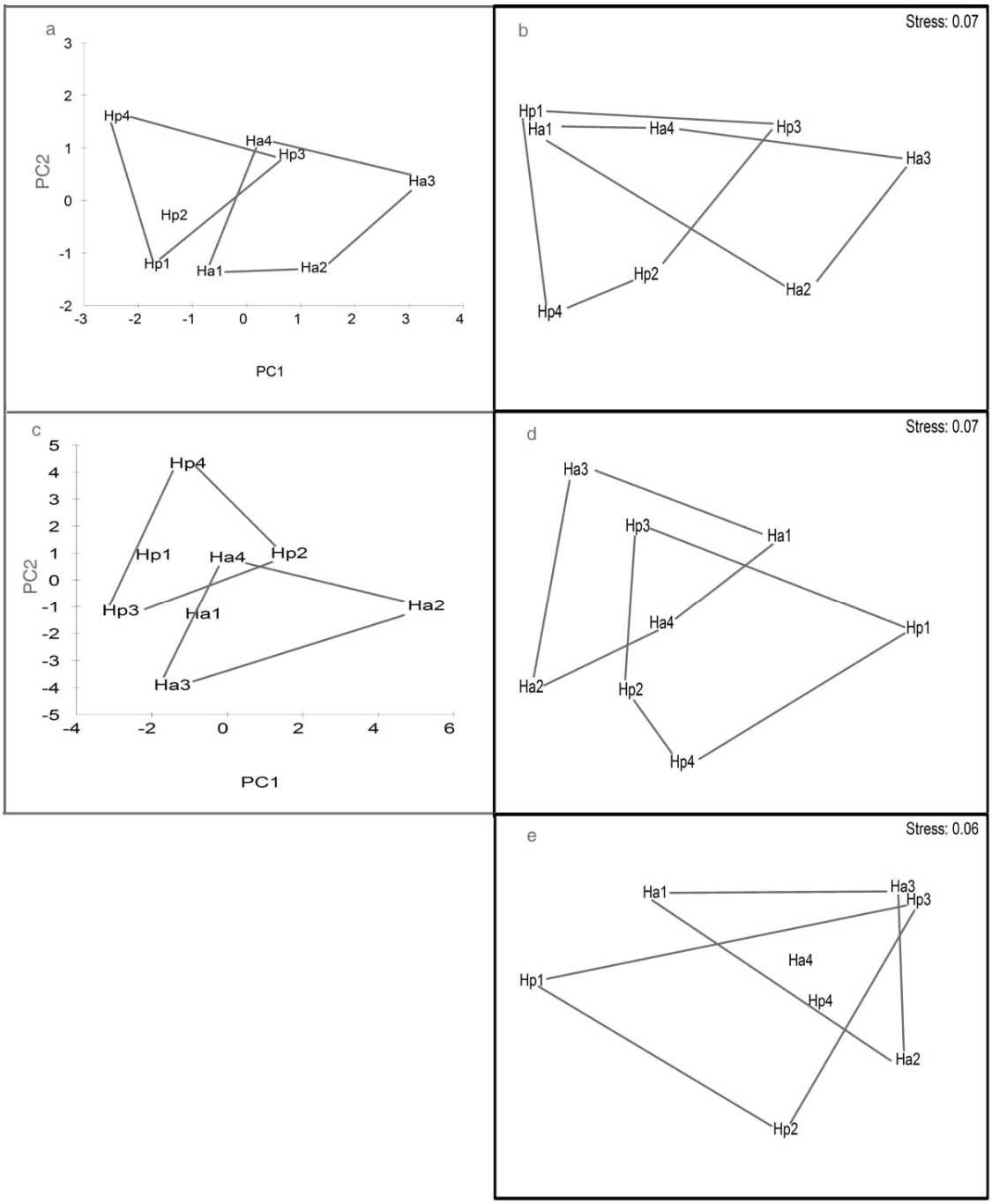


Figure 5.8. Ordinations of log-transformed abundances of insects collected using mist-blowing to establish the effect of hemipteran-tending ants (Hp - *C. sjostedti*, *C. mimosae*) and non-tending ants (Ha - *C. nigriceps* and *T. penzigi*) on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. Digits represent the sampling sessions.

CHAPTER 6: EXPERIMENTAL MANIPULATIONS TO TEST THE EFFECTS OF ANT SPECIES ON INSECT COMMUNITY STRUCTURE AND COMPOSITION ON *SENEGALIA DREPANOLOBIUM*

Introduction

Effects of ants

The interactions of ants and other related arthropods on plant canopies is a complex one and it requires close scrutiny to elucidate how ants affect the arthropods. Fritz (1983) investigated the interactions among *Formica subsericea* (Hymenoptera: Formicidae), *Vanduzea arquata* (Hemiptera: Membracidae), *Odontota dorsalis* (Coleoptera: Chrysomelidae) and *Nabicula subcoleoptrata* (Hemiptera: Nabidae), all on black locust (*Robinia pseudoacacia,* Leguminosae) in Maryland. He found that ants reduced numbers of larvae of *O. dorsalis* on those branches where it was tending *V. arquata*, but it also protected them by keeping away its predator (*N. subcoleoptrata*), which resulted in the population of *O. dorsalis* increasing in the presence of ants. This meant there was no benefit or harm to the tree due to presence of *F. subsericea* ants and *V. arquata* treehoppers. Studies on *Formica* spp. which tends *Publilia concava* (Hemiptera: Membracidae) on *Solidago altissima* (Asteraceae) showed that the ants does not exclude *Trirhabda virgata* and *T. borealis* larvae (Coleoptera: Chrysomelidae), which defoliate *S. altissima*, from the stems but they do deter their feeding (Messina, 1981). Oliveira and Freitas (1996) showed that behaviour of both immature and mature individuals of *Eunica bechina* (Lepidoptera: Nymphalidae) was finely linked with the utilization of young leaves of *Caryocar brasiliense* (Caryocaraceae), which was regularly visited by nectar-gathering ants. The ants were shown to deter females from ovipositing on *C. brasiliense* (Oliveira and Freitas, 1996). The presence of ants on tree canopies in North England resulted in a significant increase of a defoliator, *Periphyllus testudinaceus* (Hemiptera: Drepanosiphidae), while their removal resulted in a decline. At the same study site predation of *Drepanosiphum platanoides* (Hemiptera: Aphididae) by *Formica rufa* resulted in a significant decline of its population (Skinner and Whittaker, 1981). The above examples illustrate how intricate ants' associations with other animals and plants can be and the fact that presence of ants is not always beneficial to other organisms.

If properly understood, interactions between ants and other organisms could be used to predict ecological conditions within a given habitat by the presence of a particular ant species (Agosti *et al*., 2000). Lawton *et al*. (1998) showed that species richness of canopy ants in a semi-deciduous humid forest in southern Cameroon was positively correlated with changes in richness of butterflies, canopy beetles, and ground-dwelling ants. Invasion by Argentine ants (*Linepithema humile*) at Haleakala National Park, Maui, Hawaii resulted in reduced abundance of many endemic species in the shrubland ecosystem (Cole *et al*., 1992). *Solenopsis geminata* was shown to be a keystone species at the College of Tropical Agriculture (Risch and Carroll, 1982). But it contradicted the definition which indicated that loss of a keystone species would results in a collapse of the community. Removal of *S. geminata* had a very significant effect on the arthropod fauna of corn and squash plants. On corn plants, the total number of individuals and morphospecies of both herbivores and predators were significantly higher in the absence of *S. geminata* (Risch and Carroll, 1982). A similar condition was observed on squash plants: there were 15 times as many total arthropods in the absence of *S. geminata* and three times as many morphospecies.

Ants on S. drepanolobium

Results from the previous chapter suggested that the four ant species that colonize canopies of *S. drepanolobium* play a key role in determining the composition and structure of the canopy arthropod community on the trees they inhabit. To verify these observations that ant species in fact play a key role, a number of experiments were carried out involving experimentally manipulating ant species to take over adjacent trees inhabited by different ant species and later monitoring arthropod communities on these trees after takeover. At the KLEE site previous studies had shown that it was feasible to experimentally manipulate ant species to replace each other by tying together adjacent trees inhabited by different ant species (Stanton *et al*., 1999; Palmer *et al*., 2000). The conflicts involved all of the six possible combinations between the four ant species. The aim of these takeover experiments was to confirm if ant species inhabiting canopies of *S. drepanolobium* in fact regulated the canopy arthropod community and whether one or more of these ant species were keystone species in this ecosystem. If this role is confirmed it

would form the basis for recommending management methods for conservation of this ecosystem to retain the arthropod biodiversity found colonizing the canopies of *S. drepanolobium*.

Objectives

The objectives of these studies were:

i) To determine the effect of takeover between ant species on community structure and composition of canopy insects

ii) To determine what happens to insect communities inhabiting canopies of *S. drepanolobium* whenever takeover of host trees occurs between the four ant species

Hypotheses

The null hypothesis was that insect communities found in canopies of *S. drepanolobium* colonized by specific ant species would not be affected following takeover of host trees by any of the other three ant species. The alternative hypotheses were

i) Ant species behave and modify canopies differently and characteristically. Takeover of host trees by different ant species was therefore expected to alter the community structure and composition in a predictable way.

ii) The four acacia-ants modify their host trees differently and they also exhibit different characteristic aggressive behaviours. It was therefore expected that insect communities inhabiting canopies would be affected following takeover of host trees by a different ant species. It was hypothesized that the total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) would be significantly different between those tree pairs where takeover occurred and controls (trees hosting similar ant species but not involved in takeover conflicts).

Methods and Analysis

Experimental manipulations

Takeover conflicts were experimentally staged between all six possible pair-wise combinations among the four ant species inhabiting canopies of *S. drepanolobium*. Forty pairs of trees,

matched for height and canopy volume, were located for each species combination, a total of 240 pairs. For each pair involved, branches on each tree were pulled toward the other and tied together using bailing wire. The first monitoring of possible takeovers was after three months, during which pairs that had complete takeover were separated by removing the bailing wire. Complete takeovers were scored when only a single ant species could be found on branches and within the swollen thorns on both trees. One month later sampling of canopy arthropods was carried out by beating as described in Chapter Two. Subsequent monitoring of takeovers was always a month before sampling took place.

During each sampling session, four pairs of trees were sampled for each of the twelve possible outcomes in all those cases where complete takeover had taken place. For example in a conflict involving *C. sjostedti* and *T. penzigi*, four pairs of trees where *T. penzigi* had taken over trees inhabited by *C. sjostedti* would be sampled and another four pairs of trees where *C. sjostedti* had taken over trees occupied by *T. penzig*i would also be sampled. Two adjacent trees (controls) inhabited by identical ant species as those used in staging the conflicts would be sampled for each pair sampled after a takeover. This meant sampling four trees for each pair of trees where takeover was successful. The data collected from the later were to be compared to those from trees in which takeover had taken place to determine if takeover had any effect on canopy arthropods. In total three sampling sessions were carried out at intervals of four months. Other details of the methods can be found in Chapter Two.

Data analysis

Data sets collected from canopy arthropods on those pairs of trees where experimentally staged conflicts resulted in complete takeovers and from controls were analysed using PRIMER to generate the total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′). These indices were later analysed using PERMANOVA to test whether takeover between ant species had any significant effects on canopy arthropod communities.

Results

Community structure

Although twelve possible outcomes were expected with each combination, involving takeover of 20 pairs, only six combinations had takeovers with the minimum number of trees required for each sampling session (Table 6.1). Analysis was therefore limited to these six groups. Although it was intended that each tree would be sampled only once because re-sampling of the same tree could be affected by previous sampling sessions, which would have removed the majority of arthropods, a number of trees were sampled twice when it became impossible to raise a minimum of four pairs during sampling. Out of 240 pairs, only 165 pairs were recovered. Of the 75 pairs that were not recovered, tree pairs were separated either by wildlife or cattle, or labels either fell from the trees or remained on the trees but could not be located during monitoring and therefore these tree pairs were left out during the analysis.

Crematogaster sjostedti emerged the winner in most conflicts, followed by *C. mimosae* (Table 6.1). Takeover never occurred in 55.26% and 67.86% of conflicts between *T. penzigi* and *C. mimosae*, and between *T. penzigi* and *C. nigriceps* respectively. In a number of cases a third ant species not involved in the conflict would take over both trees from the two original occupants (Table 6.2). During the third monitoring and sampling sessions it was observed that in a few tree pairs that were separated during the second monitoring after complete takeovers, the displaced ant species had reclaimed back their host trees (Table 6.2). Also, some of those ant species that had taken over trees from their opponent during the conflicts had lost the two host trees to a third ant species (Table 6.2).

Effects of takeover on insect community structure

***C. sjostedti* takeover of *T. penzigi*.** At the ordinal level 66.8% of the variation was explained by the first two axes of the PCA (Table 6.3). Examination of the Eigenvectors revealed that the first axis emphasized the abundances of most orders (Table 6.3). The second axis represented a gradient between Hemiptera and Phasmatodea with little effect from the other orders (Table 6.3). These two dimensions did not reveal any pattern reflecting takeover or sampling events, with convex hulls for the two ant species overlapping (Figure 6.1a). Subjecting principal scores to PERMANOVA showed that there were no significant difference in takeover but there was a

significant difference between sampling events (Table 6.5). Pairwise comparisons revealed that the first and second sampling events were significantly different from the third sampling event (Table 6.5). A two-dimensional MDS ordination of the same data did not show any pattern for takeover or sampling events (Figure 6.1b).

The first two axes of the PCA explained 49.2% of the total variation at the family level (Table 6.4). Assessment of the Eigenvectors showed that the first axis represented a gradient between (Carabidae + Gryllidae + Blattidae) and Acrididae with minimal influence from the other families (Table 6.4). The second axis represented a gradient between (Curculionidae + Formicidae) and Buprestidae with little effect from the other families (Table 6.4). The two dimensions showed that takeover had no significant effect, with convex hulls for the two species overlapping (Figure 6.1c). A two-dimensional PCA ordination did not reveal any pattern for takeover or sampling events. However, samples for the third sampling session clustered together (Figure 6.1c). Principal scores were analysed using PERMANOVA. Results showed that there was no significant difference for takeover, but there was a significant difference between sampling events (Table 6.5). Pairwise comparisons revealed that the first and second sampling sessions were significantly different from the third sampling session (Table 6.5). Further analysis using MDS revealed the same pattern as that observed using PCA (Figure 6.1d).

At the species level a two-dimensional MDS ordination showed similar pattern to those observed at order and family levels (Figure 6.1e). A stress of 0.08 was good and justified this interpretation.

C. sjostedti* takeover of *C. mimosae. The first two principal axes of the PCA explained 56.3% of the total variation at the ordinal level (Table 6.6). Examination of the Eigenvectors revealed that the first axis was mainly affected by Hymenoptera, Mantodea, Coleoptera and Blattodea with little influence from the other orders; while the second axis was a gradient between Phasmatodea and Hemiptera with minimal effects from the other orders (Table 6.6). There was no pattern which reflected takeover or sampling events when the first two dimensions of the PCA were plotted (Figure 6.2a). Principal scores were later subjected to PERMANOVA. Results showed that there was a significant difference between sampling events but there was no significant

difference on takeover (Table 6.8). Further pairwise comparisons showed that the first sampling session was significantly different from the third sampling session (Table 6.8). Analysis of the same data using MDS did not reveal any pattern either on takeover or sampling events, but samples collected during the first sampling session tended to cluster together (Figure 6.2b).

At the family level the first two axes of the PCA captured 44.7% of the total variation (Table 6.7). Assessment of the Eigenvectors revealed that the first axis expressed abundances of most families with the exception of Mantidae (Table 6.7). The second axis represented a gradient between (Chrysomelidae + Bostrichidae) and Gryllidae with substantial influence from the other families (Table 6.7). A two-dimensional PCA plot revealed a pattern which reflected takeover but not sampling events (Figure 6.2c). However, when principal scores were analysed using PERMANOVA, results for takeover were not significant but there was a significant difference between sampling events (Table 6.8). Pairwise comparisons revealed that there was a significant difference between the first and third sampling sessions (Table 6.8). A two-dimensional MDS of the same data revealed a pattern which reflected takeover, however control samples did not cluster together with those involved in takeover conflicts (Figure 6.2d).

At the species level the data was analysed using MDS, and no pattern reflecting takeover or sampling events was observed (Figure 6.2e).

***C. mimosae* takeover of *C. sjostedti*.** At the order level 64.4 % of the total variation was captured by the first two axes of the PCA (Table 6.9). Evaluation of the Eigenvectors revealed that the first axis expressed abundances of most orders; the second axis was a gradient between Mantodea and Phasmatodea with little influence from the other orders (Table 6.9). These two dimensions revealed that takeover had no significant effect because convex hulls for *C. mimosae* and *C. sjostedti* overlapped (Figure 6.3a). A two-dimensional PCA ordination did not reveal any pattern on takeover or sampling events. There was a tendency of samples collected during the same period to be near to each other, but there was no consistency (Figure 6.3a). When principal scores were subjected to PERMANOVA results showed that there was no significant effect on takeover and sampling events (Table 6.11). The same data set was analysed using MDS, a two-dimensional configuration did not reveal any pattern on takeover or sampling events, but as

observed with PCA there was a tendency of samples collected during the same sampling event occurring next to each other but with no consistency (Figure 6.3b).

At the familial level the first two axes of the PCA explained 45.4% of the total variation (Table 6.10). Examination of the Eigenvectors revealed that the first axis expressed abundances of most families except Blattidae and Anthicidae (Table 6.10); the second axis was a gradient between (Polyphagidae + Anthicidae) and (Diapheromeridae + Mantidae) with little influence from the other families (Table 6.10). A two-dimensional PCA plot did not reveal any pattern on takeover or sampling events, but samples collected during the third sampling session clustered together (Figure 6.3c). Principal scores generated by PCA and subjected to PERMANOVA revealed no significant difference on takeover, but there was a significant difference between sampling events (Table 6.11). Pairwise comparisons showed that the first and third sampling sessions were significantly different (Table 6.11). A two-dimensional MDS ordination was similar to that obtained using PCA (Figure 6.3d). There was no pattern reflecting takeover or sampling events, but again samples collected during the third sampling session clustered together (Figure 6.3d).

At species level data was analysed using MDS, a two-dimensional configuration was similar to those obtained at order and family levels (Figure 6.3e).

C. sjostedti* takeover of *C. nigriceps. At the ordinal level the first two axes of the PCA captured 58.8% of the total variation (Table 6.12). Assessment of the Eigenvectors showed that the first axis expressed abundances of most orders except for the Phasmatodea; the second axis was a gradient between (Coleoptera + Hymenoptera) and (Blattodea + Mantodea) with little influence from the other orders (Table 6.12). These two dimensions showed that takeover had no effect on insect communities, since convex hulls for the two ant species overlapped except for *C. nigriceps* control samples (Figure 6.4a). There was also no pattern reflecting sampling events (Figure 6.4a). PERMANOVA tests were carried out on principal scores generated by PCA; results did not show any significant effect on takeover and sampling events (Table 6.14). When the same data set was analysed using MDS, the result was similar to that obtained using PCA (Figure 6.4b). A stress of 0.14 was not sufficiently good to justify further interpretation (Figure 6.4b).

The first two axes of the PCA captured 50.1% of the total variation at the family level (Table 6.13). Examination of the Eigenvectors showed that the first axis was a gradient between (Curculionidae + Cleridae + Miridae + Acrididae) and (Anthicidae + Tenebrionidae) with little influence from the other families; the second axis was a gradient between (Diapheromeridae + Chrysomelidae) and (Blattidae + Mantidae) with minimal effects from the other families (Table 6.13). These two dimensions showed that takeover had no significant effect. However, there was a tendency which indicated that takeover effect had started taking place. Control samples for *C. nigriceps* were completely isolated from the other samples, and this was what was expected if takeover had a significant effect (Figure 6.4c). Convex hulls for *C. nigriceps* control samples did not overlap with the rest of the samples (Figure 6.4c). Only convex hulls for *C. nigriceps* conflict samples and *C. sjostedti* control samples overlapped (Figure 6.4c). Principal scores were analysed using PERMANOVA, results showed that there was no significant effect on takeover, but there was a significant difference between the sampling events (Table 6.14). Further analysis using pairwise comparisons revealed that the first and third sampling sessions were significantly different (Table 6.14). A two-dimensional MDS configuration was very similar to that obtained using PCA which had indicated that takeover effect had started taking place (Figure 6.4d). There was a pattern which reflected takeover effect with convex hulls of all samples overlapping except for control samples of *C. nigriceps* (Table 6.4d). However, there was on pattern reflecting sampling events (Table 6.4d).

There was a pattern which reflected takeover similar to that observed at order and family levels, with convex hulls of all samples overlapping except control samples for *C. nigriceps* (Figure 6.4e).

C. mimosae* takeover of *C. nigriceps. At the order level the first two axes of the PCA captured 62.5% of the total variation (Table 6.15). A close examination of the Eigenvectors showed that the first axis was mainly affected by Blattodea, Mantodea and Hemiptera with little influence from other orders (Table 6.15). The second axis was a gradient between (Phasmatodea + Hymenoptera) and Hemiptera with minimal influence from the other orders (Table 6.15). These two dimensions showed that takeover had no significant effect on insect communities, with convex hulls of *C. mimosae* and *C. nigriceps* overlapping (Figure 6.5a). No pattern was detected

for takeover or sampling events (Figure 6.5a). Principal scores generated by PCA were later subjected to PERMANOVA; results did not reveal any significant effect on takeover and sampling events (Table 6.17). Further analysis using MDS did not reveal any pattern for takeover and sampling events (Figure 6.5b). With the exception of samples collected during the third sampling session from trees colonized by *C. mimosae* and *C. nigriceps* that were involved in takeover, the rest of the samples clustered together (Figure 6.5b).

At the familial level the first two axes of the PCA explained 47.2% of the total variation (Table 6.16). Evaluation of the Eigenvectors showed that the first axis was mainly affected by Miridae, Pyrrhocoridae, Acrididae and Pentatomidae with little influence from the other families (Table 6.16). The second axis was a gradient between (Gryllidae + Bruchidae + Diapheromeridae) and Chrysomelidae with minimal influence from the other families (Table 6.16). A two-dimensional PCA plot revealed a pattern on takeover but not on sampling events (Figure 6.5c). Convex hulls for all samples overlapped except for control samples for *C. nigriceps* (Figure 6.5c). If takeover had an effect those samples collected from trees that were involved in conflicts and from control samples from trees occupied by the wining ants were expected to form one group while only control samples from trees that had lost takeover wars were expected to form one group. This aspect is reflected in figure 6.5c. However, when Principal scores were analysed using PERMANOVA, results showed that there was a significant difference between sampling events, but there was no significant effect on takeover (Table 6.17). Pairwise comparisons did not show any significant difference between sampling events (Table 6.17). When the same data was analysed using MDS, a pattern reflecting takeover was observed similar to that obtained using PCA (Figure 6.5d), but there was no pattern reflecting sampling events (Figure 6.5d).

At the species level, a two-dimensional MDS ordination did not reveal any pattern on takeover or sampling events (Figure 6.5e).

***C. nigriceps* takeover *of C. mimosae*.** At the order level the first two axes of the PCA captured 62.8% of the total variation (Table 6.18). Assessment of the Eigenvectors revealed that the first axis was mainly affected by Coleoptera, Hemiptera, Phasmatodea and Mantodea with little influence from Hymenoptera, Orthoptera and Blattodea (Table 6.18). The second axis was mainly

affected by Blattodea, Orthoptera and Hymenoptera with minimal effects from the other orders (Table 6.18). These two dimensions showed that takeover had no significant effect with convex hulls for the two ant species overlapping (Figure 6.6a). There was no pattern reflecting takeover or sampling events (Figure 6.6a). PERMANOVA tests on principal scores showed that there was a significant difference between sampling events, but there was no significant effect on takeover (Table 6.20). Further analysis using pairwise comparisons revealed that the first and third sampling sessions were significantly different (Table 6.20). A stress of 0.07 for a two-dimensional MDS ordination was good and justified further interpretation (Figure 6.6b). A pattern was observed which reflected sampling events, but there was no pattern reflecting takeover (Figure 6.6b).

At the family level the first two axes of the PCA explained 46.2% of the total variation (Table 6.19). Assessment of the Eigenvectors showed that the first axis was a gradient between (Curculionidae + Miridae + Diapheromeridae + Mantidae + Acrididae) and Anthicidae with the rest of the families having little influence (Table 6.19). The second axis was a gradient between (Cleridae + Pentatomidae + Carabidae + Blattidae) and (Buprestidae + Bostrichidae) with minimal influence from the rest of the families (Table 6.19). A two-dimensional PCA configuration did not reveal any pattern for takeover and sampling events (Figure 6.6c). However, there was a tendency indicating the effect of takeover with convex hulls of samples collected from *C. mimosae* control trees not overlapping with the rest of the samples (Figure 6.6c). When principal scores were subjected to PERMANOVA, there was a significant difference between sampling events, but there were was no significant effect on takeover (Table 6.20). Pairwise comparisons revealed that the first and second sampling sessions were significantly different from the third sampling session (Table 6.20). A two-dimensional MDS ordination was slightly different from that obtained using PCA. Although there was no pattern reflecting takeover, a pattern was observed that reflected sampling events (Figure 6.6d). A similar pattern was observed at order level.

At the species level a similar pattern reflecting sampling events was observed when species data was analysed using MDS (Figure 6.6e). However, no pattern reflecting takeover was observed (Figure 6.6e).

Diversity indices

C. sjostedti* and *T. penzigi. Experimentally staged conflicts between *C. sjostedti* and *T. penzigi* resulted in some trees previously occupied by *T. penzigi* being taken over by *C. sjostedti* (Table 6.1).

C. sjostedti* and *C. mimosae. Experimentally staged conflicts between *C. sjostedti* and *C. mimosae* resulted in some trees previously occupied by *C. mimosae* being taken over by *C. sjostedti* and vice versa (Table 6.1)

C. sjostedti* and *C. nigriceps. Experimental manipulation which involved conflicts between *C. sjostedti* and *C. nigriceps* resulted in some trees previously colonized by *C. nigriceps* being taken over by *C. sjostedti* (Table 6.1).

C. mimosae* and *C. nigriceps. After staging experimental conflicts between *C. mimosae* and *C. nigriceps*, some trees previously occupied by *C. nigriceps* were taken over by *C. mimosae* and vice versa (Table 6.1).

PERMANOVA results for all the above takeovers showed that there were no significant effects on the four diversity indices at order, family and species level (Tables 6.21-6.26).

Discussion

Results obtained from the experimentally staged conflicts between the four ant species (Table 6.1) were in agreement with the past findings which indicated that *C. sjostedti* and *C. mimosae* were dominant ant species, while *C. nigriceps* and *T. penzigi* were subordinate ant species in this ecosystem (Palmer *et al*., 2000). The current studies possibly exposed what really happens under natural conditions, whereby one species may take over the host tree of another, or each species retains its host tree. In other cases a third species would take advantage and attack contesting species while they were weakened by conflict and therefore easily taking over from both. These observations may be useful in explaining particular cases, for example trees occupied by a subordinate ant species but having an insect community characteristic of a dominant ant species.

The results also revealed that *T. penzigi*, which is the least dominant ant species in this ecosystem (Palmer *et al*., 2000), was the most effective in protecting its host trees from takeover, particularly by *C. mimosae* and *C. nigriceps*. However, it rarely attacks other ant colonies and therefore very few takeover cases were reported. So, by colonizing saplings (Young *et al*., 1997) before other ant species and further protecting its host trees from takeover by the other ant species, this subordinate ant species ensures its continued survival in this ecosystem.

Previous study to determine the effect of *Camponotus acvapimensis*, *C. rufoglaucus* and *C. sericeus* on the arthropod community colonizing *Pseudocedrela kotschyi* found that there was no significant different between the three ant species (Mody and Linsenmair, 2004). However, a trend was detected for Hemiptera, with highest abundances on trees dominated by *C. sericeus* (Mody and Linsenmair, 2004). Ant-mimetic Miridae and non-ant Hymenoptera were, in contrast, least abundant on trees dominated by *C. sericeus* (Mody and Linsenmair, 2004). Results obtained from experimentally staged conflicts between the four ant species using PCA and MDS revealed patterns on takeover on samples that were collected from trees colonized by *C. sjostedti* after displacing *C. mimosae* but only at the family and species levels (Figures 6.2 c, d and e). A pattern reflecting takeover was again observed on samples collected from trees inhabited by *C. sjostedti* after displacing *C. nigriceps* on all the three taxonomic levels (Figures 6.4). Also a pattern reflecting takeover was noticed on samples collected from trees colonized by *C. mimosae* after dislodging *C. nigriceps* at the family level (Figure 6.4 c and d). However, no takeover pattern was reflected on the remaining experimental conflict pairs that were sampled. When principal component scores were analysed using PERMANOVA, results showed that there were no significant effects for takeover for all experimental conflicts. The effect of takeover could have started having impact on the insect communities and this may explain the patterns observed above that reflected takeover.

However, there was a significant difference on sampling events on experimental conflicts for samples collected from trees which involved *C. sjostedti* taking over *T. penzigi*, *C. sjostedti* taking over *C. mimosae* and *C. nigriceps* taking over *C. mimosae* at order and family levels (Tables 6.5, 6.8 and 6.20). There was also a significant difference between sampling events from samples collected from trees which involved *C. mimosae* taking over *C. sjostedti*, *C. sjostedti*

taking over *C. nigriceps* and *C. mimosae* taking over *C. nigriceps* but only at the family levels (Tables 6.11, 6.14 and 6.17). These results show that sampling events had a major effect on insect communities more than takeovers.

No significant difference was found between the four ant species on all the four diversity indices tested. Although in the previous chapter there was evidence of ant species playing a role on the structure and composition of insect communities inhabiting canopies of *S. drepanolobium*, results obtained from experimental manipulations failed to confirm this. There are two possibilities for explaining these observations that none of the ant species after all is a keystone species or the duration of experimental manipulation experiments was not long enough and therefore data obtained could not reveal the impact of the ant species. Therefore, based on results obtained from experimental manipulation experiments the null hypothesis would not be rejected. However, the second explanation carries more weight since it takes ants sometime before modifying the canopies. If insect communities are in fact affected by canopy modification then change would be predictable since the four ant species modify their canopies differently. Therefore, more research should be carried out to either confirm whether one or more of the ant species is a keystone species or none of them is a keystone species.

Assuming that one or more of the ant species is a keystone species the following scenario is likely to occur. If one or more of the ant species disappeared from this ecosystem as a result of climatic changes or overexploitation of the natural resources through overgrazing, a cascading effect on the other arthropod species would result. They would migrate, adapt to the prevailing environment or get extinct (Wilf *et al*., 2001). But the first effect would be on *S. drepanolobium*, which constitutes more than 90% of the overstorey. It will become more prone to herbivory by both vertebrate and invertebrate herbivores as a result of reduced defence. Previous studies showed that mutualistic ants defend trees against vertebrate browsers (McKey, 1974; Agosti *et al*., 2000) and insect herbivores (Koptur, 1984; Itioka *et al*., 2000; Offenberg *et al*., 2004). Decline in *S. drepanolobium* trees would result in reduced habitats and food availability for insect herbivores. This would in turn affect predators that rely on these insect herbivores as prey. Predators found on *S. drepanolobium* canopies are mainly coccinellids, mantises, spiders and lizards (personal observation).

The current study has shown that the ant species play a key role in the structure and composition of the insect community on *S. drepanolobium* canopies. The influence was mainly on the insect herbivores and sometimes on mantises. Results revealed that *C. sjostedti* mainly supported different insect community from the other three ant species. However, it is not clear how ant species influence the communities apart from modifying the canopies differently and exhibiting different aggressive behaviours. But it is expected that their loss could likely result in secondary loss of other arthropod species or change of behaviour on insects as they adapt to different environment. For example, the extinction of sea otters from the Pacific coasts of North America led to the collapse of kelp forest communities (Ebenman and Jonsson, 2005). Since more 99% of the trees are inhabited by at least one of the four symbiotic ants, almost all canopy arthropods in this ecosystem interact with ants in one way or the other. However, another scenario would be for the trees to maximise on the other defensive mechanisms such as spine length and tannin accumulation to reduce herbivory, and as a result the number of canopy arthropod species increases rather than decrease.

It also emerged that the change in insect community in canopies following a takeover is gradual and takes some time. The one year period that these trees were monitored seemed not long enough for the insect communities to stabilize following takeover wars. The modification of tree canopies following takeovers between ant species is gradual and currently there is no literature to show how long it takes a particular ant species to modify the canopy. Therefore, more research should be carried out to test this effect and document time taken by different ant species to modify their canopies following takeover conflicts and if insect communities in fact changes following takeover.

Table 6.1. Results of experimentally staged conflicts between the four ant species inhabiting *S. drepanolobium* after a period of one year. Number of pairs recovered and which ant species took over after the staged conflicts and what percentage.

Conflicts between	No of pairs recovered	%	Taken over by Cs	%	Taken over by Cn	%	Taken over by Cm	%	Taken over by Tp	%	No takeover	%
Cs Vs Tp	22	55.0	12	54.5	-		-		2	9.1	8	36.4
Cs Vs Cm	27	67.5	14	51.9	-		9	33.3	1	3.7	3	11.1
Cs Vs Cn	28	70.0	22	78.6	2	7.1	-		-		4	14.3
Cm Vs Tp	38	95.0	11	28.9	-		2	5.3	4	10.5	21	55.3
Cm Vs Cn	22	55.0	1	4.5	7	31.8	13	59.1	-		1	4.5
Cn Vs Tp	28	70.0	1	3.6	6	21.4	2	7.1	-		19	67.9
Totals	165		61		15		26		7		56	

Table 6.2. Results from experimentally staged conflicts where trees were separated after eight months after takeover was confirmed and later monitored after four months of separation.

Conflict between	Taken over after 8 months by	Taken over after 12 months by	Comments
Cs Vs Cn	Cn	-	Cs tree taken over by Cm
Cs Vs Cn	Cn	-	Cs reclaimed its tree
Cs Vs Cm	Cs	-	Cm reclaimed its tree
Cs Vs Cm	Cm		Trees deserted
Cs Vs Cm	Cm	-	Cs reclaimed its tree
Cs Vs Cm	Cm	Cn	-
Cs Vs Tp	Tp	-	Tp and Cs at Cs tree
Cs Vs Tp	Tp	Cs	-
Cn Vs Cm	Cn	-	Cm reclaimed its tree (2 pairs)
Cn Vs Cm	Cm	Cs	-
Cn Vs Tp	-	-	Cn taken by Cs and Tp
Cn Vs Tp	Cn		Tp reclaimed its tree (3 pairs)
Cn Vs Tp	Cn	-	Tp tree taken over by Cm
Cn Vs Tp	Cn	-	Cn tree taken by Cs, Tp took back their tree
Cn Vs Tp	Cn	Cs	-
Cn Vs Tp	Tp	-	Cn reclaimed its tree
Cm Vs Cn	Cm	-	Cn reclaimed its tree
Cm Vs Tp	Cm	Cs	-
Cm Vs Tp	Tp	-	Cm reclaimed its tree (2)
Cm Vs Tp	Tp	Cs	-

Table 6.3. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect orders abundance data collected using beating to test the effect of *C. sjostedti* taking over trees previously colonized by *T. penzigi* trees on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Blattodea	**-0.407**	0.280	-0.271	-0.497	-0.449
Coleoptera	**-0.541**	-0.112	-0.016	0.158	-0.103
Hemiptera	-0.241	**-0.647**	0.140	0.432	-0.225
Hymenoptera	**-0.525**	0.090	0.004	0.095	-0.138
Mantodea	-0.060	0.274	0.938	-0.082	-0.161
Orthoptera	**-0.383**	-0.264	0.133	-0.444	0.740
Phasmatodea	-0.241	**0.580**	-0.100	0.574	0.381
Eigenvalues	3.16	1.52	0.97	0.63	0.53
% Variation	45.1	21.7	13.9	9.0	7.5
Cum. % Variation	45.1	66.8	80.7	89.7	97.2

Table 6.4. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect families' abundance data collected using beating to test the effect of *C. sjostedti* taking over trees previously colonized by *T. penzigi* trees on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	**-0.317**	0.166	-0.144	0.342	-0.297
Anthicidae	0.290	-0.199	-0.001	-0.199	-0.219
Diapheromeridae	0.196	0.236	-0.374	-0.263	0.108
Blattidae	**0.346**	0.200	0.037	-0.169	-0.350
Buprestidae	-0.101	**0.366**	0.072	0.084	0.075
Carabidae	**0.406**	-0.021	0.158	0.164	0.294
Chrysomelidae	0.157	0.269	-0.458	-0.210	0.070
Cleridae	-0.165	0.081	0.496	-0.296	-0.213
Curculionidae	0.029	**0.474**	0.167	0.060	0.059
Formicidae	0.234	**0.420**	0.077	0.047	-0.067
Gryllidae	**0.364**	0.137	0.178	-0.002	0.126
Mantidae	-0.251	0.265	-0.251	-0.166	0.116
Miridae	-0.143	0.235	0.455	-0.260	0.078
Pamphagidae	-0.260	0.050	0.040	-0.067	0.658
Pentatomidae	0.221	0.078	0.094	0.647	0.125
Tenebrionidae	0.206	-0.264	0.081	-0.237	0.309
Eigenvalues	4.07	3.80	2.45	1.58	1.28
% Variation	25.5	23.8	15.3	9.9	8.0
Cum. % Variation	25.5	49.2	64.5	74.4	82.4

Table 6.5. Results of PERMANOVA performed using principal scores generated using order- and family-level data collected using beating to determine the effect of *C. sjostedti* taking over *T. penzigi* trees and sampling events on insect communities. * Significant at $\alpha = 0.05$.

Level	Source	df	SS	MS	F	P_{perm}
Order	Takeover	3	16.306	5.436	0.742	0.714
	Residual	8	58.572	7.322		
	Total	11	74.879			
	Sampling events	2	28.193	14.097	2.718	0.011*
	Residual	9	46.685	5.187		
	Total	11	74.879			
Family	Takeover	3	31.603	10.534	0.743	0.794
	Residual	8	113.413	14.177		
	Total	11	145.016			
	Sampling events	2	53.620	26.810	2.640	0.002*
	Residual	9	91.396	10.155		
	Total	11	145.016			

Level	Sampling event	t	P_{perm}
Order	First vs second sampling	0.998	0.450
	First vs third sampling	1.668	0.040*
	Second vs third sampling	2.419	0.030*
Family	First vs second sampling	1.209	0.220
	First vs third sampling	1.636	0.040*
	Second vs third sampling	2.209	0.030*

Table 6.6. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect orders abundance data collected using beating to test the effect of *C. sjostedti* taking over trees previously colonized by *C. mimosae* trees on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Blattodea	**-0.407**	0.041	-0.453	-0.528	0.082
Coleoptera	**-0.459**	0.061	-0.064	0.664	-0.483
Hemiptera	-0.103	**0.683**	0.193	0.261	0.621
Hymenoptera	**-0.542**	-0.244	0.223	0.013	0.135
Mantodea	**-0.538**	-0.148	0.009	-0.088	0.265
Orthoptera	0.021	0.297	-0.784	0.157	-0.017
Phasmatodea	0.172	**-0.599**	-0.299	0.424	0.535
Eigenvalues	2.47	1.47	1.28	0.76	0.46
% Variation	35.3	21.0	18.3	10.8	6.6
Cum. % Variation	35.3	56.3	74.5	85.4	92.0

Table 6.7. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect families' abundance data collected using beating to test the effect of *C. sjostedti* taking over trees previously colonized by *C. mimosae* trees on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	**0.348**	-0.186	0.130	0.017	-0.031
Anthicidae	-0.085	-0.268	-0.133	-0.362	-0.248
Diapheromeridae	-0.122	0.015	-0.428	-0.105	-0.029
Blattidae	**0.307**	-0.222	0.143	0.210	0.046
Bostrichidae	-0.045	**0.355**	0.416	0.018	-0.165
Buprestidae	-0.274	0.009	-0.264	0.191	0.314
Carabidae	0.271	-0.165	-0.155	0.164	-0.425
Cerambycidae	-0.242	0.243	-0.367	0.056	-0.015
Chrysomelidae	-0.175	**0.449**	0.163	0.047	-0.154
Cleridae	-0.209	-0.246	0.066	-0.374	0.345
Curculionidae	0.291	0.077	0.017	-0.366	0.230
Formicidae	**0.341**	0.069	-0.177	-0.043	0.240
Gryllidae	-0.266	**-0.352**	0.126	-0.170	0.075
Lampyridae	0.027	-0.145	0.019	-0.370	-0.428
Mantidae	**0.372**	0.028	-0.164	0.126	0.298
Miridae	0.040	0.194	0.401	-0.273	0.235
Pentatomidae	-0.196	-0.294	0.196	0.229	0.200
Tenebrionidae	-0.167	-0.299	0.233	0.399	-0.055
Eigenvalues	4.70	3.35	2.32	2.07	1.79
% Variation	26.1	18.6	12.9	11.5	10.0
Cum. % Variation	26.1	44.7	57.6	69.1	79.1

Table 6.8. Results of PERMANOVA performed using principal scores generated using order- and family-level data collected using beating to determine the effect of *C. sjostedti* taking over trees previously inhabited by *C. mimosae* and sampling events on insect communities. * Significant at $\alpha = 0.05$.

Level	Source	df	SS	MS	F	P_{perm}
Order	Takeover	3	16.335	5.445	0.799	0.691
	Residual	8	54.523	6.815		
	Total	11	70.858			
	Sampling event	2	24.919	12.460	2.441	0.016*
	Residual	9	45.939	5.104		
	Total	11	70.858			
Family	Takeover	3	44.487	14.829	1.059	0.415
	Residual	8	112.040	14.005		
	Total	11	156.527			
	Sampling events	2	54.636	27.318	2.413	0.003*
	Residual	9	101.891	11.321		
	Total	11	156.527			

Level	Sampling event	T	P_{perm}
Order	First vs second sampling	1.468	0.160
	First vs third sampling	2.098	0.020*
	Second vs third sampling	1.076	0.330
Family	First vs second sampling	1.631	0.070
	First vs third sampling	1.948	0.040*
	Second vs third sampling	1.196	0.160

Table 6.9. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect orders abundance data collected using beating to test the effect of *C. mimosae* taking over trees previously colonized by *C. sjostedti* trees on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Blattodea	**0.423**	0.017	-0.203	0.654	0.547
Coleoptera	**0.488**	-0.109	0.163	-0.426	0.227
Hemiptera	**0.407**	0.030	-0.523	-0.203	-0.001
Hymenoptera	**0.415**	-0.231	0.254	0.440	-0.697
Mantodea	0.041	**0.705**	-0.456	0.057	-0.337
Orthoptera	**0.492**	0.185	0.222	-0.358	-0.094
Phasmatodea	0.039	**0.634**	0.581	0.155	0.202
Eigenvalues	3.16	1.35	1.10	0.61	0.40
% Variation	45.1	19.3	15.7	8.7	5.7
Cum. % Variation	45.1	64.4	80.1	88.8	95.4

Table 6.10. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect families' abundance data collected using beating to test the effect of *C. mimosae* taking over trees previously colonized by *C. sjostedti* trees on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	0.244	-0.172	0.284	0.356	-0.036
Anthicidae	0.216	**0.401**	0.182	-0.047	-0.132
Diapheromeridae	0.014	**-0.399**	0.074	0.395	0.030
Blattidae	0.190	0.115	-0.172	0.113	-0.487
Bostrichidae	-0.225	0.097	-0.021	-0.339	-0.302
Buprestidae	**0.354**	-0.053	0.003	-0.152	0.284
Carabidae	0.215	-0.240	-0.327	-0.031	0.144
Cerambycidae	-0.098	-0.281	0.018	-0.082	-0.523
Chrysomelidae	0.283	0.088	0.392	-0.263	0.003
Cleridae	0.191	-0.168	-0.090	-0.481	0.145
Curculionidae	**0.384**	0.060	-0.145	0.117	0.086
Formicidae	0.293	0.135	0.271	0.213	-0.242
Gryllidae	**0.349**	-0.051	-0.056	-0.259	-0.241
Mantidae	0.006	**-0.388**	-0.251	0.054	-0.267
Meenoplidae	0.180	0.149	-0.582	0.024	0.027
Miridae	0.278	-0.264	0.076	-0.145	-0.163
Pentatomidae	-0.184	0.148	-0.029	-0.156	-0.143
Polyphagidae	0.104	**0.405**	-0.277	0.283	-0.109
Eigenvalues	5.66	2.52	2.18	2.06	1.66
% Variation	31.4	14.0	12.1	11.4	9.2
Cum. % Variation	31.4	45.4	57.5	69.0	78.2

Table 6.11. Results of PERMANOVA performed using principal scores generated using order- and family-level data collected using beating to determine the effect of *C. mimosae* taking over trees previously inhabited by *C. sjostedti* and sampling events on insect communities. * Significant at $\alpha = 0.05$.

Level	Source	df	SS	MS	F	P_{perm}
Order	Takeover	3	16.781	5.594	0.800	0.635
	Residual	8	55.921	6.990		
	Total	11	72.702			
	Sampling events	2	20.408	10.204	1.756	0.105
	Residual	9	52.294	5.811		
	Total	11	72.702			
Family	Takeover	3	35.680	11.894	0.799	0.692
	Residual	8	119.093	14.887		
	Total	11	154.773			
	Sampling events	2	52.704	26.352	2.324	0.015*
	Residual	9	102.069	11.341		
	Total	11	154.773			

Level	Sampling event	t	P_{perm}
Family	First vs second sampling	1.037	0.410
	First vs third sampling	2.172	0.040*
	Second vs third sampling	1.629	0.090

Table 6.12. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect orders abundance data collected using beating to test the effect of *C. sjostedti* taking over trees previously colonized by *C. nigriceps* trees on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Blattodea	**0.412**	**0.457**	0.149	0.334	0.133
Coleoptera	**0.358**	**-0.511**	0.032	0.375	-0.246
Hemiptera	0.093	-0.111	-0.946	0.183	0.131
Hymenoptera	**0.336**	**-0.553**	0.163	-0.155	-0.247
Mantodea	**0.300**	**0.436**	-0.195	-0.225	-0.776
Orthoptera	**0.414**	-0.047	-0.089	-0.758	0.361
Phasmatodea	**-0.565**	-0.141	-0.099	-0.255	-0.333
Eigenvalues	2.34	1.77	1.02	0.85	0.60
% Variation	33.5	25.3	14.5	12.2	8.6
Cum. % Variation	35.5	58.8	73.3	85.5	94.1

Table 6.13. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect families' abundance data collected using beating to test the effect of *C. sjostedti* taking over trees previously colonized by *C. nigriceps* trees on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	**-0.369**	-0.259	0.053	-0.008	0.275
Anthicidae	**0.357**	-0.047	-0.045	-0.270	0.376
Diapheromeridae	0.124	**0.449**	0.243	0.188	0.080
Blattidae	0.112	**-0.427**	-0.190	0.037	-0.399
Buprestidae	-0.202	-0.100	0.319	0.354	0.434
Carabidae	0.105	-0.258	-0.164	-0.053	0.416
Chrysomelidae	-0.020	**0.460**	-0.292	0.109	0.200
Cleridae	**-0.348**	0.279	0.139	-0.194	-0.241
Curculionidae	**-0.418**	-0.170	0.048	-0.117	0.003
Formicidae	-0.297	-0.083	0.211	-0.491	0.030
Gryllidae	0.225	-0.088	0.395	-0.314	-0.146
Mantidae	0.040	**-0.356**	0.121	0.426	0.032
Meenoplidae	0.013	0.056	0.602	0.125	0.005
Miridae	**-0.342**	0.034	-0.148	0.359	-0.263
Tenebrionidae	**0.320**	-0.076	0.255	0.182	-0.257
Eigenvalues	4.16	3.35	2.34	1.38	1.31
% Variation	27.7	22.3	15.6	9.2	8.7
Cum. % Variation	27.7	50.1	65.6	74.9	83.6

Table 6.14. Results of PERMANOVA performed using principal scores generated using order- and family-level data collected using beating to determine the effect of *C. sjostedti* taking over trees previously inhabited by *C. nigriceps* and sampling events on insect communities. * Significant at $\alpha = 0.05$.

Level	Source	df	SS	MS	F	P_{perm}
Order	Takeover	3	27.341	9.114	1.615	0.069
	Residual	8	45.144	5.643		
	Total	11	72.485			
	Sampling event	2	20.377	10.189	1.760	0.063
	Residual	9	52.108	5.790		
	Total	11	72.485			
Family	Takeover	3	45.562	15.187	1.316	0.226
	Residual	8	92.339	11.542		
	Total	11	137.901			
	Sampling event	2	51.859	25.930	2.712	0.007*
	Residual	9	86.042	9.560		
	Total	11	137.901			

Level	Sampling event	t	P_{perm}
Family	First vs second sampling	1.270	0.270
	First vs third sampling	2.008	0.040*
	Second vs third sampling	1.585	0.050

Table 6.15. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect orders abundance data collected using beating to test the effect of *C. mimosae* taking over trees previously colonized by *C. nigriceps* trees on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Blattodea	**-0.545**	-0.200	0.206	0.198	-0.054
Coleoptera	**-0.300**	-0.081	0.737	-0.419	0.068
Hemiptera	**-0.430**	**-0.414**	-0.184	0.034	-0.533
Hymenoptera	-0.183	**0.461**	0.226	0.751	-0.161
Mantodea	**-0.498**	-0.003	-0.304	0.070	0.767
Orthoptera	**-0.354**	**0.377**	-0.466	-0.360	-0.301
Phasmatodea	-0.145	**0.654**	0.144	-0.290	-0.056
Eigenvalues	2.52	1.86	1.10	0.77	0.44
% Variation	36.0	26.5	15.7	11.0	6.3
Cum. % Variation	36.0	62.5	78.2	89.2	95.5

Table 6.16. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect families' abundance data collected using beating to test the effect of *C. mimosae* taking over trees previously colonized by *C. nigriceps* trees on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	**-0.402**	0.005	-0.139	0.004	0.010
Anthicidae	-0.181	-0.179	0.221	-0.361	-0.277
Diapheromeridae	0.152	**-0.331**	0.007	-0.287	0.250
Blattidae	-0.295	-0.109	-0.057	-0.211	-0.284
Bostrichidae	0.128	0.216	0.124	-0.418	-0.123
Bruchidae	0.013	**-0.405**	0.173	-0.136	0.167
Buprestidae	0.153	0.244	-0.295	-0.304	-0.014
Carabidae	0.135	-0.123	-0.462	-0.282	-0.198
Chrysomelidae	-0.176	**0.343**	0.113	-0.209	-0.068
Cixiidae	0.159	0.006	-0.423	-0.159	-0.179
Cleridae	-0.117	0.229	0.412	-0.144	0.202
Curculionidae	-0.195	0.150	-0.115	-0.198	0.470
Formicidae	0.046	-0.268	0.369	-0.308	-0.253
Gryllidae	-0.045	**-0.449**	-0.106	0.047	0.263
Mantidae	-0.235	-0.281	-0.113	0.088	-0.033
Miridae	**-0.405**	-0.063	-0.134	-0.087	-0.049
Pamphagidae	0.025	-0.051	0.100	0.367	-0.510
Pentatomidae	**-0.379**	0.095	-0.020	0.040	-0.051
Pyrrhocoridae	**-0.402**	0.005	-0.139	0.004	0.010
Eigenvalues	5.23	3.74	2.52	2.29	1.48
% Variation	27.5	19.7	13.3	12.0	7.8
Cum. % Variation	27.5	47.2	60.5	72.5	80.3

Table 6.17. Results of PERMANOVA performed using principal scores generated using order- and family-level data collected using beating to determine the effect of *C. mimosae* taking over trees previously inhabited by *C. nigriceps* and sampling events on insect communities. * Significant at $\alpha = 0.05$.

Level	Source	df	SS	MS	F	P_{perm}
Order	Takeover	3	19.630	6.543	0.972	0.510
	Residual	8	53.883	6.735		
	Total	11	73.513			
	Sampling event	2	19.280	9.640	1.600	0.109
	Residual	9	54.233	6.026		
	Total	11	73.513			
Family	Takeover	3	47.501	15.834	1.053	0.415
	Residual	8	120.273	15.034		
	Total	11	167.774			
	Sampling event	2	45.048	22.524	1.652	0.040*
	Residual	9	122.726	13.636		
	Total	11	167.774			

Level	Sampling event	t	P_{perm}
Family	First vs second sampling	1.306	0.190
	First vs third sampling	1.179	0.180
	Second vs third sampling	1.398	0.050

Table 6.18. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect orders abundance data collected using beating to test the effect of *C. nigriceps* taking over trees previously colonized by *C. mimosae* trees on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Blattodea	0.107	**0.714**	0.217	0.321	0.139
Coleoptera	**-0.474**	-0.087	0.294	0.011	-0.736
Hemiptera	**-0.467**	-0.038	0.491	0.054	0.208
Hymenoptera	**-0.342**	**0.348**	0.132	-0.707	0.315
Mantodea	**-0.416**	-0.223	-0.578	-0.101	0.214
Orthoptera	-0.196	**0.557**	-0.513	-0.004	-0.390
Phasmatodea	**-0.466**	0.000	-0.107	0.620	0.314
Eigenvalues	2.83	1.57	1.15	0.80	0.43
% Variation	40.4	22.4	16.5	11.4	6.1
Cum. % Variation	40.4	62.8	79.3	90.7	96.8

Table 6.19. Eigenvectors and Eigenvalues of correlation matrix generated by PCA from log-transformed insect families' abundance data collected using beating to test the effect of *C. nigriceps* taking over trees previously colonized by *C. mimosae* trees on insect communities.

Variable	PC1	PC2	PC3	PC4	PC5
Acrididae	**-0.302**	-0.169	-0.057	-0.449	0.237
Anthicidae	**0.318**	-0.176	0.033	-0.036	0.379
Diapheromeridae	**-0.377**	-0.130	0.184	-0.181	0.319
Blattidae	0.214	**-0.342**	0.404	0.009	0.005
Bostrichidae	0.129	**0.328**	-0.171	-0.073	-0.087
Buprestidae	-0.120	**0.435**	-0.174	0.286	-0.082
Carabidae	0.128	**-0.354**	0.423	0.247	0.001
Chrysomelidae	0.141	0.050	0.472	-0.012	-0.410
Cleridae	-0.159	**-0.435**	0.021	0.030	-0.310
Curculionidae	**-0.432**	-0.065	-0.068	0.095	-0.301
Formicidae	-0.183	-0.021	0.210	0.509	-0.055
Gryllidae	0.083	-0.018	0.322	0.483	0.384
Mantidae	**-0.353**	0.154	-0.030	0.205	0.404
Miridae	**-0.399**	-0.195	0.067	0.104	-0.127
Pentatomidae	0.128	**-0.354**	-0.423	0.247	0.001
Eigenvalues	3.92	3.01	2.31	1.73	1.43
% Variation	26.2	20.1	15.4	11.5	9.5
Cum. % Variation	26.2	46.2	61.6	73.2	82.7

Table 6.20. Results of PERMANOVA performed using principal scores generated using order- and family-level data collected using beating to determine the effect of *C. nigriceps* taking over trees previously inhabited by *C. mimosae* and sampling events on insect communities. * Significant at $\alpha = 0.05$.

Level	Source	df	SS	MS	F	P_{perm}
Order	Takeover	3	14.987	4.996	0.672	0.855
	Residual	8	59.519	7.440		
	Total	11	74.506			
	Sampling event	2	35.774	17.887	4.156	0.001*
	Residual	9	38.733	4.304		
	Total	11	74.506			
Family	Takeover	3	37.674	12.558	1.017	0.471
	Residual	8	98.776	12.347		
	Total	11	136.450			
	Sampling event	2	52.589	26.294	2.822	0.001*
	Residual	9	83.861	9.318		
	Total	11	136.450			

Level	Sampling event	t	P_{perm}
Order	First vs second sampling	2.154	0.070
	First vs third sampling	2.008	0.040*
	Second vs third sampling	1.856	0.080
Family	First vs second sampling	1.571	0.070
	First vs third sampling	1.928	0.040*
	Second vs third sampling	1.456	0.040*

Table 6.21. Results of PERMANOVA to test the effects of *C. sjostedti* taking over trees occupied by *T. penzigi* on total number of taxa (S), the Shannon-Wiener diversity index (H´), Margalef's richness index (d) and Pielou's evenness index (J´) at order level. * = Significant at α = 0.05.

Level	Diversity variable	Source	df	SS	MS	F	P-value
Order	S	Takeover	3	24.625	8.208	0.650	0.882
		Residual	4	50.500	12.625		
		Total	7	75.125			
	D	Takeover	3	3.465	1.155	0.879	0.600
		Residual	4	5.253	1.313		
		Total	7	8.718			
	J′	Takeover	3	0.924	0.308	1.516	0.221
		Residual	4	0.812	0.203		
		Total	7	1.736			
	H′	Takeover	3	2.497	0.832	0.797	0.652
		Residual	4	4.178	1.045		
		Total	7	6.675			
Family	S	Takeover	3	50.125	16.708	0.555	0.886
		Residual	4	120.500	30.125		
		Total	7	170.625			
	D	Takeover	3	3.935	1.312	0.872	0.641
		Residual	4	6.015	1.504		
		Total	7	9.950			
	J′	Takeover	3	0.961	0.320	1.699	0.138
		Residual	4	0.754	0.189		
		Total	7	1.715			
	H′	Takeover	3	2.940	0.980	0.725	0.803
		Residual	4	5.407	1.352		
		Total	7	8.347			

Level	Diversity variable	Source	df	SS	MS	F	P-value
Species	S	Takeover	3	81.625	27.208	0.718	0.771
		Residual	4	151.500	37.875		
		Total	7	233.125			
	d	Takeover	3	4.646	1.549	0.961	0.523
		Residual	4	6.450	1.612		
		Total	7	11.096			
	J′	Takeover	3	1.070	0.357	2.033	0.076
		Residual	4	0.702	0.175		
		Total	7	1.772			
	H′	Takeover	3	3.499	1.166	0.761	0.779
		Residual	4	6.131	1.533		
		Total	7	9.630			

Table 6.22. Results of PERMANOVA to test the effects of *C. sjostedti* taking over trees occupied by *C. mimosae* on total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) at order, family and species levels. * = Significant at $\alpha = 0.05$.

Level	Diversity variable	Source	df	SS	MS	F	P-value
Order	S	Takeover	3	18.000	6.000	0.686	0.755
		Residual	4	35.000	8.750		
		Total	7	53.000			
	d	Takeover	3	2.520	0.840	0.546	0.907
		Residual	4	6.153	1.538		
		Total	7	8.672			
	J′	Takeover	3	0.642	0.214	0.778	0.691
		Residual	4	1.100	0.275		
		Total	7	1.742			
	H′	Takeover	3	1.646	0.549	0.481	0.937
		Residual	4	4.565	1.141		
		Total	7	6.211			
Family	S	Takeover	3	46.125	15.375	1.034	0.512
		Residual	4	59.500	14.875		
		Total	7	105.625			
	d	Takeover	3	2.724	0.908	0.542	0.946
		Residual	4	6.698	1.675		
		Total	7	9.422			
	J′	Takeover	3	0.588	0.196	1.068	0.372
		Residual	4	0.734	0.184		
		Total	7	1.322			
	H′	Takeover	3	2.330	0.777	0.733	0.768
		Residual	4	4.239	1.060		
		Total	7	6.569			

Level	Diversity variable	Source	df	SS	MS	F	P-value
Species	S	Takeover	3	57.375	19.125	0.950	0.557
		Residual	4	80.500	20.125		
		Total	7	137.875			
	d	Takeover	3	3.596	1.199	0.612	0.864
		Residual	4	7.840	1.960		
		Total	7	11.435			
	J′	Takeover	3	0.600	0.200	1.049	0.378
		Residual	4	0.762	0.191		
		Total	7	1.362			
	H′	Takeover	3	2.497	0.832	0.694	0.771
		Residual	4	4.796	1.199		
		Total	7	7.293			

Table 6.23. Results of PERMANOVA to test the effects of *C. mimosae* taking over trees previously occupied by *C. sjostedti* on total number of taxa (S), the Shannon-Wiener diversity index (H´), Margalef's richness index (d) and Pielou's evenness index (J´) at order, family and species levels. * = Significant at $\alpha = 0.05$.

Level	Diversity variable	Source	df	SS	MS	F	P-value
Order	S	Takeover	3	29.000	9.667	0.586	0.916
		Residual	4	66.000	16.500		
		Total	7	95.000			
	d	Takeover	3	2.725	0.908	0.338	1.000
		Residual	4	10.750	2.688		
		Total	7	13.475			
	J′	Takeover	3	0.586	0.195	0.256	1.000
		Residual	4	3.054	0.763		
		Total	7	3.639			
	H′	Takeover	3	2.251	0.750	0.459	0.976
		Residual	4	6.540	1.635		
		Total	7	8.791			
Family	S	Takeover	3	66.750	22.250	0.754	0.742
		Residual	4	118.000	29.500		
		Total	7	184.750			
	d	Takeover	3	5.062	1.687	0.495	0.991
		Residual	4	13.644	3.411		
		Total	7	18.705			
	J′	Takeover	3	0.529	0.176	0.376	0.990
		Residual	4	1.872	0.468		
		Total	7	2.401			
	H′	Takeover	3	3.710	1.237	0.672	0.893
		Residual	4	7.356	1.839		
		Total	7	11.066			

Level	Diversity variable	Source	df	SS	MS	F	P-value
Species	S	Takeover	3	81.750	27.250	0.779	0.725
		Residual	4	140.000	35.000		
		Total	7	221.750			
	d	Takeover	3	6.432	2.144	0.539	0.967
		Residual	4	15.910	3.978		
		Total	7	22.342			
	J′	Takeover	3	0.506	0.169	0.359	0.990
		Residual	4	1.878	0.470		
		Total	7	2.384			
	H′	Takeover	3	4.185	1.395	0.697	0.883
		Residual	4	8.009	2.002		
		Total	7	12.194			

Table 6.24. Results of PERMANOVA to test the effects of *C. sjostedti* taking over trees occupied by *C. nigriceps* on total number of taxa (S), the Shannon-Wiener diversity index (H´), Margalef's richness index (d) and Pielou's evenness index (J´) at order, family and species levels. * = Significant at $\alpha = 0.05$.

Level	Diversity variable	Source	df	SS	MS	F	P-value
Order	S	Takeover	3	28.625	9.542	1.497	0.167
		Residual	4	25.500	6.375		
		Total	7	54.125			
	d	Takeover	3	3.738	1.246	0.966	0.536
		Residual	4	5.158	1.290		
		Total	7	8.896			
	J′	Takeover	3	0.929	0.310	0.894	0.639
		Residual	4	1.385	0.346		
		Total	7	2.314			
	H′	Takeover	3	3.155	1.052	1.228	0.232
		Residual	4	3.425	0.856		
		Total	7	6.580			
Family	S	Takeover	3	48.000	16.000	0.985	0.511
		Residual	4	65.000	16.250		
		Total	7	113.000			
	d	Takeover	3	5.347	1.782	0.702	0.763
		Residual	4	10.153	2.538		
		Total	7	15.500			
	J′	Takeover	3	0.800	0.267	0.757	0.765
		Residual	4	1.410	0.352		
		Total	7	2.210			
	H′	Takeover	3	3.700	1.233	0.882	0.617
		Residual	4	5.595	1.399		
		Total	7	9.294			

Level	Diversity variable	Source	df	SS	MS	F	P-value
Species	S	Takeover	3	77.250	25.750	1.256	0.291
		Residual	4	82.000	20.500		
		Total	7	159.250			
	d	Takeover	3	8.890	2.963	1.027	0.469
		Residual	4	11.546	2.886		
		Total	7	20.436			
	J′	Takeover	3	0.833	0.278	0.793	0.685
		Residual	4	1.400	0.3350		
		Total	7	2.234			
	H′	Takeover	3	5.090	1.697	1.151	0.291
		Residual	4	5.895	1.474		
		Total	7	10.985			

Table 6.25. Results of PERMANOVA to test the effects of *C. mimosae* taking over trees occupied by *C. nigriceps* on total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) at order, family and species level. * = Significant at α = 0.05.

Level	Diversity variable	Source	df	SS	MS	F	P-value
Order	S	Takeover	3	18.875	6.292	0.498	0.951
		Residual	4	50.500	12.625		
		Total	7	69.375			
	d	Takeover	3	3.690	1.230	0.434	0.963
		Residual	4	11.329	2.832		
		Total	7	15.019			
	J′	Takeover	3	0.554	0.185	0.466	0.980
		Residual	4	1.585	0.396		
		Total	7	2.140			
	H′	Takeover	3	1.941	0.647	0.485	0.939
		Residual	4	5.649	1.412		
		Total	7	7.590			
Family	S	Takeover	3	70.125	23.375	1.222	0.400
		Residual	4	76.500	19.125		
		Total	7	146.625			
	d	Takeover	3	8.483	2.828	0.972	0.521
		Residual	4	11.632	2.908		
		Total	7	20.115			
	J′	Takeover	3	0.301	0.100	0.464	0.949
		Residual	4	0.866	0.216		
		Total	7	1.167			
	H′	Takeover	3	4.918	1.639	0.952	0.526
		Residual	4	6.891	1.723		
		Total	7	11.809			

Level	Diversity variable	Source	df	SS	MS	F	P-value
Species	S	Takeover	3	78.125	26.042	1.278	0.327
		Residual	4	81.500	20.375		
		Total	7	159.625			
	d	Takeover	3	9.879	3.293	1.099	0.395
		Residual	4	11.983	2.996		
		Total	7	21.862			
	J′	Takeover	3	0.309	0.103	0.471	0.958
		Residual	4	0.873	0.218		
		Total	7	1.182			
	H′	Takeover	3	5.139	1.713	0.968	0.479
		Residual	4	7.078	1.770		
		Total	7	12.217			

Table 6.26. Results of PERMANOVA to test the effects of *C. nigriceps* taking over trees occupied by *C. mimosae* on total number of taxa (S), the Shannon-Wiener diversity index (H′), Margalef's richness index (d) and Pielou's evenness index (J′) at order, family and species levels. * = Significant at α = 0.05.

Level	Diversity variable	Source	df	SS	MS	F	P-value
Order	S	Takeover	3	13.875	4.625	0.536	0.911
		Residual	4	34.500	8.625		
		Total	7	48.375			
	d	Takeover	3	1.956	0.652	0.531	0.915
		Residual	4	4.913	1.228		
		Total	7	6.868			
	J′	Takeover	3	0.779	0.260	0.938	0.496
		Residual	4	1.107	0.277		
		Total	7	1.886			
	H′	Takeover	3	1.975	0.659	0.647	0.806
		Residual	4	4.071	1.018		
		Total	7	6.046			
Family	S	Takeover	3	30.250	10.083	0.524	0.861
		Residual	4	77.000	19.250		
		Total	7	107.250			
	d	Takeover	3	4.394	1.465	0.482	0.929
		Residual	4	12.166	3.042		
		Total	7	16.560			
	J′	Takeover	3	0.834	0.278	1.025	0.419
		Residual	4	1.085	0.271		
		Total	7	1.920			
	H′	Takeover	3	2.921	0.974	0.528	0.875
		Residual	4	7.382	1.846		
		Total	7	10.303			

Level	Diversity variable	Source	df	SS	MS	F	P-value
Species	S	Takeover	3	30.000	10.000	0.500	0.894
		Residual	4	80.000	20.000		
		Total	7	110.000			
	d	Takeover	3	4.713	1.571	0.528	0.908
		Residual	4	11.898	2.974		
		Total	7	16.610			
	J′	Takeover	3	0.940	0.313	0.940	0.478
		Residual	4	1.332	0.333		
		Total	7	2.272			
	H′	Takeover	3	3.016	1.005	0.541	0.865
		Residual	4	7.429	1.857		
		Total	7	10.445			

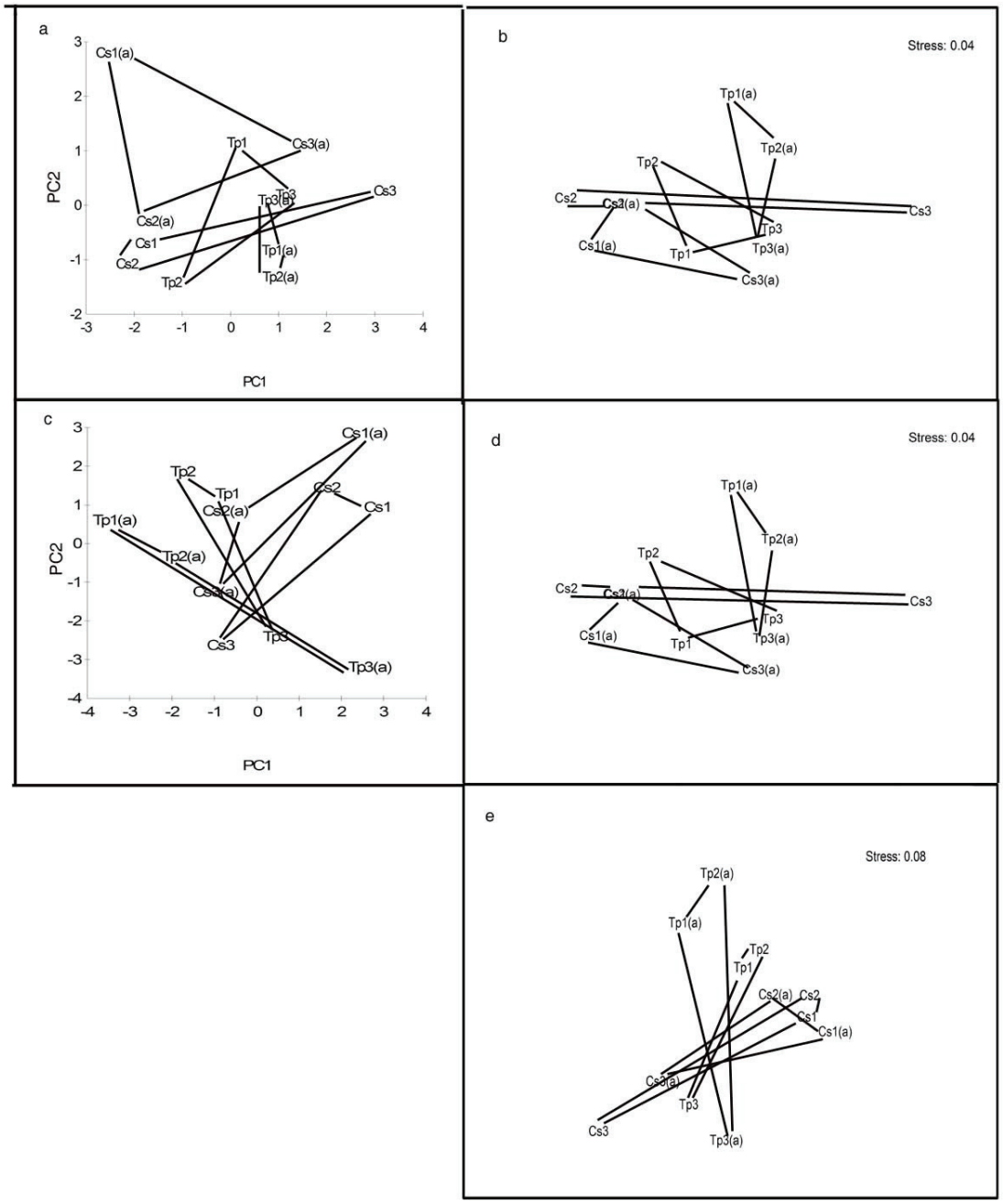


Figure 6.1. Ordinations of log-transformed abundances of insects collected using beating to test the effect of *C. sjostedti* (Cs) takeover *T. penzigi* (Tp) trees on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. Digits represent the sampling sessions.

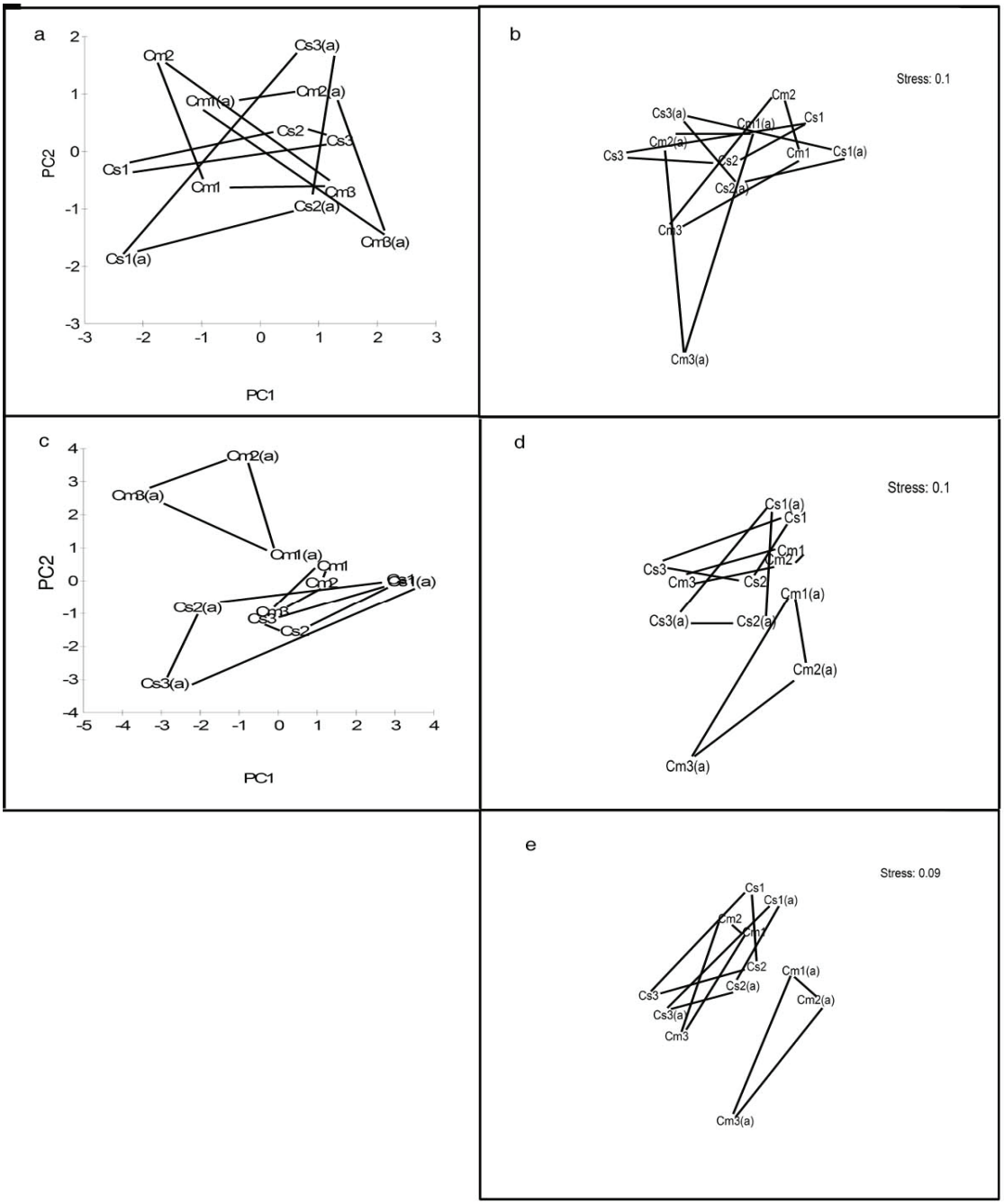


Figure 6.2. Ordinations of log-transformed abundances of insects collected using beating to test the effect of *C. sjostedti* (Cs) takeover *C. mimosae* (Cm) trees on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. Digits represent the sampling sessions.

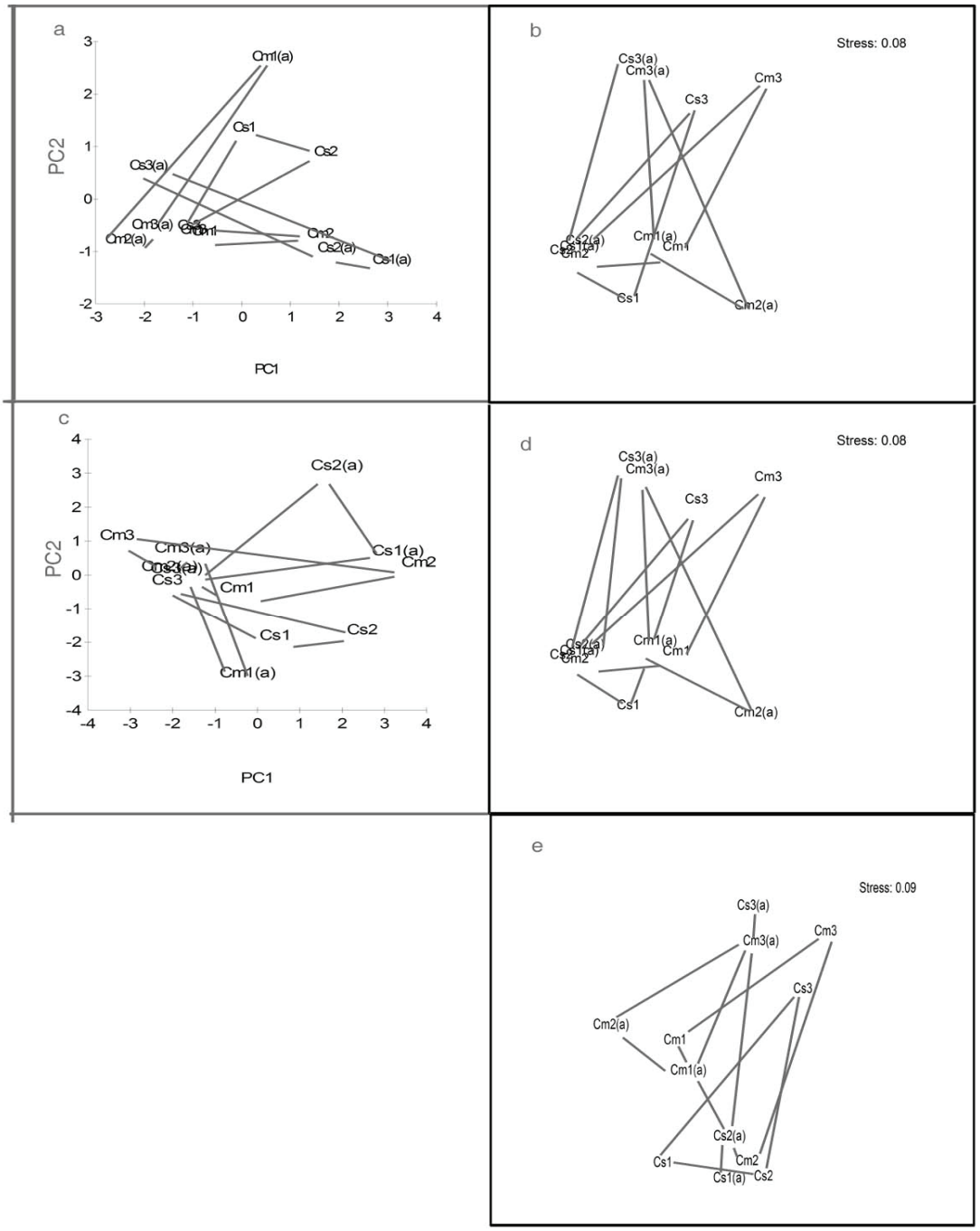


Figure 6.3. Ordinations of log-transformed abundances of insects collected using beating to test the effect of *C. mimosae* (Cm) takeover *C. sjostedti* (Cs) trees on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. Digits represent the sampling sessions.

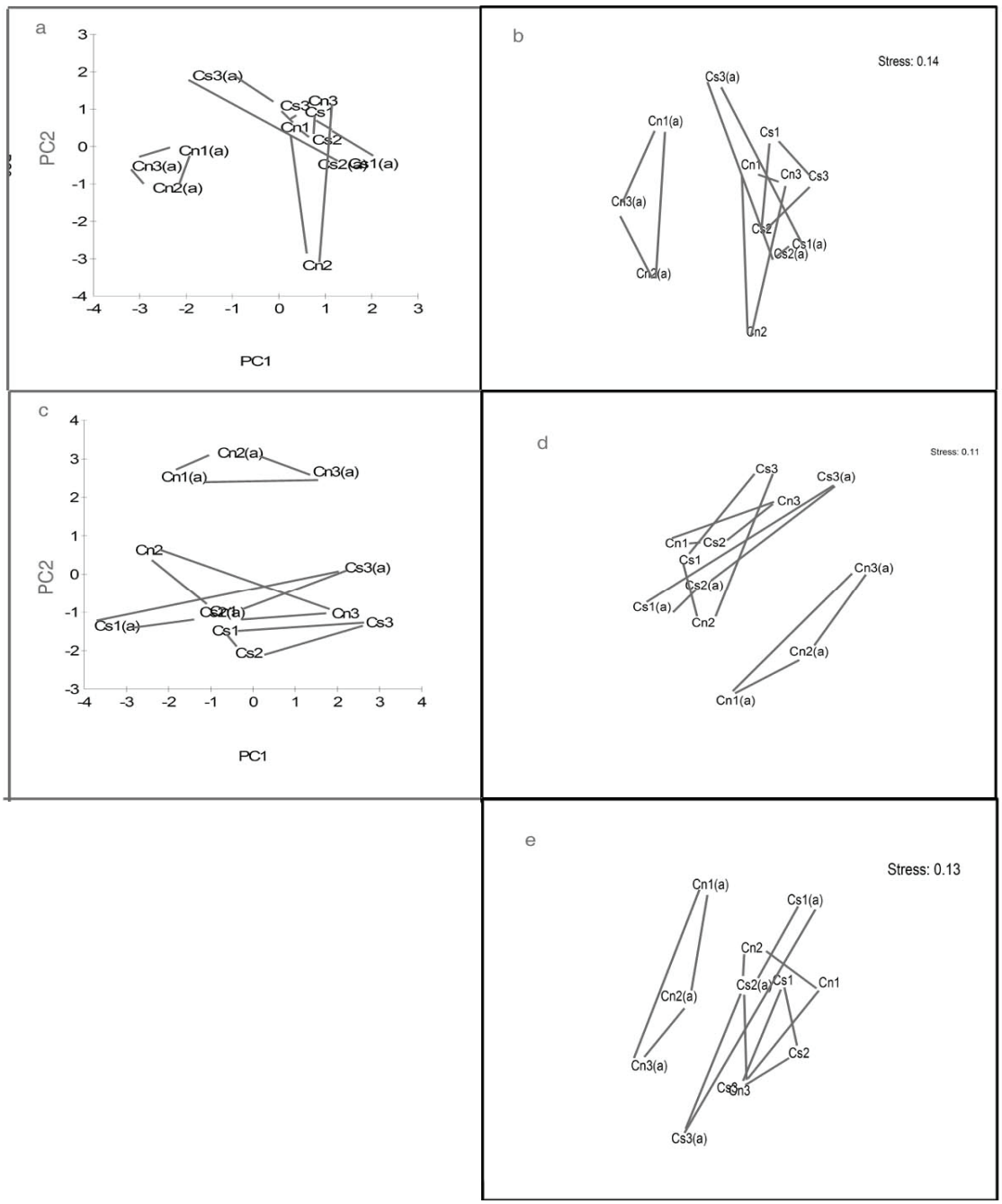


Figure 6.4. Ordinations of log-transformed abundances of insects collected using beating to test the effect of *C. sjostedti* (Cs) takeover *C. nigriceps* (Cn) trees on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. Digits represent the sampling sessions.

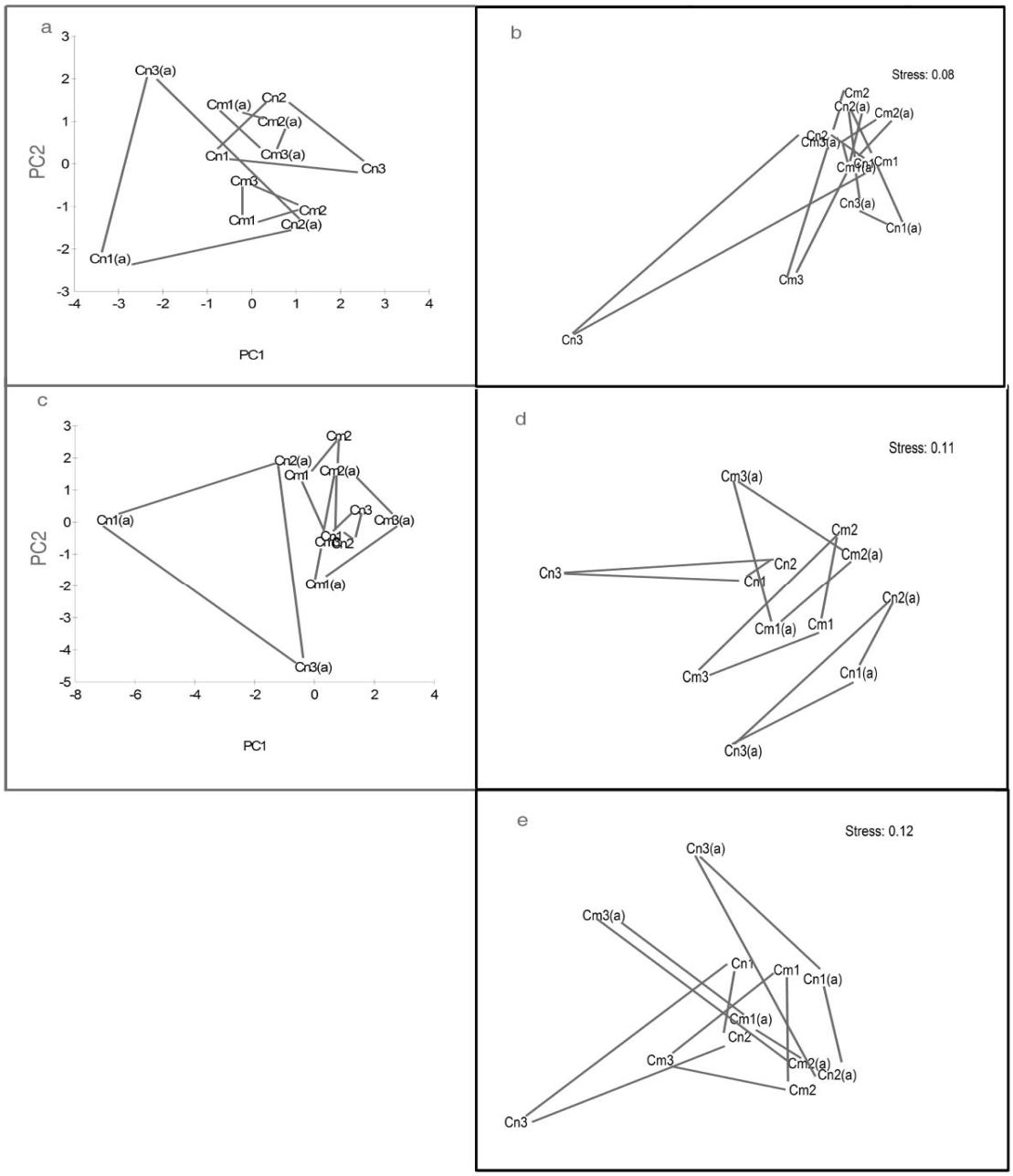


Figure 6.5. Ordinations of log-transformed abundances of insects collected using beating to test the effect of *C. mimosae* (Cm) takeover *C. nigriceps* (Cn) trees on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. Digits represent the sampling sessions.

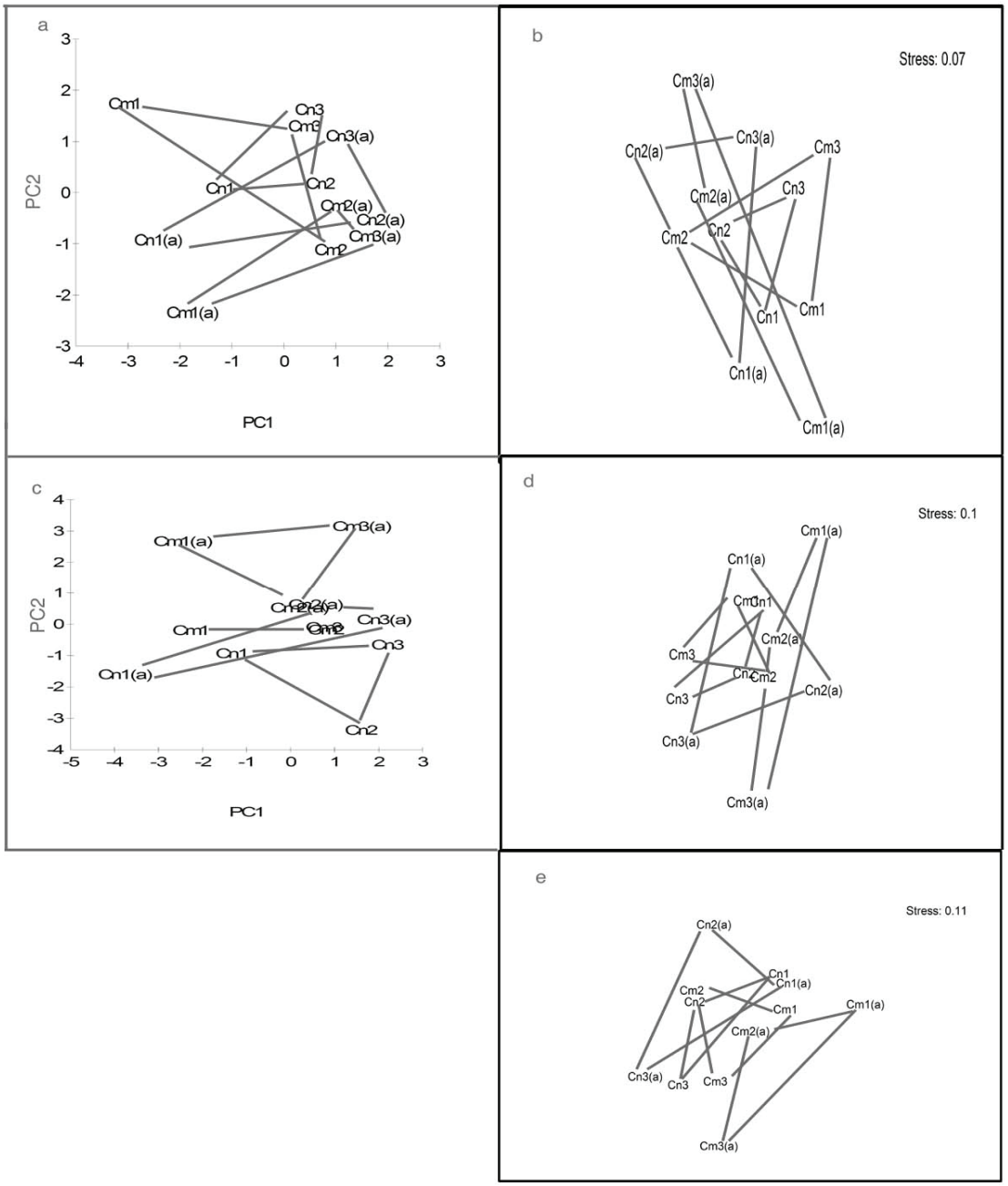


Figure 6.6. Ordinations of log-transformed abundances of insects collected using beating to test the effect of *C. nigriceps* (Cn) takeover *C. mimosae* (Cm) trees on insect communities; (a) First two dimensions of a PCA of orders (b) Two-dimensional MDS of orders (c) First two dimensions of a PCA of families (d) Two-dimensional MDS of families (e) Two-dimensional MDS of abundances of species. Digits represent the sampling sessions.

CHAPTER 7: GENERAL DISCUSSION

Insects play critical roles in the structure and function of tropical savannas throughout the world (Andersen and Lonsdale, 1990). Herbivorous insects are undoubtedly important in savannah ecosystems, but have been largely ignored in studies of herbivory in favour of native ungulates and domestic cattle (Andersen and Lonsdale, 1990). Ants in particular form relationships that range from parasitism to mutualism with other ants and other organisms (MacMahon *et al*., 2000). They have strong symbiotic relationships with plants as seed dispersers, pollinators, defoliators and guardians (MacMahon *et al*., 2000). Ant-plant associations have arisen independently in many plant taxa, and are often thought to represent good examples of coevolution (Speight *et al*., 1999). In the tropics around the world, myrmecophytes occur in at least 141 plant genera from 47 plant families (Fonseca, 1999). In Laikipia ecosystem, Kenya, four symbiotic ants coexist with *S. drepanolobium*.

The current study determined the structure and composition of terrestrial ant community and their potential as indicators of environmental change resulting from livestock grazing. The study also elucidated the role of symbiotic ants in the composition and structure of canopy arthropods on *S. drepanolobium*.

Diversity of ants on black cotton ecosystem and their potential as indicators

Ant community

Sixteen ant species belonging to six subfamilies were identified. This was the first time that the diversity of the terrestrial ant community occurring on black cotton ecosystem was investigated. Although there are thousands of individuals of the four primary ant symbionts on the canopy of each *S. drepanolobium* tree, the numbers collected on the ground using pitfall traps was very low. Previous research postulated that these ant species must leave the trees and forage on the ground to supplement their protein needs (Palmer, 2003). However, findings from this study indicate that large numbers of arthropod species coexist with these ants on canopies. It is assumed that carcases resulting from mortality of the various arthropods may be supplying the required proteins for these ants. The other source of proteins would be remains from prey captured by mantises, spiders and lizards. However, more research is required to verify this hypothesis.

Ordination of the ant community using PCA and MDS showed that there was difference between the blocks; however, there was no effect on treatments. There was an interaction effect between block location and treatments, but further analysis did not reveal any effect between treatments in all the blocks. The ant community occurring in south block was significantly different from that found in Central and North blocks. This was not expected since blocks were within a radius of approximately 5 kilometres of one another. However, Warui (2005) made similar observation while working on the impact of wildlife and cattle grazing on spider biodiversity. The spider data showed that the south block was different from the other blocks. According to data from previous study in this same area (Young *et al*., 1998), there was a north-south gradient, which also suggested that the blocks differ. The current study did not investigate climatic factors but according to Young (personal communication) the south block receives more rain than the other blocks. It is also possible that edaphic factors are different.

PERMANOVA results on terrestrial ant community showed that there was a significant difference between treatments but further analysis did not reveal any significant difference between treatment plots. However, analysis of insect samples collected from the canopies did not reveal any significant difference between treatments. But previous studies on the same KLEE site had shown some significant differences between treatment plots. Warui (2005) showed that spider samples collected using pitfall traps from cattle plots (C, MWC and WC) had significantly lower Margalef's richness index and total number of taxa compared to '0' and MW plots. *Saccostomus mearnsi* found in plots where ungulates were excluded showed a 40% higher abundance compared to those occurring on plots which ungulates were allowed (Keesing, 1998). Another study on herbivory of *S. drepanolobium* seedlings on the KLEE plots showed that seedlings on plots that had no ungulates suffered damage faster than those in plots where ungulates were allowed (Shaw *et al*., 2002).

Bioindication

Monitoring and managing of biological systems is essential because humans depend on living systems for food and other essential needs (Kimberling *et al*., 2001). Human disturbance result in a decline in species richness, change in abundance patterns, disruption of patterns of endemism, and modification of ecosystem structural properties (Kitching *et al.*, 2000; Kimberling *et al*.,

2001). Therefore, there is need for biological indicators to detect and predict the influence of anthropogenic impacts on the environment (Marc *et al*., 1999; Kimberling *et al*., 2001; Büchs, 2003). A biotic indicator was initially defined as an organism that reacts to harmful substances by changing its life functions or by accumulating substances (Büchs, 2003). The understandings of biotic indicators were therefore focused more in the sense of test organisms and indicators were used in the environment to detect factors such as air pollution (Büchs, 2003). In this thesis the term bioindicator will refer to species, functional group or a community that will detect and respond to anthropogenic impacts.

Characteristics of ideal bioindicators include presence in high numbers under natural conditions, relatively small individual territory, sensitivity to environmental stressors, rapid response to change to provide early warning of change, and ease of sampling (Noss, 1990; Kremen *et al*., 1994; Lobry de Bruyn, 1999; Torre *et al*., 2000; McGeoch *et al*., 2002; Büchs, 2003; Linton and Warner, 2003). Ants possess most of these features of ideal bioindicator (Lobry de Bruyn, 1999; Nash *et al*., 2001). Perner and Malt (2003) classified bioindication into three categories, environmental indicators that reflect the state of the environment, ecological indicators that reveal the impacts of environmental change, and biodiversity indicators that particularly indicate the diversity of species, taxa, or entire communities within an area. Using this classification, use of ant as bioindicators would be classified as ecological bioindication.

Invertebrates are an important component of most terrestrial ecosystems and a key element in the energy flow and nutrient turnover within a community (Tassone and Majer, 1997). Terrestrial invertebrates are regarded as good biological indicators because they are universal, diverse, easy to sample, and ecologically significant (Kimberling *et al*., 2001; Andersen *et al*., 2002, 2004). However, invertebrates are routinely ignored in land monitoring and assessment programmes, largely because their excessive numbers and taxonomic challenges are too intimidating for most land-management agencies (Andersen *et al*., 2002). Some invertebrate groups have been used as bioindicators, including spiders (Marc *et al*., 1999; Perner and Malt, 2003; Finch, 2005), beetles (McKie and Cranston, 1998; Bohac, 1999; McGeoch *et al*., 2002; Perner and Malt, 2003; Moretti and Barbalat, 2004; Finch, 2005), pollinators (Kevan, 1999), moths (kitching *et al*., 2000) and soil-dwelling Diptera (Frouz, 1999). Hoschitz and Kaufmann (2004) recommended use of soil

nematode communities as bioindicators of climatic change. Soil macrofauna (earthworms, ants and termites) were proposed as bioindicators of soil health (Lobry de Bruyn, 1997). Other potential indicators of ecological change include Miridae (Fauvel, 1999).

Previous studies investigated the impact of grazing on the ecosystem by wildlife and livestock with a view to identifying a bioindicator for monitoring feeding pressure. Perner and Malt, (2003) postulated that changes in land use, habitat fragmentation and environmental stress often affect species diversity in ecosystems. Grazing and trampling modify the microclimate, as well as the physical structure of vegetation and the soil surface, thereby influencing the quality of the environment and the accessibility of oviposition sites by insects (Hutchinson and King, 1980; O'Neill *et al*., 2003). O'Neill *et al*. (2003) showed that abundances of some grasshopper species would increase on ungrazed plots while other species would increase on grazed plots, but they found no strong evidence to show that these changes were in fact caused by grazing. Studies carried out in Arizona by Rambo and Faeth (1999) on insects, showed that species richness was not different between grazed and ungrazed habitats but insect abundance increased between 4 and 10 folds in ungrazed vegetation. However, Hutchinson and King (1980) showed that sheep stocking affected the abundance and biomass of all invertebrates. Ants increased in numbers and biomass with each increase in sheep stocking; all other invertebrates were reduced substantially at the highest stocking level (Hutchinson and King, 1980).

Ants are good indicator taxa of disturbance but their use in assessing or monitoring grazing effects in rangelands is still in its formative years (James *et al*., 1999). Ants are relatively sedentary and responsive to changes occurring at relatively small scales in space and time (Bestelmeyer and Wiens, 1996; Rojas and Fragoso, 1999). Lobry de Bruyn (1999) recommended their use as bioindicators of soil function in rural environment, while Agosti *et al*. (2000) suggested their use in biodiversity inventory and monitoring programs owing to their relative stability, moderate diversity and sensitivity to microclimate. Ants are the most commonly used invertebrate indicators in Australian land management in detecting ecological change associated with human land use (Read and Andersen, 2000; Andersen *et al*., 2002, 2004). Nash *et al*. (2001, 2004) investigated ants as indicators of grazing pressure and unsustainable management, but their findings showed that ants have limited utility as indicators of rangeland condition. However, ants

have been used successfully as indicators to monitor success of mine-sites restoration (Majer, 1992; Majer and Nichols, 1998; Andersen *et al*., 2004). As indicators of ecosystem condition, ant assemblages often reflect the degree of habitat disturbance and/or succession in a community (Roth *et al*., 1994). Despite increasing appreciation that ants provide a useful indication of change in biological integrity associated with land use, their viability as indicators remains controversial (Andersen *et al*., 2004).

Even though use of ants as bioindicators for impact caused by livestock grazing on rangeland is still in its formative stages, the current study investigated the potential of terrestrial ants that coexist with symbiotic ants inhabiting canopies of *S. drepanolobium* as indicators of environmental change caused by livestock and wildlife feeding. Results showed that the ant community did not respond to different grazing pressures and therefore could not be used as bioindicators of livestock and wildlife feeding on black cotton ecosystem. However, it was recommended that further research be undertaken and focus on functional group/s or particular species that may be sensitive to feeding pressure and therefore can act as bioindicators in this ecosystem. On a large scale, research should be carried out to fully determine which invertebrates are affected by livestock and wildlife feeding and on what aspects before any of the invertebrate groups can be fully accepted for use as bioindicators for livestock grazing. Ecologists have argued for use of several indicators other than one (Büchs, 2003).

A comparison of insect diversity under two sampling methods

Efficacy of using different sampling methods

The major use of sampling in entomology is to determine the number of insects in a given area or location, usually for pest control or conservation purposes. The other major use is to sample insects for identification and use their numbers to boost our understanding of the population dynamics of the insect/s in question and make predictions of their future abundance.

Canopy arthropods play essential roles in the functioning, biodiversity, and productivity of forest ecosystems (Werner, *et al*., 2004). Regrettably quantitative sampling of arboreal arthropods poses formidable challenges (Barker and Sutton, 1997; Werner, *et al*., 2004). The earliest canopy observations were made from the ground level, either using binoculars or relying upon materials

that had fallen on the ground (Lowman and Wittman, 1996). However, a range of methods for sampling canopies have been developed in the recent past. Nevertheless, use of these sampling methods depends on a number of factors including the objectives of the study, which part of the canopy is being investigated, and the amount of funding available (Barker and Sutton, 1997). However, care should be taken to avoid disturbing canopy components being sampled by sampling equipment (Barker and Sutton, 1997). Some of the methods commonly used in sampling canopy arthropods include beating (McCaffrey *et al*., 1984; Fauvel, 1999; Maudsley *et al*., 2002; Jiménez-Valverde and Lobo, 2005), branch-clipping (Basset *et al*. 1996; Hijii *et al*., 2001), fogging/mist-blowing (Southwood *et al*., 1982; Brown and Hyman, 1986; Lawman and Wittman, 1996; Chey *et al*., 1998), and the use of tower cranes (Parker *et al*., 1992; Allen, 1996), a single rope technique (Laman, 1995; Barker and Sutton, 1997; Ter Steege, 1998) and portable platforms (Nadkarni, 1988).

In the past different sampling methods were compared to determine their efficiency in sampling particular taxa and if they could compliment each other and improve sample collection. Werner *et al*. (2004) showed that there was no difference on the mean number of larval thrips when they compared pole-pruner, shotgun and certified tree climber in sampling basswood thrips, *Thrips calcaratus* (Thysanoptera: Thripidae) from the foliage of basswood canopies. However they showed that certified tree climber was the most preferred but costly, pole-pruner could not sample very high canopies and shotgun was not recommended near human habitation areas (Werner *et al*., 2004). Beating, suction, plant removal and stem eclectors (a device which measures active density of the stem fauna) were compared in sampling spiders in a maize field (Meissle and Lang, 2005). These methods differed in their capture efficiency with regard to abundance, family composition, species richness and power to detect effects. Suction samplers performed best and were recommended for sampling spiders in maize fields (Meissle and Lang, 2005). Buffington and Redak (1998) investigated the efficacy of vacuum sampler in sampling arthropods by comparing it with sweep-net, they showed that vacuum sampler collected more individuals in three out of the six orders, and also more arthropod species in two orders compared to sweep-nets. This showed that vacuum sampler was superior to sweep-nets.

A variety of techniques for sampling canopy arthropods are currently available but for the current study only beating and mist-blowing were used. These two were considered adequate because the tallest heights of the targeted trees were only 2.5 metres. Although the heights of *S. drepanolobium* can go up to 7 metres and in rare cases more than 7 metres (personal observation) all four symbiotic ants colonize trees within 1.0-2.5 metres while tall trees are occupied by *C. sjostedti* and small trees by *T. penzigi*. The two methods performed fairly well, and there was no significant difference when the two were compared using diversity indices. The two methods each missed approximately 20 morphospecies collected by the other method. This showed that none of the methods was perfect. These results support use of more than one sampling method so that they can compliment each other.

Community structure and composition

Plants over evolutionary time have evolved an enormous range of mechanical and chemical defences against animals that eat them (Buckley, 1987; Howe and Westley, 1988; Coley and Barone, 1996; Speight *et al*., 1999; Gadd *et al*., 2001). Herbivores require plant materials for nourishment and are also capable of evolution (Howe and Westley, 1988). Over time herbivores have adapted to breaking plant defences such as spines, digesting plant fibres, and detoxifying plant poisons (Coley and Barone, 1996; Howe and Westley, 1988). Insect herbivores too must feed and therefore they have developed ways of evading these defensive mechanisms by not consuming defended plants or plant parts and by detoxifying allelochemicals to less toxic forms (Rhoades, 1985; Coley and Barone, 1996; Herrera and Pellmyr, 2002). This discussion shows that there is a dynamic, evolutionary 'arms race' between insect herbivores and their hosts, with the development of novel plant defences being followed by adaptations of herbivores to overcome these defences (Speight *et al*., 1999).

Natural selection is the process that compels relentless and intricate contest between plants and herbivores (Howe and Westley, 1988). One of the challenges of modern ecology is to understand how plants escape from herbivores in time and space (Howe and Westley, 1988). The fundamental issue is that plant species evolve secondary compounds in response to attacks by insects, while insects meet the challenge by evolving new detoxification systems (Howe and Westley, 1988).

Ants are one of the most abundant, diverse and ecologically dominant animal groups in the world (Hölldobler and Wilson, 1990). Ecologically they are important because they function as predators and prey, as detritivores, mutualists, and herbivores (Agosti *et al*., 2000). They protect plants directly from herbivores (Agrawal and Dubin-Thaler, 1998; Oliveira *et al*., 1999) or from competition with other plants (Herrera and Pellmyr, 2002). The coevolution of ants and plants has resulted in a variety of elaborate and complex interactions collectively known as ant-guard systems (Herrera and Pellmyr, 2002).

Ant-guard systems involving extra-floral nectaries are often complicated by the presence of Hemiptera (Dansa and Rocha, 1992; Del-Claro and Oliveira, 1999; Oliveira *et al*., 1999) or Lepidoptera larvae (Pierce *et al*., 2002) that secrete nectar-like fluids collectively known as honeydew. Many ant species harvest the honeydew and, in return, protect hemipterans from predators and parasites (Buckley, 1987; Del-Claro and Oliveira, 1999). Janzen (1979) indicated that the presence of hemipterans was part of the cost of the plant-guard system in the same way as the provision of extra-floral nectaries and other rewards. The majority of ant-plant symbioses are currently regarded as true mutualisms, in which ants obtain shelter, nourishment or both and plants obtain protection against both arthropod and vertebrate herbivores (Janzen, 1966; Agosti *et al*., 2000).

Having explored the various mechanisms that plants use to avoid herbivory and how herbivores break these barriers to feed on these plants, the current study was carried out to determine the arthropod community, its structure and composition on canopies of *S. drepanolobium* which are defended by, spines, tannins and symbiotic ants. Some of these ant species have symbiotic association with hemipterans. The study also investigated if the canopy arthropod community was affected by these ant species, ant-hemipteran-mutualism, block location and livestock grazing.

Insect community found on canopies of S. drepanolobium

Most herbivorous insects are loosely associated with a larger plant taxon such as a genus or family, apart from the symbiotic ants occupying the canopies of *S. drepanolobium* other invertebrates colonizes these canopies and utilizes other available niches within the plant. These

herbivorous insects may also be feeding on other plant species found on this ecosystem. During the current study a total of 117 morphospecies were identified comprising 25 families and seven orders from canopies of *S. drepanolobium*. This was a big number, particularly for a plant that has several defensive mechanisms and in a species poor ecosystem. However, insect species were not categorized according to their feeding habits and therefore some of them may be general feeders or tourists. Studies carried out in Papua New Guinea rain forest by Erwin (1982) had estimated 138 monophagous species inhabiting one tree species, but Basset *et al*. (1996) drastically reduced this number to between 23 and 37 species by indicating that some insect species shared the tree species, others were transient species, and some were generalists wood-eating insects.

It is generally assumed that defence is costly because investments in defence come at the expense of investments in growth and reproduction (Rohner and Ward, 1997). Presence of mutualistic ants and the stipular thorns are partly effective in defending *S. drepanolobium* against vertebrate herbivores, but the current study has shown that they are not effective in defending the tree against insect herbivores. As a result the ants and even the plant have allowed predators such as playing mantises, spiders and lizards to inhabit the canopy and in return attack and feed on insect herbivores, thereby reducing their damage to the plant. The presence of predators such as praying mantis, spiders and lizards on the canopies of *S. drepanolobium* which feed on insect herbivores found on these canopies can in fact be regarded as a defence mechanism for the plants. Plants have provided the habitat while the predators' attacks and feeds on herbivores consuming the plants leaves and sometimes stems.

Studies at Mpala Research Centre have indicated how the four-ant species coexist through succession (Young *et al*., 1997), competition-colonization trade-off (Palmer *et al*., 2003) and niche-partitioning (Palmer, 2003) on a limited resource (*S. drepanolobium*). However, more studies should be carried to determine which mechanisms contribute to the coexistence of the more than 100 insect species found coexisting with these four ant species on *S. drepanolobium*. Understanding the interactions between species or populations is a prerequisite for predicting ecological phenomena at all levels of biological organisation (Abrams, 1987; Fagundes *et al*.,

2005), therefore there is need to understand the various interactions between insects, acacia-ants and *S. drepanolobium* in order to understand this ecosystem.

Factors affecting arthropod community

The current study showed that the arthropod community was not affected by location of blocks and feeding pressure, but it was affected by ant species and ant-hemipteran mutualism. The blocks were not far apart and therefore vegetation was relatively similar. However, data of terrestrial ants collected during the same time had indicated that the blocks were different. Although no effect of feeding by livestock and wildlife was found during the current study, Brown and McDonald (1995) had listed livestock grazing as one the most important factors affecting productivity and species composition of arid rangelands. Very heavy grazing results in a decline in the number of species, a reduction in abundance of the remaining species and dominance by a few species (James *et al*., 1999). Previous studies by Rambo and Faeth (1999) had shown that livestock grazing affects insect abundance but not species richness, while that of O'Neill *et al*. (2003) showed that some insect species would increase in grazed habitats while some would increase in ungrazed habitats.

The current study has shown that ant species play a great role in shaping the composition and structure of insect community on canopies of *S. drepanolobium*. The study also revealed that ants do not interfere with natural enemies, since the following groups of predators were encountered in the canopies praying mantises, coccinellids, spiders and lizards (personal observation). Stuntz *et al*. (2003) investigated the effect of non-myrmecophilic epiphytes on arboreal ants of *Annona glabra* (Annonaceae) trees; they found that epiphytes had no influence on composition of ant assemblages. Previous study had indicated that ants play a major role in structuring of arboreal arthropod communities because they exert a constant and high predation pressure (Stuntz *et al*., 2003). Basset (1996) whilst working on arboreal herbivores of Papua New Guinea found that ant abundance was one of the factors that explained the variance in species richness and the ratio of specialist to generalist chewers among tree species. Experimental studies of a diverse range of plant species often show that nectar-collecting ants remove herbivores and thus benefit plants (Rashbrook *et al.*, 1992; Oliveira and Freitas, 1996). In managed ecosystems, such as agricultural

systems, where ants are both pests and pest control agents, they play a role in shaping communities through species interactions including competition (Roth *et al*., 1994).

The reliability of ant defence is frequently compromised by conflicts of interest, because some ants that defend nectar-producing plants also defend sugar-secreting hemipterans (Howe and Westley, 1988). However, the direct effects of ant-tended herbivores (hemipterans and lepidopterans) are detrimental to the fitness of their host plants, but increased ant densities on extrafloral nectaries plants as a result of these herbivores may be of indirect benefit to the plant (Rashbrook *et al.*, 1992). Ants tending hemipterans show a generalized aggressive response toward other insects on the host plant (Fritz, 1983). Gaume *et al*. (1998) while studying the association between *Leonardoxa africaca* and *Aphomomyrmex afer* showed that the benefits of an ant-plant mutualism depended on the type of hemipteran tended by the ants. They found that the net benefits to the plant of maintaining ants appear to be much greater with pseudococcids as the third partner as compared to coccids. At the study site, two of the ant species tend coccids but only one was aggressive while the other was not and in fact the less aggressive ant (*C. sjostedti*) was found to accommodate the highest number of insect species in this ecosystem. During the current study ant-hemipteran mutualism was found to have an effect on community structure. The effect was on all four diversity indices tested at the three levels order, family and species. There is likelihood that ant species, hemipterans and *S. drepanolobium* have an evolutionary link.

The other factor which had an effect on arthropod community was sampling sessions. This is was likely due to seasonal effects though there was no consistent since sampling sessions were not organized to coincide with the seasons. Watanabe and Ruaysoongnern (1989) had shown that arboreal arthropods are more abundant during the rainy season. In general, insect populations are depressed during the dry seasons, with a marked rebound at the beginning of the wet season followed by a gradual increase until the onset of the following dry season (Coley and Barone, 1996).

Experimental manipulations to test the effects of ant species on insect community structure and composition on *S. drepanolobium*

Ants as keystone species

Keystone species are animal or plant species with a wide-ranging influence on community composition, and their removal or extinction could result in changes in competitive relationships, and relative abundances of other species in a community (Howe and Westley, 1988; Ernest and Brown, 2001; Payton *et al*., 2002). If a competitive keystone disappears, other plants or animals that play similar roles in the community prosper (Howe and Westley, 1988). Identifying keystone species can be problematic (Mills *et al*., 1993). Approaches used include experimental manipulations, comparative studies, historical reconstruction and adaptive management but no robust methodologies have been developed (Power *et al*., 1996; Payton *et al*., 2002).

Disease-producing organisms can also function as keystone species, where their impact on predator or herbivore populations has significant flow-on effects for dominant elements of the wider community (Payton *et al*., 2002). Examples are the rinderpest virus and the anthrax bacterium (*Bacillus anthracis*), which have periodically devastated grazing mammal populations in parts of Eastern and Southern Africa (Payton *et al*., 2002). Keystone plant species are also recognized for their importance in sustaining wildlife, and in tropical rainforests the best example are the figs (Moraceae: *Ficus*) whose combined year-round production of fruit support frugivorous mammals and birds (Harrison, 2003). Another keystone species is *Euphausia superba* a prey species throughout most of the Southern Ocean, in particular the Antarctic Peninsula/Scotia sea region (Reid and Croxall, 2001). Other examples of confirmed keystone species include *Piper* (Fleming, 1985), prairie dogs (*Cynomys* spp.) (Kotliar *et al*., 1999; Fahnestock and Detling, 2002), plateau pika (*Ochotona curzoniae*) (Lai and Smith, 2003), *Aloe dichotoma*, *A. pillansii* and *Pachypodium namaquanum* (Midgley *et al*., 1997), and *Daphnia* (Martin-Creuzburg *et al*., 2005).

Keystone species can exert effects, not only through the commonly known mechanism of consumption, but also through such interactions and processes as competition, mutualism, dispersal, pollination and disease (Power *et al*., 1996). In the current study ant species exert their influence on canopy arthropods through mutualism, diverse aggressive behaviours and canopy

modification. By exhibiting the different behaviour patterns, the acacia-ants are likely to influence the canopy arthropods differently. These are some of the cues that might contribute to making these acacia-ants keystone species. Identifying keystone species is difficult and it would be unwise to fully conclude that one or more of the ant species are keystone species after carrying out experiments for approximately two years, although the findings showed that one or more of the ant species may be keystone species. Therefore there is need to verify the current findings. Experiments should be carried out, which would involve excluding one of the ant species from trees and monitoring changes taking place on the arthropod community. The keystone concept has great relevance for identifying the most suitable areas for biodiversity preserves (Power *et al*., 1996). It may be eventually used in deciding whether to conserve the black cotton ecosystem if it is finally concluded that in fact some of the ant species are keystone species. Ambiguity in the use of the term keystone and the lack of an operational definition has led to criticism of its continued application in research and policy contexts (Power *et al*., 1996). However, the current definitions still holds and I would recommend research findings to continue being interpreted based on them until such a time when a consensus on an operational definition would be achieved.

The overstorey in this black cotton ecosystem is 99% *S. drepanolobium*. There is a possibility that the tree has a major influence on the canopy arthropods and the effect of ant species and ant-hemipteran mutualism is at a fine spatial scale. Trees have been regarded as insects' islands because they provide habitat to a wide variety of insect species (Krüger and McGavin, 2000), therefore decimation of *S. drepanolobium* trees from Savannah ecosystem would be a big loss of insect habitat as well as source of food to mammalian and insect herbivores.

Conclusion and recommendations

The current studies have shown that terrestrial ant community of black cotton ecosystem cannot be used as biological indicators of grazing pressure and therefore as a tool of rangeland management to detect and predict the impact caused by livestock/wildlife feeding. However, there is consensus from past studies that use of ants as bioindicators is still in its formative stages

and it may take time before its potential is fully appreciated or the concept may be dropped out altogether.

The large numbers of insect species identified during the current study coexisting with symbiotic ants on *S. drepanolobium* have shown that symbiotic mutualisms are much more complicated than what the current literature reveals. In this case although the ant species may defend the acacia plants against herbivory from vertebrates and invertebrates, they also coexist with other arthropod herbivores and predators. How these various interactions benefit the plants/ants or compete with plants/ants is not well understood. The study has shown that mutualism is not necessarily between two or a few species but can involve a large number of species coexisting together and interacting at various levels. However, more research is required in this area to identify the role played by the various members.

This study recommends that the black cotton ecosystem be conserved and more research be undertaken to verify the following:

i) whether ant communities are potential indicators of livestock grazing, particularly on those areas under intense grazing pressure;
ii) what mechanisms support coexistence between acacia-ants, *S. drepanolobium*, hemipterans and arthropod community; and
iii) the role of ant species as keystone species in this ecosystem.

Once these questions are answered the rangeland managers and ecologists will have information that can assist them in making decisions regarding this ecosystem.

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