

**TEMPORAL AND SPATIAL COMPOSITION OF
ARBOREAL INSECTS ALONG THE
OMARURU RIVER, NAMIBIA**

BY

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DECLARATION OF INDEPENDENT WORK

DECLARATION WITH REGARD TO INDEPENDENT WORK

I, Gertruida Louisa Theron, identity number 64100400233 and student number 2008024496, do hereby declare that this research project submitted to the University of the Free State for the Degree MAGISTER SCIENTIAE, is my own work and that I have not previously submitted the same work for a qualification at/in another University/Faculty.

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ABSTRACT

Insects play a major role in any ecosystem and are also of extreme importance to the well-being of humans. Amongst others, they are pollinators that indirectly determine food security. On a more negative side, they can cause great crop damage and act as vectors for many diseases. It is thus of utmost importance to understand their biology. In this context a study was undertaken to analyze the temporal and spatial composition of arboreal insects along the Omaruru River in central Namibia. This river is one of the ephemeral rivers in Namibia, running along an east-west rainfall and altitudinal gradient.

Three typical Namibian tree species (*Acacia erioloba*, *Acacia tortilis* and *Faidherbia albida*) were selected as host species and their canopies sampled over a period of one year. An anaesthetising insecticide, Pyrethroid, was used to fog the tree. Insects dropped onto plastic sheets suspended underneath each sample tree. This material was collected, stored in 70% Ethanol and then sorted and identified into relative taxonomic units (RTUs).

The data obtained was used to compare the insect diversity and composition of the three selected host species. Results indicated that there are no statistical differences regarding canopy associated insects between the three tree species. Not only do they have similar numbers of RTUs, but they also share a high percentage (50% and higher) of the same RTUs.

The influence of aridity was also investigated by comparing the different sampling stations with each other. The stations lie within different rainfall regimes and show an increase in mean temperature and a decrease in humidity from east to west. The effect of rainfall was eliminated because the trees make use of year-round groundwater to fulfil their requirements.

Results indicated that the sampling stations differ from each other with regard to their insect diversity. The further apart the stations are from each other the less similar they are regarding recorded arboreal insect diversity. There was a noticeable decrease in RTU numbers from east to west.

Lastly the effect of seasonality was also investigated. Samples were taken on a bi-monthly, basis allowing comparison of the three main seasons (pre-rainy, rainy and dry). Results indicated an increase during and after the rainy season and a decrease during the dry season.

Finally, when deciphering the temporal and spatial composition of arboreal insects along the Omaruru River in Namibia, seasonality seem to be the most meaningful determining factor, followed by locality (site), in turn followed by host (tree) species.

These results are largely in accordance with the results of other studies and, when linked to climate change, can provide valuable information to decision makers on various levels. An increase in temperature can cause a shift in insect distribution into areas presently not occupied by them, changing ecosystem function of the area (e.g. insect-plant interaction and disease transmission) in the process.

Key words: *insect diversity, host species, aridity, seasonality, relative taxonomic units, climate change.*

UITTREKSEL

Insekte speel 'n betekenisvolle rol in enige ekosisteem en is as sulks ook belangrik vir die vooruitgang van die mens. Onder andere is hulle bestuiwers wat indirek voedselsekuriteit bepaal. Aan die negatiewe kant veroorsaak hulle ook aansienlike oesskade en is hulle draers van baie siektes. Dit is dus van uiterste belang dat hulle biologie, diversiteit en volopheid ontleed en verstaan word. In hierdie konteks is 'n studie van die verspreiding en samestelling van insekte oor tyd en ruimte langs die Omaruru Rivier in sentraal Namibië uitgevoer. Hierdie rivier is een van die nie-standhoudende riviere in Namibië en volg 'n oos-wes reënval- en hoogte bo seevlak gradient.

Drie boomsoorte tipies aan Namibië (*Acacia erioloba*, *Acacia tortilis* en *Faidheria albida*) is gekies as gasheer spesies en opnames in die loof van die bome is oor 'n periode van een jaar gedoen. 'n Verdowende insekdoder, Pyrethroid, is gebruik om die bome te berook wat gelei het tot die afval van insekte op plastiek seile wat onder elke boom gespan is. Hierdie materiaal is versamel en in 70% Etanol gestoor, waarna hulle gesorteer en geïdentifiseer is as relatiewe taksonomiese eenhede (RTU's) vir elke orde.

Die versamelde data is gebruik om die insek diversiteit en samestelling van die drie gasheer spesies te vergelyk. Resultate het aangetoon dat daar geen statistiese verskille, wat betref loof-geassosieerde insekte, tussen die drie boom spesies bestaan nie. Nie alleen het hulle min of meer dieselfde getal taksonomiese eenhede nie, maar hulle deel ook 'n groot persentasie (50% en meer) van dieselfde taksonomiese eenhede.

Die invloed van ariditeit is ook ondersoek deur die verskillende opname stasies met mekaar te vergelyk. Die stasies val in verskillende reënval streke en toon 'n toename in temperatuur en afname in humiditeit van oos na wes. Die uitwerking van reënval is nie in berekening gebring nie omdat die bome van ondergrondse

water, wat dwarsdeur die jaar beskikbaar is gebruik maak om aan hulle behoeftes te voldoen.

Resultate het aangetoon dat die opnamestasies wel van mekaar verskil ten opsigte van hul insekdiversiteit. Hoe verder die stasies van mekaar geleë is, hoe meer verskil hulle van mekaar wat betref versamelde loof insekdiversiteit. Daar was 'n merkbare afname in taksonomiese eenhede van oos na wes.

Die effek van seisoenaliteit is ook ondersoek. Opnames is op 'n twee-maandelikse basis gedoen wat dus daartoe gelei het dat al drie die seisoene (voor-reën, reën en droë) met mekaar vergelyk kon word. Resultate het 'n toename in getalle aangetoon gedurende en na die reënseisoen en 'n afname gedurende die droë seisoen.

Ten slotte, wanneer die samestelling van insekte oor tyd en ruimte langs die Omaruru Rivier in Namibië ontleed word, blyk dit dat seisoenaliteit die mees bepalende faktor is, gevolg deur lokaliteit (versamelplek), om die beurt gevolg deur gasheer (boom) spesie.

Hierdie resultate is grootliks in ooreenstemming met ander studies en wanneer dit gekoppel word aan klimaatsveranderinge kan dit van groot waarde vir besluitnemers op verskeie vlakke wees. 'n Toename in temperatuur kan aanleiding gee tot 'n verskuiwing in insek verspreiding na gebiede waar hul voorheen nie voorgekom het nie, wat sodoende edosisteem funksie (bv. Insek-plant interaksie en siekteoordrag) in die gebied kan verander.

Sleutelwoorde: *insek diversiteit, gasheerspesie, ariditeit, seisoenaliteit, relatiewe taksonomiese eenhede, klimaats-verandering.*

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 Namibia and its insects

Of the estimated 35 000 insect species occurring in Namibia only about 18% are described of which 24% are endemic with a high concentration occurring in western Namibia along the escarpment and on the Namib gravel plains (Simmons *et al.*, 1998). According to Marais (1998) the biggest problem in Namibia is the lack of knowledgeable scientists, capable of studying the insect fauna and their ecological importance. There is an urgent need for understanding processes in order to manage natural resources sustainably. Thus, much baseline information is needed, which can potentially contribute towards making better conservation decisions.

Namibia is a large country, covering an area of about 823,680 km² and its coastline of approximately 1 570 km separates the mainland from the Atlantic Ocean (Mendelsohn *et al.*, 2003). Two overwhelming features of Namibia's climate are the scarcity and unpredictability of rainfall. Over much of the country and for most of the year, the climate can be described as arid. It is, however, not so much the low rainfall, but the low relative humidity (dry air) that makes Namibia a dry country. The dry air results in fewer clouds being formed which then leads to high radiation from the sun and high daytime temperatures. Water evaporates rapidly, leaving the earth dry. (Mendelsohn *et al.*, 2003).

The distribution of rain in Namibia is variable and unpredictable. Rainfall is highly seasonal with well marked dry and wet seasons. Moorsom (1995) and Barnard (1998) defined Namibia's seasons as follows: a dry season, extending from April/May to September/October and a wet season, from November to April,

when most of Namibia's rain falls. Even within the rainy season rainfall is highly irregular with long dry spells between rain events. Moorsom (1995) further defines it by saying that May to September can be classified as winter, when rainfall is unlikely; spring and early summer stretches from September to November and this is also referred to as the pre-rainy season. The first rains usually commence in October, although mainly in the northern parts of the country. For the rest of the country the rainy season usually only commences in November. January and February are generally regarded as the wettest months, with a lesser amount of rainfall during March. Towards the end of April, however, the rainy season comes to an end. In Namibia, the isohyets generally lie northwest to southeast, with rainfall decreasing from northeast to southwest (Chapter 2, Figure 1).

Because not much is known about the Namibian insect biodiversity a study was conducted to assess insect diversity along an east-west aridity gradient in western central Namibia. The study, however, only investigated tree-living (arboreal) insects of selected orders and three tree species commonly found along the dry river courses in Namibia were used as focus species.

1.2 Literature study

The majority of structured studies on arthropod/insect arboreal biodiversity have been conducted in the humid tropical forest biome (e.g. Paarman & Stork, 1987; Noyes, 1989; Longino & Colwell, 1997 and Kaspari & Weiser, 2000). Basset (2001) did a review from studies concerned with mass-collecting (>1000 individuals) to identify how much was known at that time and which taxon, collecting method or bio-geographical regions were favoured and which neglected. He came to the conclusion that the canopies of lowland wet and subtropical forests have been studied more often than those of lowland dry and montane forests. The areas best studied appeared to be Panama, Costa Rica, Manaus and Sulawesi, with the Afrotropical region and the mainland of southeast

Asia most neglected. Krüger & McGavin (1997) stated that most entomologists utilised canopy fogging as the primary investigative technique and that insect communities in tropical savannah tree canopies are comparatively poorly studied, with very few studies having been conducted anywhere in an African savannah habitat. Denlinger (1980) studied the seasonal and annual variation of insect abundance in the Nairobi National Park in Kenya and Krüger & McGavin (1997 and 1998) studied the insect fauna of *Acacia* species in Mkomazi Game Reserve, northeast Tanzania. Closer to home, Moran & Southwood (1982) compared the guild composition of arthropod communities in trees in South Africa (Grahamstown & Hogsback) with those in Britain (Ascot, Berkshire and Richmond). Moran *et al.* (1994) also investigated herbivorous insect species in the tree canopies of a relict South African forest.

Climate change is one of the most pressing issues of the 21st century. For the scientist, the most important question is: What will the effects of climate change be on biodiversity? Pearson & Dawson (2003) stated that there is clear evidence that future climate change will have a significant impact on the distribution of species. The majority of the studies related to climate change focus on the possible effect of changing temperature and or precipitation on plants and their associated fauna (Masters *et al.*, 1998, Andrew & Hughes, 2005, Deutsch *et al.*, 2008 and Schweiger *et al.*, 2008). Herbivorous insects are widely used in these studies because their ability to disperse and relatively fast rate of reproduction, allow them to act as rapid sensors of climate change (Hodkinson & Bird, 1998). Marsh (1986) as well as Kaspari & Weiser (2000) stated that ant activity clearly follows a moisture gradient. Changes in rainfall (moisture), due to climate change, will therefore affect the distribution and/or composition of ants, and most probably that of all other life-forms. Honey bees are regarded as the most economically valuable pollinators of agricultural crops worldwide and Le Conte & Navajas (2008) investigated the impact of climate change on honey bee populations. Malaria is responsible for the deaths of many people worldwide every year and the potential impact of climate change on the outbreaks thereof is

of importance for governments worldwide. Various studies had been conducted on the potential impact of climate change on malaria and other diseases of importance to mankind (e.g. Martens, *et al.*, 1995, Githeko *et al.*, 2000 and Gage *et al.*, 2008).

Namibia provides a unique opportunity to study plant and animal distribution patterns related to rainfall gradients. It has a strong climatic gradient from coastal desert to inland savannah. Marsh (1986; 1990) studied ant biology, ecology and biodiversity along a climatic gradient within the Namib Desert where he concentrated on the hyper-arid coastal desert (Namib Desert biome). More recently, Vohland & Deckert (2005) studied termites along a north-south transect in Namibia and South Africa and Vohland *et al.* (2005) studied the impact of different grazing systems on the diversity of beetles in southern Namibia. With the exception of the studies conducted by Marsh (1986; 1990), the majority of projects undertaken in Namibia, however, run along a north-south gradient. In contrast this study focused on an east-west gradient, along one of Namibia's ephemeral rivers, which is largely similar to the Kuiseb River used by Marsh (1986;1990). Apart from the research done by a former student of the Polytechnic of Namibia (Kasch, 2002), who looked at the influence of aridity on insect biomass along the Omaruru River, no evidence could be found of any other study, on arboreal insects, undertaken in Namibia along an east-west gradient and along an ephemeral river. The student used the same sampling sites, but only sampled two trees per species per sampling site and concentrated mainly on biomass and not much sorting and identification was done.

Perennial rivers are found only at the northern and southern borders of Namibia and all such rivers originate in neighbouring countries. All the rivers that actually originate in Namibia are ephemeral rivers in that they are usually dry and only flow after strong rains have fallen in their catchments. These rivers are very important because they support approximately 20% of the population and are an important source of water for people and fodder for domestic animals and wildlife

(Jacobson *et al.*, 1995). Flooding of these rivers is extremely important because it channels huge quantities of water, as well as organic matter and nutrients, which are all very valuable sustenance for the riparian vegetation. Seeds are washed down from the catchments which can affect the distribution of vegetation downstream. Changes in vegetation can change the distribution of wildlife. Flooding also helps to replenish the ground water (Loutit, 1991).

1.3 Why trees?

Trees provide an excellent framework for research on insect community dynamics because they can be considered discrete and long lasting ecological units (Southwood & Kennedy, 1983). Trees also have great niche diversification because of structural complexity (Lawton & Price, 1979). Moran and Southwood (1982) regard trees as ideal habitats for studying insects. They used trees to study inter-specific comparisons, as well as comparisons of fauna on conspecific trees within and across countries.

In this study the east-west flowing Omaruru River constituted the larger study area and the three widely representative focus trees species were *Acacia erioloba* E. Meyer (Fabaceae; camel-thorn), *Faidherbia albida* (Del.) A. Chev (Fabaceae; anaboom) and *A. tortilis* (Forsk.) Hayne (Fabaceae; umbrella-thorn). Large trees growing in ephemeral rivers do not depend on rainfall as much as trees growing away from rivers, as they obtain their required water and nutrients from an edaphic environment with little differences across the rainfall gradient. Do *et al.* (2005) stated that, in dry tropics, groundwater is the major environmental variable that controls canopy dynamics. In the case of the focus tree species, which are aided by long tap-roots, nutrients are obtained from ephemeral westward-flowing river beds. The Omaruru River originates approximately 60km east of the town of Omaruru where rainfall can be in excess of 400 mm per year, but by the time it reaches the coast, rainfall has declined to near zero (Jacobson *et al.*, 1995).

Due to the fact that the riparian trees obtain their water requirements from a year-round underground water supply, flowering and new growth commence during the same period each year. In contrast, outside the river beds, where water and nutrient supplies are more unpredictable, this is not the case. This synchronized pattern helps to decrease/limit the number of ecological interactions determining diversity, with temperature, humidity and maybe altitude constituting the major constraints.

Insects have complex life-cycles and a series of life stages can be found in many species. Some groups are hemimetabolous (the hatching eggs develop into nymphs, which resemble the adults in both body form and feeding habits) whilst other groups are holometabolous (the eggs hatch into caterpillars or grub-like larvae which are quite unlike the adults in both feeding habits and appearance). Juvenile stages of the latter groups specialize for rapid feeding and growth, and usually consume completely different resources from those used by adults. One has to keep this in mind when collecting and identifying insects. The different stages may inhabit different parts of the tree and may even be active during different seasons. However, as stated by Erwin (1989), by sampling during different seasons it is possible to collect species normally living inside the wood or bark, because at some point in time they disperse and lay eggs on different surfaces of the plant. Basset (2001) also noted that some insect orders may be abundant, but difficult to sample, for example Isoptera (especially termite workers, who rarely move beyond their galleries), photophobic Blattodea (who tend to hide under the bark) and minute Thysanoptera (who may be very seasonal).

1.4 Objectives of the study

For this study the following questions were posed: (1) How does the entomological diversity found in the canopies of each of the selected tree species compare overall?; (2) What quantitative and qualitative influence does increased aridity across a transect have on the faunal composition associated with the canopies of the three tree species?; (3) What quantitative and qualitative influence does seasonality have on the faunal composition associated with the canopies of the three tree species?.

It is envisaged that this study will not only provide a better understanding of the effects of increased aridity across a transect on species abundance and diversity, but that it will also provide valuable insight into the importance of riparian systems as biodiversity sinks in larger water scarce landscape systems. Specifically adapted desert fauna therefore play a secondary role in the context of the study, with the focus rather being on the impact of increased aridification on diversity indices and community structure.

Agriculture plays an important role in Namibia. Changes in the abundance and distribution of insects (due to climate change for example) might influence the productivity of Namibia's agricultural sector and, as a result, its economy as well. Understanding the impact of climate change on species will help scientists to suggest which species, habitats and regions are most at risk from climate change, which in turn will aid government bodies in making sound environmental policy decisions. Another advantage of this study is that it will provide insight into arid region landscape ecology, specifically arid region ecosystem function.

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CHAPTER 2

MATERIALS AND METHODS

2.1 Study area

Sampling was done at five study sites along the Omaruru River (Figure 1; Table 1), one of the twelve major ephemeral rivers in Namibia, between longitudes 21° and 22° S, and latitudes 14° and 17° E. The river originates in the Etjo Mountain, about 60 km east of the town of Omaruru, and runs for 330 km in an east-west direction with a catchment area of 13 100 km² (Jacobson *et al.*, 1995). The mountainous catchment area receives 200-450 mm rain per annum (Geyh & Ploethner, 1995). The river then runs through private farms, the town of Omaruru and communal settlements such as Okombahe and NaiNais. At Okombahe the river supports a community farming with wheat (*Triticum* spp) and maize (*Zea mays*) crops. Groundwater rising to the surface also provides water for livestock in the region and supports a dense forest of ana trees (*Faidherbia albida*) on which the livestock depend. Approximately 40 km from where the Omaruru runs into the sea (close to Henties Bay) the Omdel Dam was built in 1993. Its purpose is to contain silt-laden flood waters, allowing the silt to settle. Silt-free water is then drained into the sandy riverbed downstream, replenishing the aquifer. (Jacobson *et al.*, 1995). The Omaruru River supplies water to Henties Bay, Swakopmund, Arandis and Rössing mine. The climate of the Omdel region itself is hyper-arid with an annual rainfall of less than 50 mm (Geyh & Ploethner, 1995).

Most botanists in Namibia use the system of vegetation types proposed by Giess (1971). According to Giess (1971) three major vegetation zones can be distinguished, namely deserts, savannas and woodland. These are determined primarily by rainfall and to a lesser extent by temperature. These three zones can again be subdivided, into 13 biomes on the basis of their characteristic plant species. The Omaruru River originates in the thorn bush savannah biome, then runs through the semi-desert and savannah transition biome and finally through

the central Namib biome, where it runs into the Atlantic Ocean just north of Henties Bay. Although the vegetation differs among these three biomes, the riverine vegetation shows less variation, to the extent that the first two sample sites (Otjikoko farm and Omaruru town) are very similar to each other.

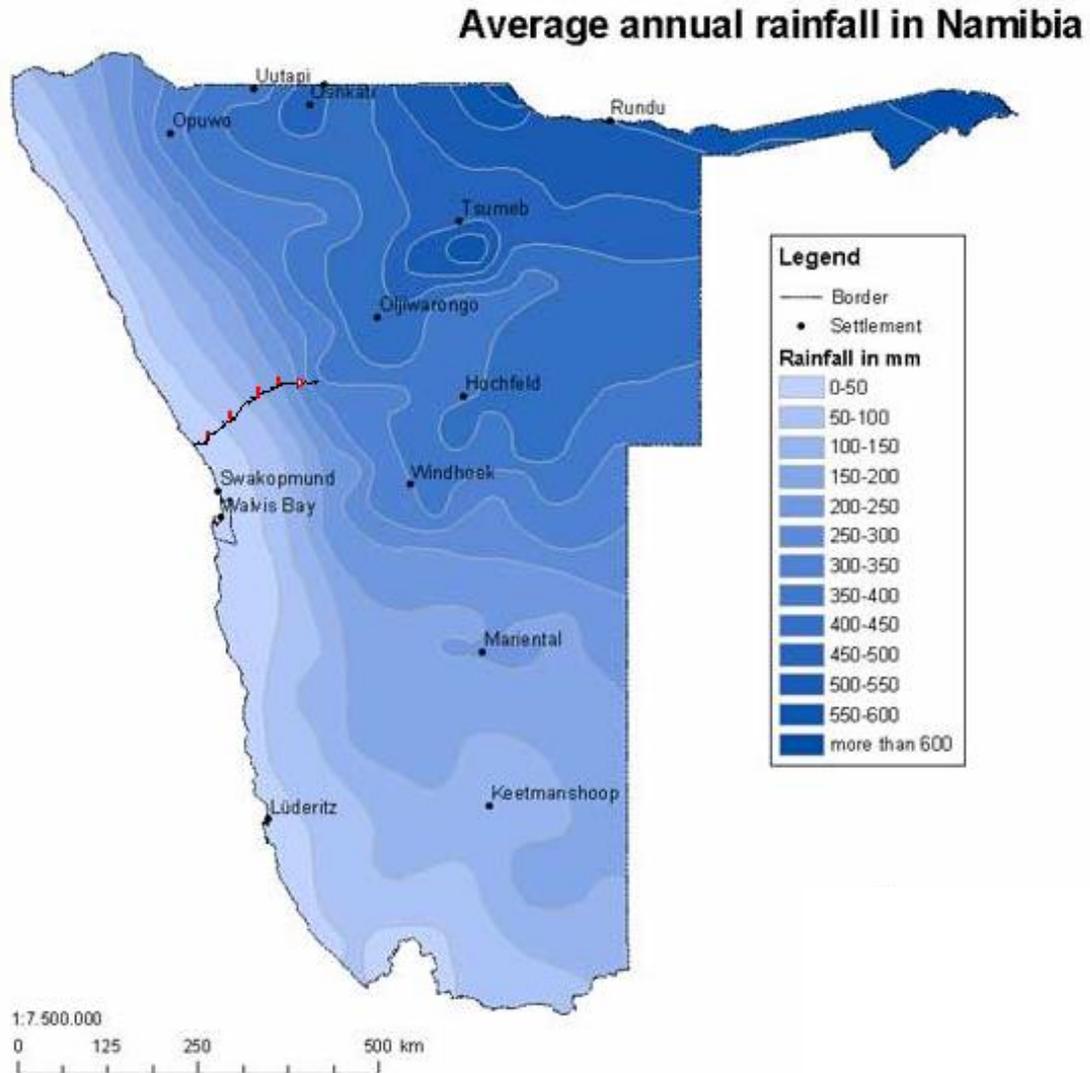


Figure 1. Mean annual rainfall in Namibia and position of sampling sites (red blocks) situated along the Omaruru River (modified from Mendelsohn *et al.*, 2003).

At the first two sampling sites from the origin of the Omaruru River (Otjikoko and Omaruru) the riparian vegetation consists mainly of *Acacia* species, *Faidherbia albida*, *Ziziphus mucronata* and *Boscia albitrunca*. Dense undergrowth and a variety of grasses form part of the riverine vegetation. Further to the west, at Okombahe, the riverine vegetation becomes less dense. The number of trees per species decrease, but the species composition remains fairly similar. The undergrowth is however, considerably less diverse, as well as the grass diversity. At NaiNais the vegetation is even more exposed with almost no undergrowth and very little grass. Trees are further apart from each other and there is little canopy overlap. At the most western site (Omdel Dam) there is almost no undergrowth (bushes and shrubs). Grass is visible only during some months and the area is mainly comprised of open gravel plain. *Faidherbia albida* and *Acacia tortilis* are the dominant tree species. Many *Prosopis* trees are also found, but *Acacia erioloba* is scarce. The sample trees were restricted to a narrow line along the edge of the river, but were sufficient distances apart to be considered independent units (each tree not affected by the fogging of neighbouring trees). Otjikoko and Omaruru are 40 km apart, Omaruru and Okombahe 60 km apart, Okombahe and NaiNais 70 km apart and NaiNais and Omdel 90 km apart.

Table 1. Farms/areas along the Omaruru River (Namibia) where insect sampling took place from May 2004 to April 2005.

Rainfall gradient	Sampling site	Name of farm/area
50 - 100 mm	Site 5	5 km down river from Omdel Dam
100 - 150 mm	Site 4	50 km SE of Uis town (NaiNais)
200 - 250 mm	Site 3	Okombahe town area
250 - 300 mm	Site 2	Omaruru town area
300 - 350 mm	Site 1	Otjondijisse (Otjikoko Hunting Farm)

2.2 Selected tree host species

Species were selected on the basis of their widespread distribution to allow for future comparison between other areas with the same host species. In addition, the study required that host tree species should be found in abundance at each of the study locations along the Omaruru River.

2.2.1 *Acacia erioloba* E. Meyer

The camelthorn is a symbol of Namibia. In high rainfall areas with deep sandy soil the tree species can grow quite high (over 8 m), but in drier, more inhospitable habitats, it doesn't grow that tall (about 1-3 m on rocky outcrops) and can become gnarled and deformed in appearance (Von Koenen, 2001 and Curtis & Mannheimer, 2005). In favourable habitats the camelthorn can grow up to 17 m high (Roodt, 1998). It is the most widespread *Acacia* species in Namibia, occurring throughout most of the country (Figure 2). *Acacia erioloba* can be found in a wide range of vegetation types and in almost all habitats. It mostly grows on sand, but can also grow on clay, gravel and stony or rocky areas. It is one of the more prominent tree species in the Namib Desert (Palgrave, 1977; Van Wyk & Van Wyk, 1997 and Curtis & Mannheimer, 2005).

A. erioloba can be distinguished from other acacias by the blue-green colour of the foliage, the almost black bark and the untidy, pendant, broken branches and twigs. Young twigs are noticeably angled (zigzagged) between pairs of large, white thorns. The most outstanding characteristic is the large ear-shaped pods (Roodt, 1998). The pods provide an excellent fodder for stock and farmers have reported a noticeable increase in milk-yield of cows that have been fed them (Palgrave, 1977 and Roodt, 1998).

The wood of *Acacia erioloba* is dark red-brown and very strong, resistant to borers and termites and in the past had been used for mine props and wagon-building. It also makes good firewood. The camelthorn is a deciduous tree

which loses its leaves for a short period only. However, due to the fact that the roots can tap subterranean water, they have foliage virtually throughout the year and the value for animals of the shade which they provide in desert areas cannot be over-estimated (Palgrave, 1977 and Roodt, 1998).

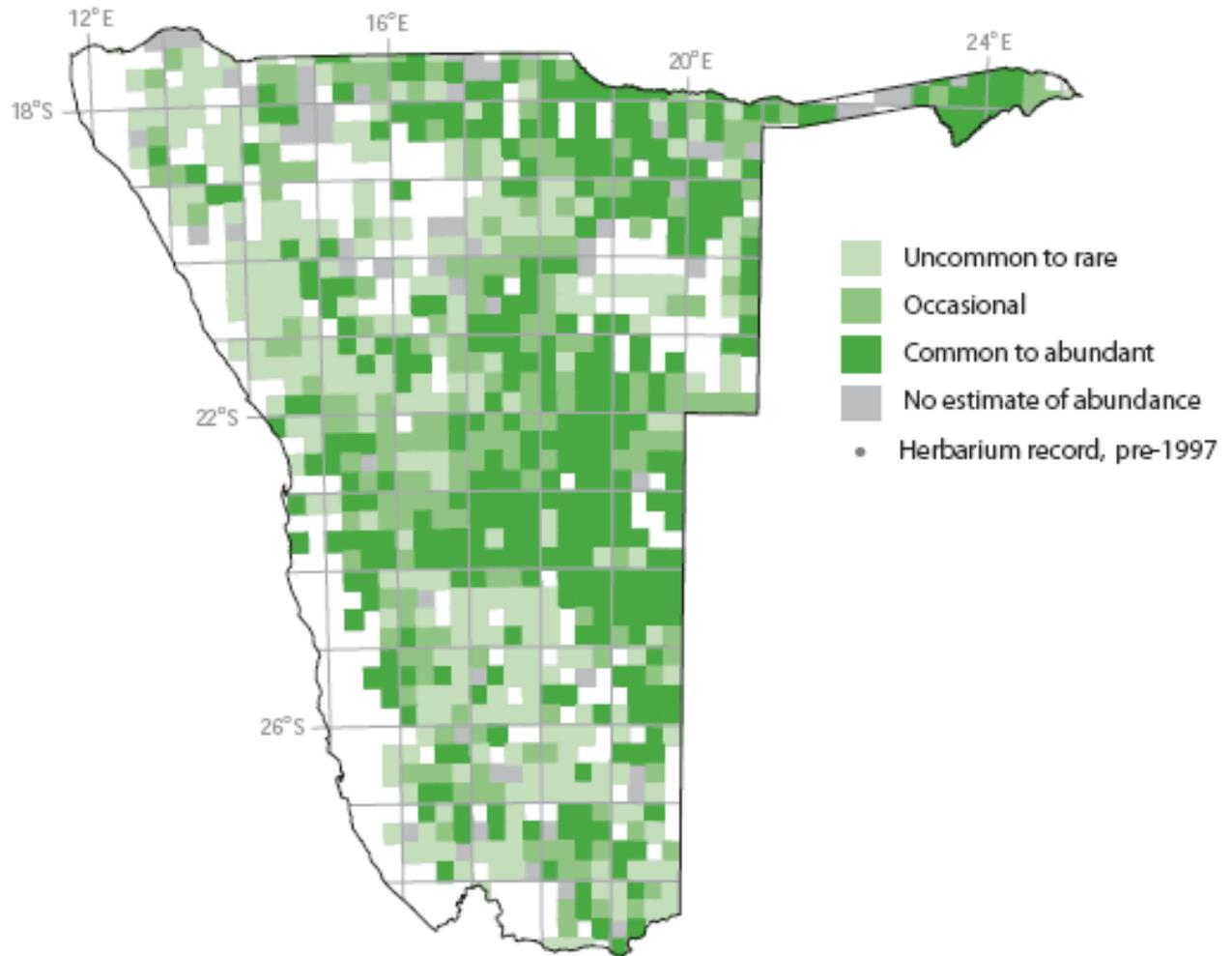


Figure 2. Distribution of *Acacia erioloba* in Namibia (Curtis & Mannheimer, 2005).

2.2.2 *Faidherbia albida* (Del.) A. Chev.

This tree, also known as the anaboom, is widely distributed in semi-arid Africa. In Namibia it occurs mainly in the north western and central western parts, is

occasionally present along the eastern part of the Okavango River and is common in the extreme eastern areas of Caprivi (Figure 3). The anaboom grows mainly in dry riverbeds and along the banks of perennial rivers (Curtis & Mannheimer, 2005). It grows to more than eight meters in height (Curtis & Mannheimer, 2005), with spreading branches and a rounded crown in mature plants, but slender and more upright in young ones (Van Wyk & Van Wyk, 1997). It bears finely pinnate leaves and thorns. In mid-winter it unfolds cream-coloured spiky flowers (Von Koenen, 2001).

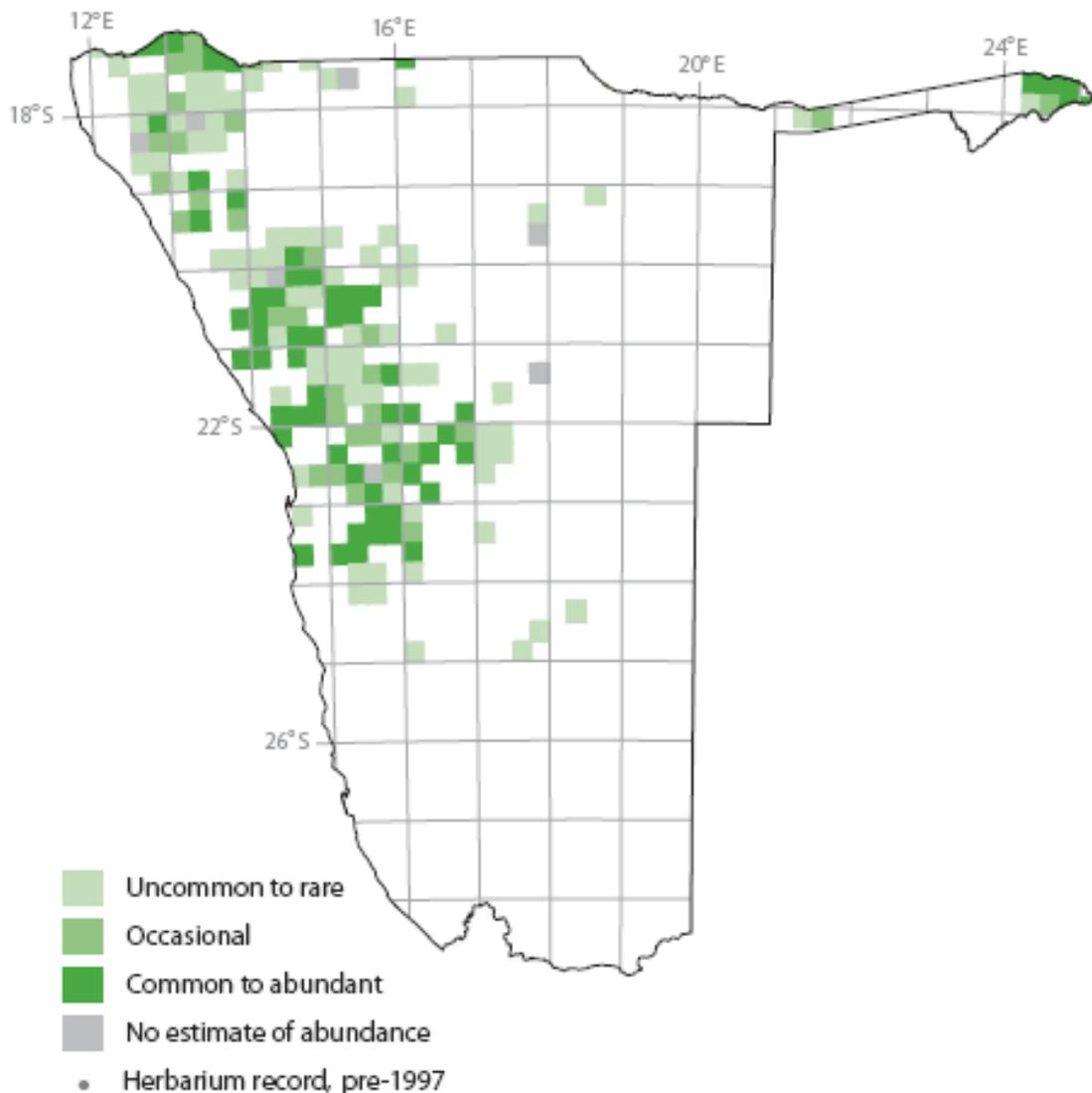


Figure 3. Distribution of *Faidherbia albida* in Namibia (Curtis & Mannheimer, 2005).

Faidherbia albida is a multipurpose tree widely used by Namibians for food, beverage and medicinal purposes. Livestock and game eat the leaves and pods (Van Wyk & Van Wyk, 1997 and Curtis & Mannheimer, 2005).

What makes this tree even more popular in Namibia is that apart from the fact that it provides valuable fodder, it also doesn't compete much with crops for water resources, especially with those growing during the wet season. This is due to a process referred to as reverse phenology. As described by Roupsard *et al.* (1999) the tree bears leaves and fruit during the dry season. After the first rains leaves are shed and growth resumes only at the end of the wet season. This phenology was confirmed by Curtis & Mannheimer (2005). In Namibia their leaves are essentially evergreen, but most leaves are shed in summer, from December to March, with new leaves formed from July to September.

F. albida has a deep tap-root system (with depths of up to 30 m) which allows it to extract water from deep soil layers or from the water-table. This is probably the reason why growth can occur during the dry season. The deep roots also allow the tree to sustain growth, without competing too much with crops for water uptake (Roupsard *et al.*, 1999).

2.2.3 *Acacia tortilis* (Forsk.) Hayne

This flat-crowned acacia is synonymous with the African savannah landscape. The English common name Umbrella thorn describes the umbrella shape and the Afrikaans common name Haak-en-steek describes the thorns of the species (Roodt, 1998). They form small or medium-sized trees with the crown typically flattened and spreading outwards. They occur in dry areas, bushveld and grassland (Palgrave, 1977 and Van Wyk & Van Wyk, 1997).

This species is commonly found on plains and along rivers, mostly in the central interior of Namibia, extending to the northwest and scattered in the northeast and southeast (Figure 4). It is most abundant and dominant on the north central plateau (Curtis & Mannheimer, 2005).

The taproot is exceptionally deep, enabling the plant to tap water at great depths. The pods are unique to acacias in that they are completely distorted, to form untidy clusters, sometimes curled into a corkscrew spiral. The leaves and pods, which are browsed by stock and game, are very nutritious and the bark is eaten by elephant. The tree also yields an edible gum favoured by many animals. Otherwise the tree is of little commercial value. It is easily raised from seeds, and although rather slow-growing, is very hardy and drought-resistant (Palgrave, 1977 and Roodt, 1998).

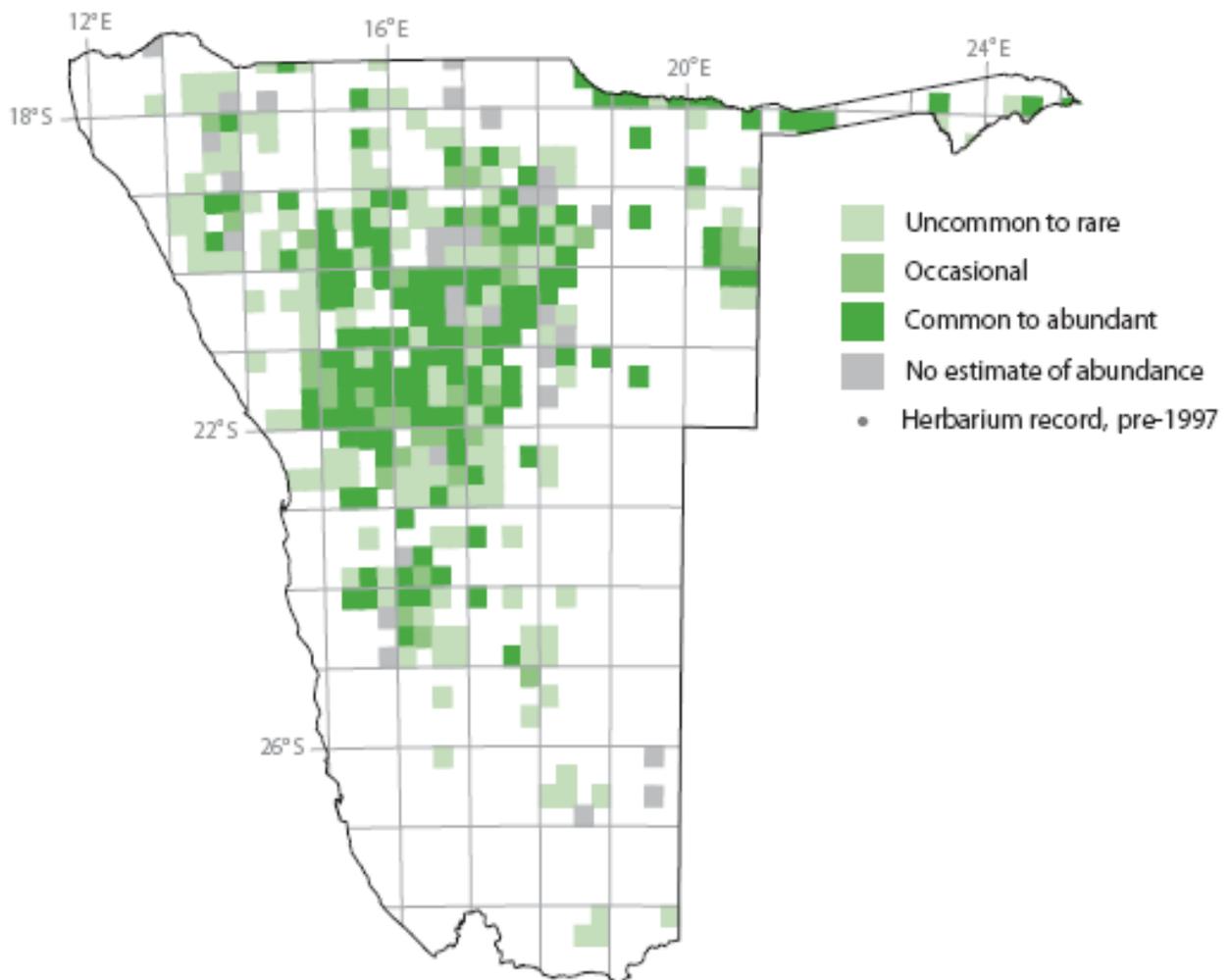


Figure 4. Distribution of *Acacia tortilis* in Namibia (Curtis & Mannheimer, 2005).

In Namibia, apart from using it as shade, *Acacia tortilis* is also utilized for food and industrial purposes (Curtis & Mannheimer, 2005).

When considering the three tree species that were sampled during the study, there is little structural difference between them. Both the camelthorn and the umbrella thorn belong to the *Acacia* genus and the anaboom was once also classified as *Acacia albida* – due to its similar characteristics. The morphological similarity might imply similar niches and therefore similar insect population dynamics. One major difference, however, is the reverse phenology processed by *Faidherbia albida*. This may lead to seasonal distribution differences of the associated insect species.

Therefore, by sampling trees all dependant on similar edaphic conditions, and trees similar in morphology, differences in associated insect diversity can be explained by investigating differences in the aridity gradient, which is determined by factors such as temperature, precipitation and evaporation rate.

2.3 Experimental design

A reconnaissance trip was undertaken, during April 2004, to the various proposed sampling sites (Table 1) along the rainfall gradient. At each site four individuals for each of the three tree species were identified (*i.e.* 12 trees at each sampling site,) and a GPS reading taken for each (Table 2, Figure 5). Trees whose canopies were isolated from surrounding trees were selected. This was to prevent that neighbouring trees skew the data. Where possible, trees of similar height, trunk diameter and canopy circumferences were also selected. It was however, not always possible because *F. albida* in general has thicker stems than *A. tortilis* and *A. erioloba* trees of approximately the same height/age, and they also tend to grow into taller or more slender trees than the two acacia species. It was also not possible to find four individuals of each species at each of the sites. At Okombahe, as well as at Omdel, only two *A. erioloba* trees could be found for each site and of this total three were smaller than the average trees

selected. At both these sites there were no other individuals within a 1 km range to all the other sample trees. At NaiNais, only three *A. tortilis* trees could be found and at Otjikoko only three suitable *F. albida* trees were found. Although there were other *Faidherbia* trees, none of them were suitable because they were too high for fogging from ground level. In total then 54 trees were sampled (19 *Acacia tortilis*, 16 *Acacia erioloba* and 19 *Faidherbia albida*). (The complete study design was only filled at Omaruru, with four individuals for each of the three tree species.)

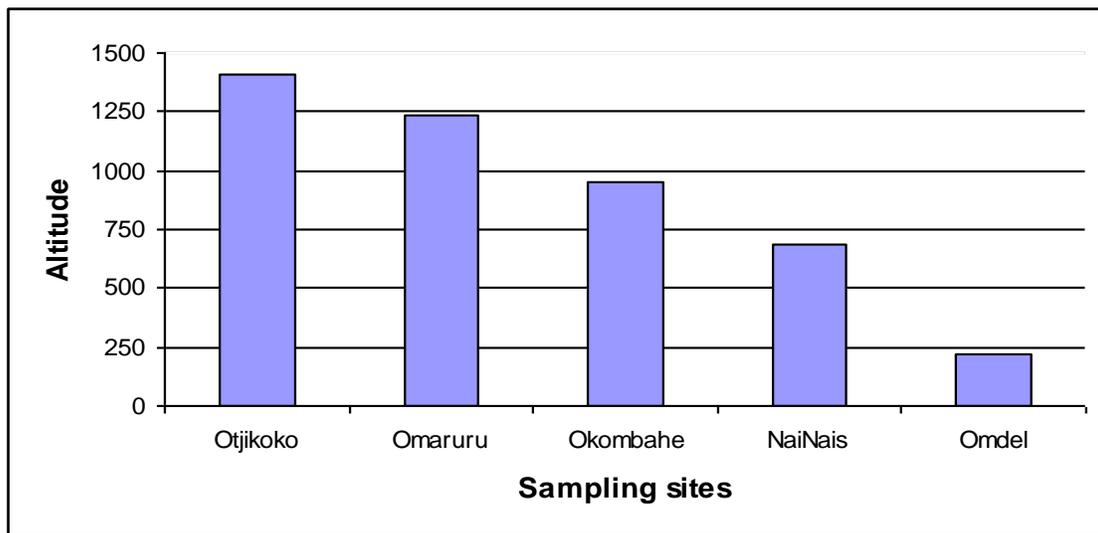


Figure 5. Average altitude of sample sites along the Omaruru River (Namibia).

For each tree species (at each site) the four individuals were given a unique number, for example At1; At2; At3 and At4. Each tree was spot-marked with red spray-paint, with the number of spots corresponding to the tree number. A piece of white and red chevron tape was also tied around the trunk of each tree to help with easy location until the trees became familiar later on during the project. The immediate area surrounding each tree was cleared of debris and the branches of nearby trees, as well as all low-hanging branches of the sample tree were pruned back and all dead material at the base of the tree was removed. This was to allow setting up of the collecting sheets and for easy movement around the tree when fogging.

Studying tree-living insects can be a difficult task. Studying insects in *Acacia* species is also a 'thorny task'. The first person who attempted to quantitatively collect insects from tree canopies was O.W. Richards from the University of Oxford who, in 1929 hoisted light traps up into the canopies. However, it was only during the early 1970's, with the development of fogging and light-trapping techniques, that insect mass-collecting started to progress with a noticeable increase during 1993 (Basset, 2001). The use of insecticides has been a major breakthrough and it is now the most utilized method, despite the fact that some species are not collected, like those hidden in crevices, under bark or mining in leaves (Marques, *et al.* 2006). Pyrethroid is a non-residual insecticide with high knock-down but low killing effect. The advantage thereof is that insects can be collected without being killed and can therefore also be used for investigations of life history strategies, as explained by Paarmann & Stork (1987). Another advantage, especially for this study, is the fact that only insects from the tree that has been fogged will collect on the sample sheets. With light traps insects are being lured from a wider area and one cannot use the data to differentiate between different tree species for example.

Table 2. Geographic coordinates and altitude for each study tree sampled along the Omaruru River (Namibia) during May 2004 – April 2005.

Waypoint nr	Sampling station	Tree nr	Latitude			Longitude			Altitude
			Degrees	Min	Sec	Degrees	Min	Sec	
L1B1	Otjikoko	Fa1 + Fa2	21	12	23.2	16	18	28.3	1413
L1B2		Ae1	21	12	24.2	16	18	29.3	1405
L1B3		Fa3	21	12	24.9	16	18	28.2	1404
L1B4		At1	21	12	24.7	16	18	25.7	1411
L1B5		At2	21	12	24.5	16	18	26.2	1411
L1B6		At3	21	12	23.6	16	18	27.4	1408
L1B7		At4	21	12	24.6	16	18	29.4	1403
L1B8		Ae2	21	12	26.1	16	18	28.6	1405
L1B9		Ae3 + Ae4	21	12	27.3	16	18	34	1408
L2B1	Omaruru	At1	21	24	28.8	15	58	39.6	1232
L2B10		Ae3	21	24	27.7	15	58	42.2	1230
L2B11		Ae4	21	24	25.3	15	58	40.7	1234
L2B12		Fa4	21	24	24.3	15	58	43.5	1235
L2B2		Fa1	21	24	29.1	15	58	38.7	1233
L2B3		At2	21	24	30.3	15	58	39.5	1232
L2B4		Fa2	21	24	28.2	15	58	38.4	1233
L2B5		Fa3	21	24	30.3	15	58	37.7	1231
L2B6		Ae1	21	24	30.8	15	58	39.3	1231
L2B7	At3	21	24	31.1	15	58	40.6	1234	
L2B8	At4	21	24	30.2	15	58	41.3	1237	
L2B9	Ae2	21	24	29	15	58	41.6	1231	
L3B1	Okombahe	Ae1	21	21	8	15	24	59.5	951
L3B10		Ae2	21	21	9.4	15	25	11	949
L3B2		At1	21	21	8.5	15	25	1.9	950
L3B3		At2	21	21	6.9	15	25	2.8	950
L3B4		At3	21	21	7	15	25	4	950
L3B5		At4	21	21	6	15	25	4.1	949
L3B6		Fa1	21	21	1.9	15	24	58	947
L3B7		Fa2	21	21	4	15	24	58.9	948
L3B8		Fa3	21	21	3.6	15	25	5.5	947
L3B9	Fa4	21	21	3.6	15	25	5.5	951	
L4B1	NaiNais	At1	21	28	39.7	15	2	16.3	685
L4B10		Ae4	21	28	29.8	15	2	9	686
L4B11		Fa4	21	28	31.6	15	2	13.6	688
L4B2		At2	21	28	39.2	15	2	15.8	687
L4B3		At3	21	28	40.3	15	2	15.8	689
L4B4		Ae1	21	28	38	15	2	15.8	693
L4B5		Fa1	21	28	41.9	15	2	14	693
L4B6		Ae2	21	28	41.8	15	2	13.8	695
L4B7		Fa2	21	28	31.7	15	2	8.8	675
L4B8	Fa3	21	28	31.4	15	2	8.8	676	
L4B9	Ae3	21	28	30.4	15	2	8.5	682	
L5B1	Omdel	Fa1	21	54	2.1	14	29	43.7	212
L5B2		Ae1	21	54	1.8	14	29	45.9	210
L5B3		Fa2	21	54	2.6	14	29	46.9	212
L5B4		At1+2, Ae2	21	54	2.3	14	29	48.4	214
L5B5		Fa3	21	54	4	14	29	45.7	214
L5B6		At3	21	54	2.7	14	29	37.6	221
L5B7		Fa4	21	54	4.8	14	29	34	220
L5B8		At4	21	54	2.6	14	29	41.3	225

2.4 Sampling

Fogging was conducted on a bi-monthly basis, always working in the same order along the rainfall gradient (from east to west). Sampling was done during the following periods: May 2004 and July 2004 (Winter/Dry season); September 2004 and November 2004 (Spring/Pre-rainy season); January 2005 and March 2005 (Summer/Rainy season).

Sampling sessions were at least one and a half month (mostly two) apart to allow ample time for insect re-colonisation in the tree canopies. Lucky *et al.* (2002) stated that previous experiments showed re-population occurred after about 10 days. Erwin (1989) suggested that re-population in tropical forests takes place within 10-30 days, and when fogging at Tambopata and Pacaya-Simiri (Peru) he found that re-fogging after 10-30 days resulted in as diverse and abundant an insect sample as the initial one. He therefore concluded that the arboreal fauna is highly mobile and that the canopy and sub-canopy acted as horizontal highways across which mass daily faunal movement of arboreal insect species takes place.

Fogging was conducted at dawn, to take advantage of the calmer weather conditions that generally occur in the morning, and also to capture both diurnal insects (before alate species fly off) and nocturnal insects (already settled for the day). Albeit that Andrew & Hughes (2005) for example sampled between 07:00 and 11:00, it was found to be too late in the day for the harsh conditions at the study sites, since the wind usually started blowing from around 10:00. The actual sampling time differed depending on the season, but this usually commenced from around 05:30 to 06:00.

Similar studies that have been conducted (mostly in the tropics) used funnel-shaped trays to collect dropping insects (Erwin, 1989, Krüger & McGavin, 1998 and Marques *et al.*, 2006). However, in the open savannah areas of Namibia there is enough space around each tree to allow for a bigger collecting area.

Nine white plastic sheets, each approximately 1 m by 1,2 m were positioned underneath each tree (in three rows and three columns) with the trunk of the tree more or less in the middle, suspended on 1 m long metal droppers to prevent terrestrial insects from crawling onto the sheets. The sheets overlapped each other and were secured around the trunk of the tree as tightly as possible – resulting in a $\pm 10 \text{ m}^2$ surface area (Figures 6 & 7).



Figure 6. Plastic sheets suspended on metal droppers underneath sample trees (Omaruru River, Namibia). (Photo: J. Theron, 2005)



Figure 7. Sheets positioned around the trunk of a tree to be sampled (Omaruru River, Namibia). (Photo: J. Theron, 2005)

Pyrethroid insecticide was mixed with paraffin (400 ml insecticide to 5 l paraffin). From ground level this was blown into the canopies of individual trees as a smoke-like fog by using a Motan Swingfog SN 50 disperser (Figure 8). This procedure provided rapid knockdown on the above-mentioned sheets.



Figure 8. Motan Swingfog SN 50 disperser used to knock down insects from trees (Omaruru River, Namibia). (Photo: J. Theron, 2005)

The advantage of this method is the degree to which the mist can be directed accurately into the canopy from ground level. Fog was released for about one to two minutes or until the entire canopy was covered in fog (Figures 9a and b). Fogging during wind-still conditions allowed for easy assessment of when sufficient fogging had been conducted.



a



b

Figures 9a and b. Fog released into the trees (Omaruru River, Namibia). (Photos: J. Theron, 2005).

Bigger insects were hand-sampled using forceps as soon as they dropped, and placed into a plastic sampling bottle, containing 70% Ethanol. This was done prior to folding the sheets with material in order to avoid damage to the specimens (Figure 10).



Figure 10. Larger insects on a collecting sheet (Omaruru River, Namibia). (Photo: J. Theron, 2005)

After about 40-45 minutes the sheets for each tree were removed from the droppers and folded to ease subsequent handling (Figure 11).



Figure 11. Folding sheets for transportation purposes (Omaruru River, Namibia) (Photo: J. Theron, 2005)

Careful folding allowed easy and secure handling of sampled material. Krüger & McGavin (1997) used a drop-time of 1 hour. However, during this study it was found that species started to recover after about 40 minutes. Some small locusts (Orthoptera) and silverfish (Thysanura) were even more resistant and had to be captured by hand as soon as possible to avoid them crawling or jumping from the sheets. The nine sheets and a sampling bottle for each tree were contained together (Figure 12).



Figure 12. Sheets and sampling bottles for 8 trees sampled (Omaruru River, Namibia). (Photo: J. Theron, 2005)

The sheets were removed in the same order in which the trees were fogged, in order to allow the insects the same time span to drop onto the sheets. After all sheets were picked up, the nine sheets for each tree were opened one by one and the knocked-down material collected by using a hand-held vacuum machine (Figure 13). All this material (per tree) was then added to the same sampling bottle in which the larger specimens had already been placed (Figure 14).



Figure 13. Insects being vacuumed from the sheets (Omaruru River, Namibia). (Photo: J. Theron, 2005)



Figure 14. Final sample for 8 trees (Omaruru River, Namibia). (Photo: J. Theron, 2005)

In the lab and between sampling regimes this material was sorted into orders and eventually morphospecies (or recognizable taxonomic units) and referred to as RTUs (Figure 15).



Figure 15. Sorting canopy insects into morphospecies (RTUs). (Photo: J. Theron, 2005)

Some of the bigger orders (*e.g.* Coleoptera), some of which formed the bulk of the study, were also sorted into families. All the fauna (per tree per sampling regime) were then quantified and recorded on a data-sheet, under the following headings: Site; Date; Tree species.; Tree nr.; Order; Family; Number of individuals; Comments and Collection number.

Identification was done by Eugene Marais, the resident entomologist of the National Museum of Namibia. The complete reference collection, together with all the sampled material of the project, was transferred to the National Museum of Namibia in Windhoek for further identification and safe-keeping.

Macro- and micro-climatological data were gathered during the course of the study and rain gauges were put up at each site. A data-logger for measuring temperature and relative humidity were also placed at each site. Each data-logger was secured onto a branch of a tree between smaller branches and leaves to avoid direct sunlight as far as possible. The position of each data-logger was logged onto a GPS.

2.5 Data analysis

A mixed model analysis of variance (ANOVA PROC MIXED (SAS Institute 2010)) was used to examine the fixed effects of tree species, season, and sample location, as well as the random effect of replicate trees, which was tested within tree species and sample location. Separate ANOVA tests were performed for these effects on i) number of individuals, ii) RTU richness, and iii) diversity of four orders, *i.e.* Coleoptera, Diptera, Hemiptera and Hymenoptera. Least square means for each level of the main effects, namely tree species, season, and sample location were also reported. The SAS program's CATMOD (categorical modelling) procedure was also used to look at the interaction between the three tree species and relative representation of the four insect orders. These results were compared to the results of Chi-square analysis. The Chi-square analysis was also used to investigate the proportion of different phagy types (plant eating insects) on the three tree species sampled. The Sørensen's Quotient of Similarity was used to determine which sites and tree species had the most similar communities of insects.

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CHAPTER 3

TAXON SUMMARY

Data loggers, placed at each site, took temperature and Relative Humidity readings daily at 06:00, 14:00 and 22H00. These variables were used to verify and quantify the aridity gradient across the study area. A summary of all insect orders sampled is also given below, after which only the four biggest orders (Coleoptera, Hemiptera, Hymenoptera and Diptera) will be discussed in more detail. The occurrence of phytophagy was also investigated and the results given below.

3.1 Abiotic measurements

Temperature and Relative Humidity, captured by data loggers, showed marked seasonality in the study area, with warm, wet summers (November to April) and drier, cooler winters (May to September). Mean monthly maximum temperatures (taken at 14:00) during the study ranged between 18,14°C and 43,26°C (Figure 1) and the mean monthly minimum temperature (taken at 06:00) from 6,7°C to 20,34°C (Figure 2).

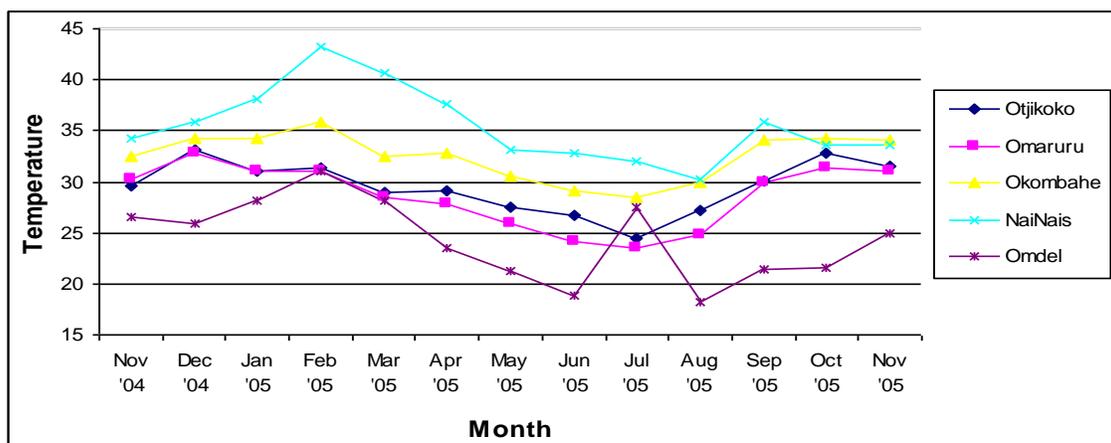


Figure 1. Mean monthly maximum temperatures, taken at 14:00, at each sampling site along the Omaruru River (Namibia) in 2004-2005. (Note temperature spike in July for Omdel due to east winds.

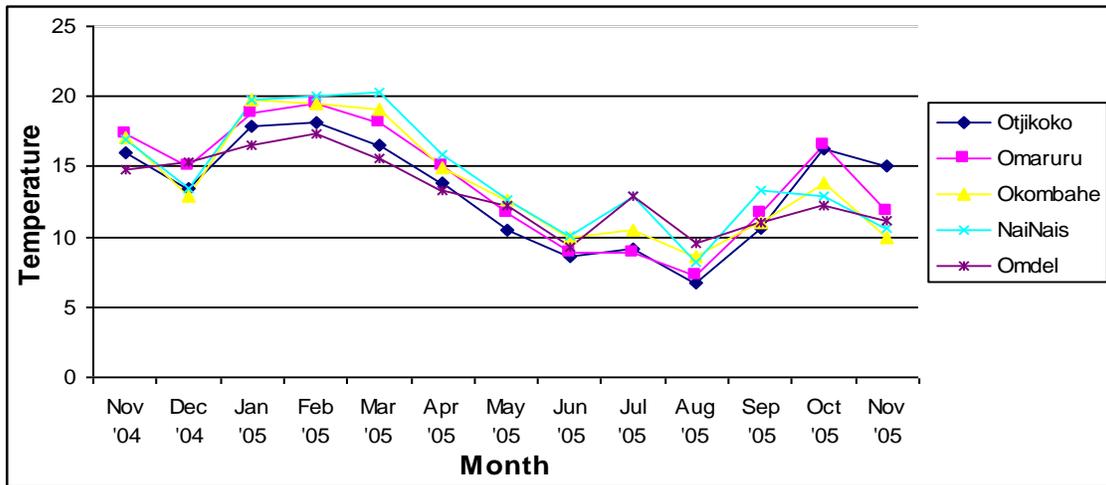


Figure 2. Mean monthly minimum temperatures, taken at 06:00, at each sampling site along the Omaruru River (Namibia) in 2004-2005. (Note temperature spike in July for Omdel and NaiNais due to east winds).

In both graphs it is clear that the temperature is generally higher at more western sample sites. NaiNais (site #4) has higher temperatures than Okombahe (site #3), Okombahe higher than Omaruru (site #2) and Omaruru higher than Otjikoko (site #1, moving from west to east). Omdel, although being the most western sampling site, generally has lower temperatures due to the proximity to the coast and the presence of fog. During July, however, Omdel showed an exceptional increase in both minimum and maximum temperatures, due to strong east winds (also known as berg winds).

The results for both maximum RH (Figure 3) as well as minimum RH (Figure 4) showed a decrease (drier conditions) from April through to September. These months are generally seen as the winter or dry months in Namibia (Chapter 1 - Study Area). September to November is seen as the pre-rainy season and an increase in RH can be seen for both min. and max. RH. From November/December to January there is a slight RH decrease before the start of the main rainy season in January. January through to March/April then show the highest RH (both min. and max), and are also the wettest months. Omdel appears to be completely different from the pattern of the rest. From March to June/July the max. RH for Omdel was considerably lower than that of the other stations, indicating that it was much drier, even early in the morning at 06:00.

This was because of east wind conditions starting to develop and reaching its peak in June and July. For the rest of the year the 06:00 readings for Omdel tended to be higher than those of the other stations. Omdel is the closest to the sea and moist fog regularly reaches as far inland as Omdel, which increases the RH.

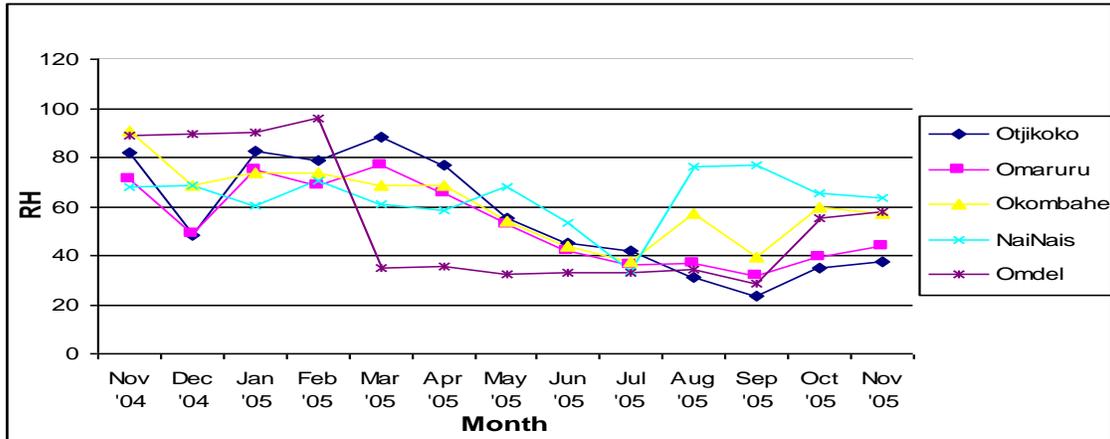


Figure 3. Maximum Relative Humidity, taken at 06:00, from November 2004 until November 2005 at the five sampling sites (Omaruru River, Namibia).

The minimum RH (14:00) shows Omdel to be considerably wetter than the other stations for January through to December. This is again because Omdel lies within the fog zone. However, even for the minimum RH a drop can be seen in July when the east wind season peaks.

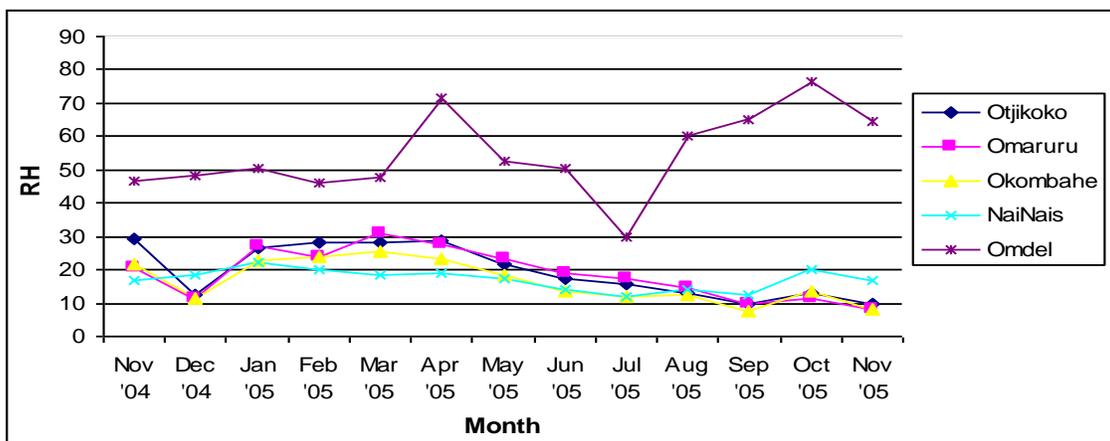


Figure 4. Minimum Relative Humidity, taken at 14:00, from November 2004 until November 2005 at the five sampling sites (Omaruru River, Namibia).

Rainfall gauges were placed at each sample site. For each site, with the exception of Omdel Dam, data was obtained at the end of the study period. However, the data proved to be unreliable due to various reasons and it was therefore decided not to make use of the rainfall data. The Weather Bureau of Namibia, situated in Windhoek, could also not provide rainfall data for the specific sample sites, due to the fact that the areas are not densely populated and no permanent weather stations are in place. Figure 1 in Chapter 2, however, shows that the sample sites are situated along a clear and steep rainfall gradient.

Although no formal vegetation study was done, field observations indicated a noticeable decrease in vegetation from east to west. As the rainfall drops from east to west, so does the vegetation diversity. This means fewer micro-habitats available and therefore less species (not only insects). Although all three tree species can be found at all five sampling sites other species (shrubs, grasses, other trees, ext.) become progressively less from east to west. The plant communities therefore differ and so the number of niches available.

3.2 General results and discussion

A total of 363 076 individuals were collected and sorted during the survey. This total, of which 98.9% were insects and 1.1% arachnids, represented 22 taxonomic orders. The three most abundant groups (in descending order) were Hymenoptera (45%) (of which Formicidae comprised 38%), followed by Coleoptera (21,7%) and Hemiptera (19,7%), together representing 86,4% of the total sample (Figure 5 and Table 1). This closely corresponds with what Basset (2001) found in tropical rain forests.

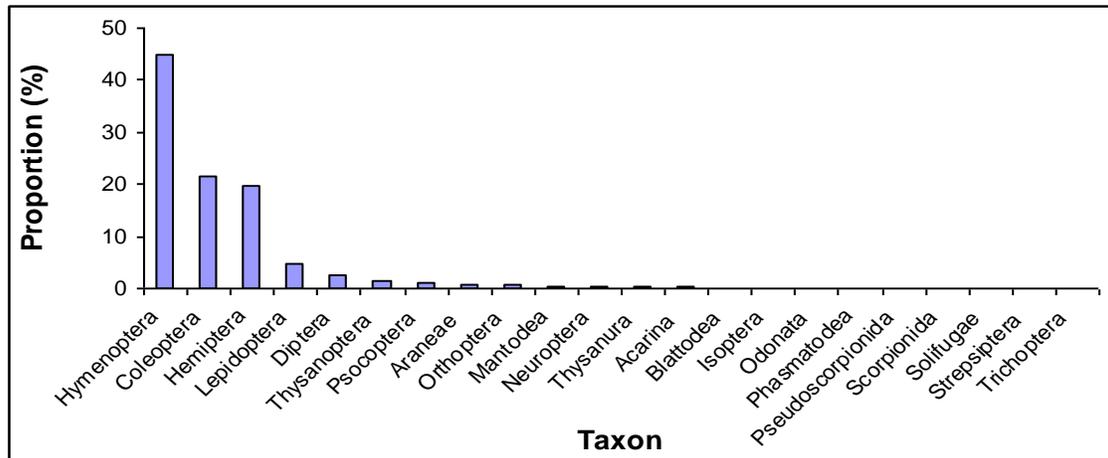


Figure 5. Abundance proportion (%) of arthropods obtained from the canopies of 54 trees, sampled between May 2004 and April 2005 along the Omaruru River (Namibia), in decreasing rank of dominance. (Formicidae included in the Hymenoptera).

Twenty of the orders sampled (90,9%) occurred on all three tree species. Odonata and Trichoptera (only one individual) were only collected from *Faidherbia albida*. Similar to the results of Marques *et al.* (2006) Formicidae was the most abundant taxon. Although present, certain orders were considered to be present in insufficient numbers to provide meaningful data. These orders, *i.e.* Trichoptera, Strepsiptera, Phasmatodea, Odonata, Isoptera, Blattodea, Thysanura, Neuroptera, Mantodea, Orthoptera and Thysanoptera, were excluded from further analysis. Although Lepidoptera was the fourth largest order as far as abundance is concerned, many of the adults can, to a certain extent, be described as tourists – only resting in the tree canopies and cannot be considered to be ecologically associated with the trees. Many were also not accurately identified, due to the fact that most of them were damaged during sampling and/or placed in alcohol vials together with the bulk sample from the sheets and therefore not in a condition for proper identification and accurate distinction. Lepidoptera, therefore, was also not used in any further analysis.

Table 1. Total capture (individuals) and proportion (%) of arthropod taxa obtained from the canopies of three different tree species at the five sampling sites along the Omaruru River (Namibia). (At: *Acacia tortilis*; Ae: *Acacia erioloba* and Fa: *Faidherbia albida*).

Taxon	At		Ae		Fa		All spp	
	Total (individuals)	Proportion (%)	Total (individuals)	Proportion (%)	Total (individuals)	Proportion (%)	Total (individuals)	Proportion (%)
Acarina	405	0.4	163	0.1	92	0.1	660	0.2
Araneae	1146	1.1	1091	1.0	1180	0.7	3417	0.9
Blattodea	165	0.2	218	0.2	50	<0.1	* 433	0.1
Coleoptera	9297	8.5	47230	42.4	26240	16.3	* 82767	21.7
Diptera	2440	2.2	5715	5.1	2221	1.4	* 10376	2.7
Hemiptera	26100	28.7	17790	16.0	13344	8.3	* 57234	15.8
Hymenoptera	36053	33.0	31050	27.9	104458	65.0	171561	45
-Formicidae	[31869]	[29.2]	[16048]	[14.4]	[96740]	[60.2]	[144657]	[38.0]
-Others	[4184]	[3.8]	[15002]	[13.5]	[7718]	[4.8]	[26904]	[7.0]
Isoptera	3	<0.1	2	<0.1	4	<0.1	9	<0.1
Lepidoptera	6950	6.4	3090	2.8	8458	5.3	* 18498	4.9
Mantodea	701	0.6	465	0.4	720	0.4	* 1886	0.5
Neuroptera	297	0.3	497	0.4	226	0.1	* 1020	0.3
Odonata	0	0	0	0	1	<0.1	1	<0.1
Orthoptera	1035	0.9	819	0.7	1307	0.8	* 3161	0.8
Phasmatodea	78	<0.1	14	<0.1	0	0	92	<0.1
Pseudoscorpionida	4	<0.1	3	<0.1	5	<0.1	12	<0.1
Psocoptera	2114	1.9	1689	1.5	902	0.6	* 4705	1.2
Scorpionida	13	<0.1	15	<0.1	29	<0.1	57	<0.1
Solifugae	61	<0.1	30	<0.1	41	<0.1	132	<0.1
Strepsiptera	9	<0.1	8	<0.1	4	<0.1	21	<0.1
Thysanoptera	3923	3.6	767	0.7	1047	0.7	* 5737	1.5
Thysanura	307	0.3	685	0.6	304	0.2	1296	0.3
Trichoptera	0	0	0	0	1	<0.1	1	<0.1
Total	91101	100	111341	100	160634	100	363076	100

* Taxa includes immatures

..... Dominant taxon

..... Dominant taxon excluding ants

The arthropods collected were also grouped into 11 feeding guilds (Table 2), similar to what Moran & Southwood (1982) and Andrew & Hughes (2005) did. If a feeding guild could be exclusively assigned at the order level, the group was not further subdivided. This was the case for spiders (Araneae), caterpillars (Lepidoptera), thrips (Thysanoptera), booklice (Psocoptera), mantids (Mantodea), stick insects (Phasmatodea), cockroaches (Blattodea) and silverfish (Thysanura).

For orders containing a range of feeding guilds (for example Coleoptera), the order was subdivided into families. The order Hemiptera was divided into two suborders: Homoptera (Auchenorrhyncha + Sternorrhyncha) and Heteroptera. Ants were considered a separate group. Flies (Diptera) and ticks (Acarina) were placed in an artificial 'various' group as they included a variety of feeding guilds. Also included in 'various' were dung beetles (Coleoptera: Scarabaeidae: Aphodiinae) and bees (Hymenoptera: Anthophoridae).

The specificity of phytophagy (eating of plants) was also investigated. Analysis was done using data from Coleoptera, Diptera and Hemiptera only. Although some other insect orders also included phytophagous species, for example Orthoptera, they were excluded due to the fact that they represented such a small percentage of the total sample. The phytophagous insects were grouped as monophagous – present and therefore presumed to be feeding on only one of the three tree species, oligophagous – present and therefore presumed to be feeding on two of the three tree species or polyphagous – present and therefore presumed to be feeding on all three tree species.

Cates (1980) listed resource abundance and predictability and plant chemistry as the main factors determining herbivore feeding patterns. The majority of phytophagous insects often restrict their diet to one or two species of plants (monophagous-oligophagous) (Bernays & Graham, 1988), despite the ability to utilize alternate hosts (Michaud, 1990) and are usually well adapted to the defence mechanisms of their host plants (Cates, 1980). In contrast, polyphagous insects consume various host species (Michaud, 1990), but are usually not so well adapted to the defence mechanisms of their host plants (Cates, 1980).

Table 2. Feeding guild divisions for all arboreal insect samples taken along the Omaruru River (Namibia) during 2004/5.

Feeding Guild	Taxa included
Predators	Arachnida: [Spiders; Pseudoscorpions; Scorpions; Solifuges] + Coleoptera: [Rove beetles (Staphylinidae); Ladybirds Coccinellidae); Drilid beetles (Drilidae); Chequered beetles (Cleridae); Carabids (Carabidae); Ant beetles (Anthicidae)] + Hemiptera: [Assassin bugs (Reduviidae); Gnat bugs (Enicocephalidae); Stink bugs (Pentatomidae, Subfam.: Asopinae)] + Hymenoptera: [Spider-hunting wasps (Pompilidae); Paper wasps (Vespidae); Mud daubers (Sphecidae); Potter wasps (Eumenidae)] + Mantodea + Neuroptera: [Green lacewings (Chrysopidae); Brown lacewings (Hemerobiidae); Mantidflies (Mantispidae); Antlions (Myrmeleontidae)]
Parasitoids	Hymenoptera: [Braconid wasps (Braconidae); Calcidid wasps Chalcididae); Cuckoo wasps (Chrysididae); Ichneumon wasps (Ichneumonidae); Parasitic wasps (Parasitica); Tiphid wasps (Tiphidae)]
Leaf chewers	Coleoptera: [Apionids (Apionidae); Jewel beetles (Buprestidae); Leaf beetles (Chrysomelidae); Snout weevils (Curculionidae); Scarab beetles (Scarabaeidae); Tapering darkling beetles (Tenebrionidae)] + Orthoptera: [Short-horned grasshoppers (Acrididae); Bush hoppers (Euschmidtidae); Crickets (Gryllidae); Bush crickets (Tettigoniidae); Armoured ground crickets (Bradyporidae)] + Phasmatodea: Stick insects + Lepidoptera: larvae
Sapsuckers	Coleoptera: (Nitidulidae) + Heteroptera: [Thread bugs (Berytidae); Twig wilters (Coreidae); Dictyopharid planthoppers (Dictyopharidae); Moth bugs (Flatidae); Lantern bugs (Fulgoroidea); Seed bugs (Lygaeidae); Capsids (Miridae); Shield bugs (Pentatomidae); Pill bugs (Plataspidae); Fire bugs (Pyrrhocoridae); Shield-backed bugs (Scutelleridae); Inflated stink bugs (Tessaratomidae); Lace bugs (Tingidae)] + Homoptera: [Planthoppers (Issidae); Treehoppers (Membracidae); (Trioziidae); Homoptera bugs] + Thysanoptera: Thrips
Scavengers	Blattodea: Cockroaches + Coleoptera: [Spider beetles (Ptinidae); Darkling beetles (Tenebrionidae)] + Psocoptera: Booklice + Thysanura: Silverfish
Seed feeders	Coleoptera: Seed weevils (Bruchidae) + Heteroptera: Broad-headed bugs (Alydidae)
Wood feeders	Coleoptera: [Auger borers (Bostrichidae); Longhorn beetles (Cerambycidae); Gnawing beetles (Trogossitidae)]
Flower feeders	Coleoptera: [Hide beetles (Dermestidae); Blister beetles (Meloidae); Soft-winged flower beetles (Melyridae); Tumbling flower beetles (Mordellidae)] + Hymenoptera: [Pollen wasps (Masaridae); Leafcutting bees (Megachilidae)]
Nectar feeders	Hymenoptera: Anthophoridae
Various	Flies: (Diptera) + Ticks: (Acarina) + Moths + Butterflies: (Lepidoptera) + Hister beetles (Coleoptera: Histeridae) + Dung beetles (Coleoptera: Scarabaeidae: Aphodiinae) + Nectar feeders (Hymenoptera: Anthophoridae)
Ants	Hymenoptera: (Formicidae)
Tourists	Coleoptera: [Predaceous water beetles (Dytiscidae); Water scavenger beetles (Hydrophilidae); Pond skaters (Gerridae)] + Heteroptera: [Saucer bugs (Naucoridae); Backswimmers (Notonectidae)]

The distribution of phytophagy by morphospecies (RTUs) among the three different tree species (*A. tortilis*, *A. erioloba* and *F. albida*) was relatively even (chi-square test: $\chi^2 = 5.68$, $df = 6$, $P = 0.4599$; log-linear analysis: $\chi^2 = 1.16$, $df = 2$, $P = 0.5609$). Thus, no tree species appeared to have more species-specific RTUs within the relevant orders than any of the other tree species (Figure 6). The results indicated that a certain tree species was not more likely to have tree-specific RTU groups than others.

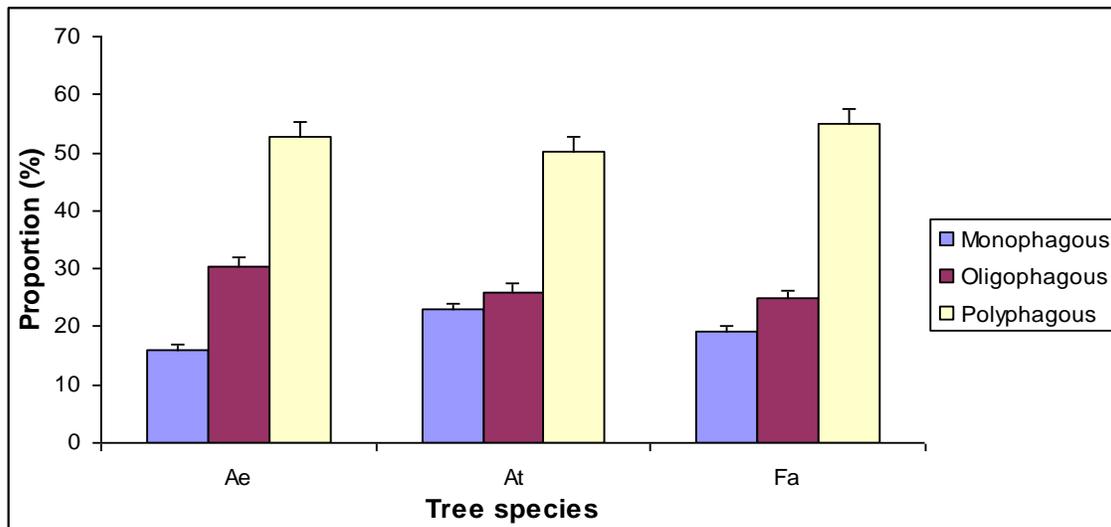


Figure 6. Proportion of phagous groups in each of the tree species (\pm se) sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

Tree-specific phytophagy did however differ among the orders that were considered (chi-square test: $\chi^2 = 13.02$, $df = 6$, $P = 0.0428$; log-linear analysis: $\chi^2 = 33.62$, $df = 2$, $P = <0.0001$). Coleoptera had more monophagous RTUs (recorded only on one tree species) than the other orders (Figure 7). Some orders tended to be more likely to have tree-specific RTU groups than others. The data suggested that Hemiptera were overall more generalist than Coleoptera throughout the study area.

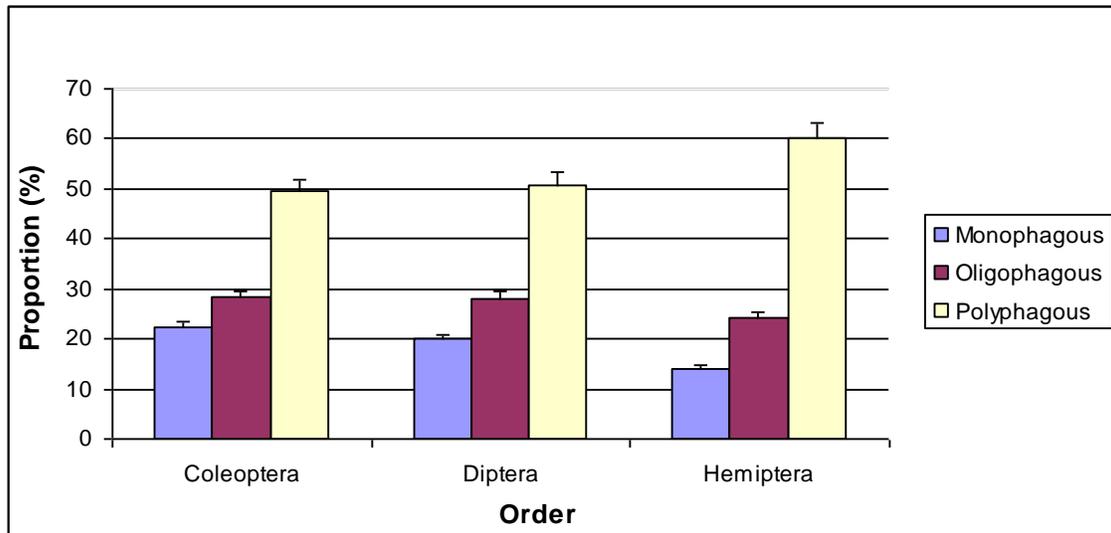


Figure 7. Proportion of phagous groups by insect order (\pm se) sampled at five sites along the Omaruru River (Namibia) during 2004/5.

Analyses suggested there was no specific interaction between a tree species and an insect order with regard to the proportion of individuals found in the three phytophagous groups (log-linear analysis: $\chi^2 = 1.32$, $df = 4$, $P = 0.8587$). The effects that were observed with regard to insect order were constant across all tree species. If there would have been an interaction, it would have meant that orders had different proportions of RTUs in the various phagy groups and that those proportions changed depending on the tree species that they were found on. However, that was not the case.

3.3 References

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CHAPTER 4

TEMPORAL AND SPATIAL COMPOSITION OF COLEOPTERA

4.1 Introduction

The order Coleoptera (beetles) is not only the largest order within the Insecta, but also the largest order of all living organisms (Scholtz & Holm, 1985). Lucky *et al.* (2002) labelled Coleoptera as the most species-rich group of insects, with new species being described at the rate of about 2300 annually. This was also confirmed by the results of this study.

Coleoptera vary in size from minute to very large, and can clearly be distinguished from other insect orders in that their forewings are modified into hardened cases (elytra) which fold over the membranous hind wings (when at rest) to protect them. Their mouthparts are adapted for chewing (Picker *et al.*, 2003). They vary greatly in size, shape and colour, as well as with regard to their biological requirements. Their trophic range allow them to be grouped into numerous feeding guilds (Chapter 3, Table 2).

Climate change is a natural phenomenon, but climate change due to human interference (anthropomorphic climate change) is happening at a rate that far exceeds the natural rate. Insects are poikilothermic animals and temperature therefore plays a vital role in their life cycles (Carroll *et al.*, 2004). The effect of temperature increase, due to climate change, has been investigated by numerous scientists during the last decade or so.

The distribution of herbivorous insects is usually determined by the availability of their food source. However, other factors such as temperature, moisture, the presence of other organisms, amongst others, also play an important role (Buse

et al., 2001). Insects have relatively shorter life cycles than, for example trees, and can therefore adapt relatively rapidly to environmental changes.

Carroll *et al.* (2004), as well as Hicke *et al.* (2006), investigated the effect of climate change on the distribution of the mountain pine beetle (*Dendroctonus ponderosae*) and came to the conclusion that an increase in temperature will allow this beetle to expand its range northwards into areas where it is currently not occurring due to climatic limitations. Infestation of the host tree in areas previously considered as climatically hostile is therefore likely to occur (Carroll *et al.*, 2004). This example serves to remind us that the outbreak frequency of many other insect pests is also most likely to increase due to climate change (Hicke *et al.*, 2006). Smith *et al.* (2000) found that changes in temperature with elevation (altitude) has an influence on the development and behaviour of dung beetles and Haidekker & Hering (2008) stated that water temperature determines the distribution and species richness of stream fauna.

Namibia is primarily an arid country, with the exception of the north eastern region. According to Lioubimtseva (2004) there is still much uncertainty about the influence of climate change on arid environments and some researchers argue that the predicted increase in atmospheric CO₂ will enhance productivity and increase water use efficiency of vegetation, thereby improving the vegetation in arid environments. Others, however, argue that a further increase in temperature may cause further intensification of aridity. There is thus a clear need for more research in this field.

4.2 Materials and Methods

The Materials and Methods for the complete survey are provided in Chapter 2.

4.3 Results and Discussion

A total of 82 767 individuals (82 593 adults and 174 larvae) were collected, representing 21.7% of the total sample. The collected adult beetles were grouped into 285 morphospecies, referred to hereafter as Relative Taxonomic Units or RTUs. They were further also divided into eight feeding guilds (Figure 1), namely flower feeders (18 RTUs); leaf chewers (118 RTUs); predators (62 RTUs); scavengers (16 RTUs); seed feeders (24 RTUs); aquatic species (3 RTUs); wood feeders (21 RTUs) and various, include dung beetles and other non-phytophagous groups (23 RTUs). The three aquatic species sampled should henceforth be considered as tourists. Adult Dytiscidae are aquatic predators and adult Hydrophilidae (2 spp) are either aquatic predators or scavengers on decomposing plant matter, but they play no significant role as members of the arboreal feeding guilds.

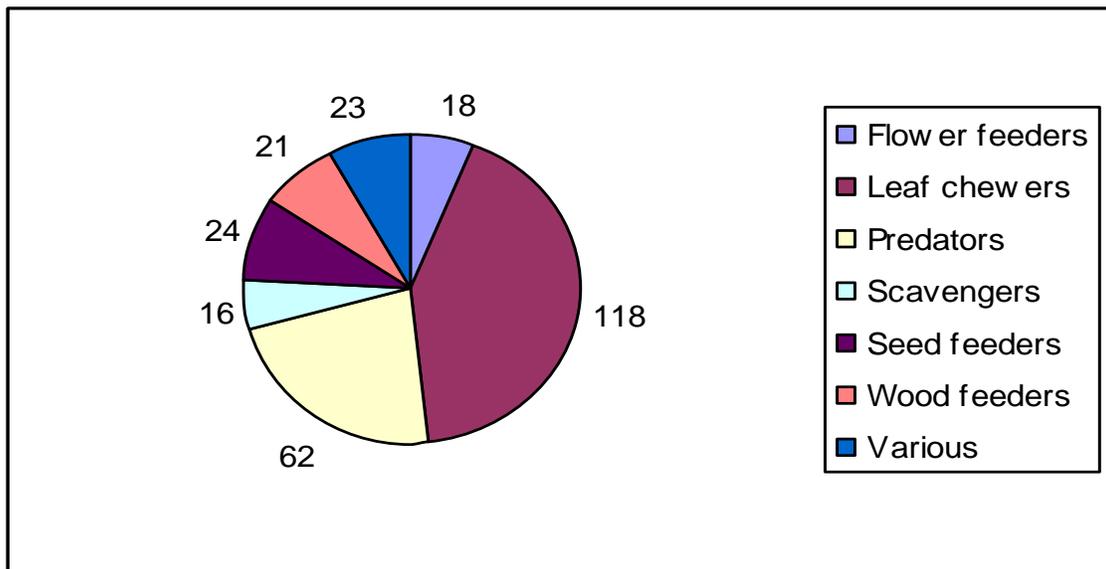


Figure 1. The feeding guild distribution of arboreal Coleoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

4.3.1 RTU comparison between three tree species

Acacia tortilis showed the highest richness with 186 RTUs, followed by *Acacia erioloba* with 172 RTUs and *Faidherbia albida* with 164 RTUs in declining order (Figure 2). However, *A. erioloba* showed the greatest abundance (47 232) across all samples, followed by *F. albida* (26 242) and then *A. tortilis* with the lowest (9293). Species richness appeared to be more or less similar, indicating similar number of niches available on all three tree species. However, the abundance per tree species was very different (Figure 3). *F. albida* appeared to have some or other limiting resource, like nutrition or shelter for example, with *A. tortilis* even more limited.

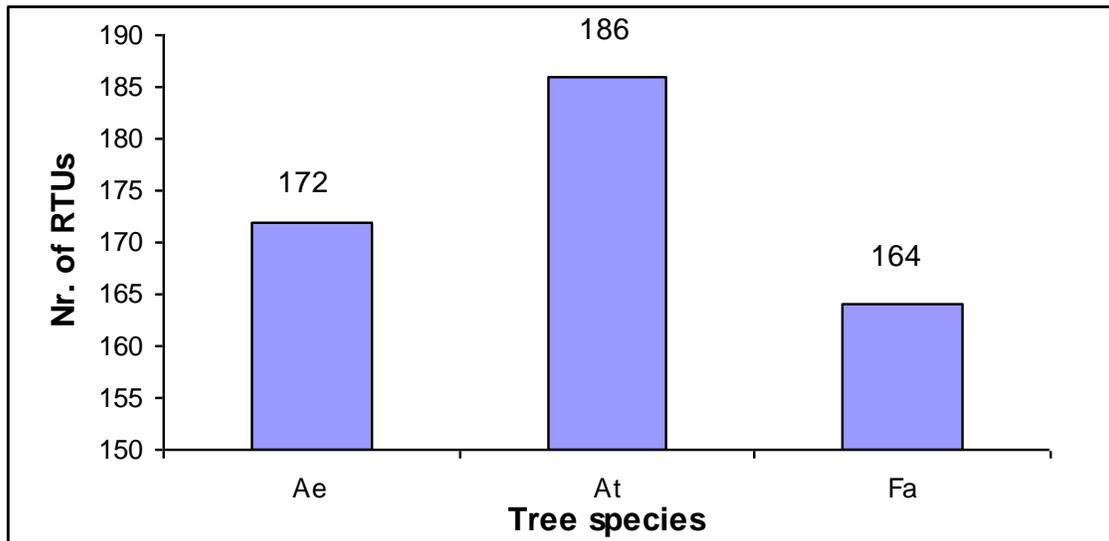


Figure 2. Species richness per tree species for arboreal Coleoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

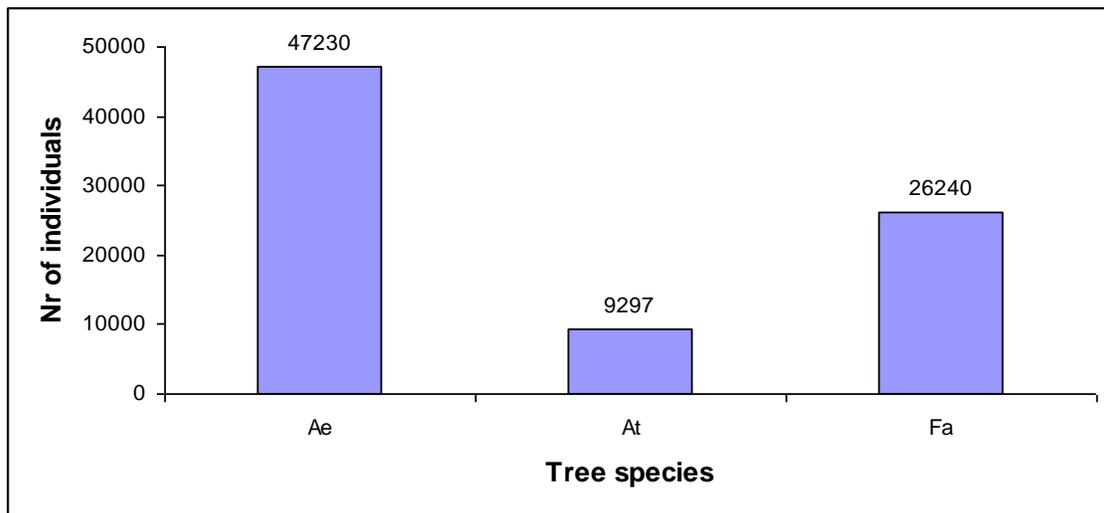


Figure 3. Specimen abundance per tree species for arboreal Coleoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

The mean species richness found in each sample (according to the mixed model analysis of variance (ANOVA PROC MIXED (SAS Institute 2010)), did not vary among the three tree species ($F = 0.44$, $df = 2.47$, $P = 0.649$), but the abundance found in each sample was higher in *A. erioloba* than *F. albida* or *A. tortilis* ($F = 3.66$, $df = 2.47$, $P = 0.033$, Table 1). The three tree species sampled seemed to have similar niche availability for Coleoptera. The high abundance value for *A. erioloba* corresponded with those of Hymenoptera and Diptera. *A. erioloba* seemed to have a rich supply of resources available to the arboreal insects.

Table 1. Least square means (ANOVA; PROC MIXED (SAS Institute 2010)) for number of RTUs (species richness) and number of individuals (abundance) per tree species for arboreal Coleoptera, sampled at five sites along the Omaruru River (Namibia) during 200/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

	Least square means		
	<i>Ae</i>	<i>At</i>	<i>Fa</i>
Species richness	13.54	13.37	12.33
Abundance	474.90	99.78	276.82

Although the abundance per tree species varied greatly, the different tree species all harboured very similar feeding guilds, with dominance regarding leaf chewers and predators (Figure 4). This dominance is probably on account of a rich feeding resource for both guilds, *i.e.* plant material for leaf feeders and prey items for predators.

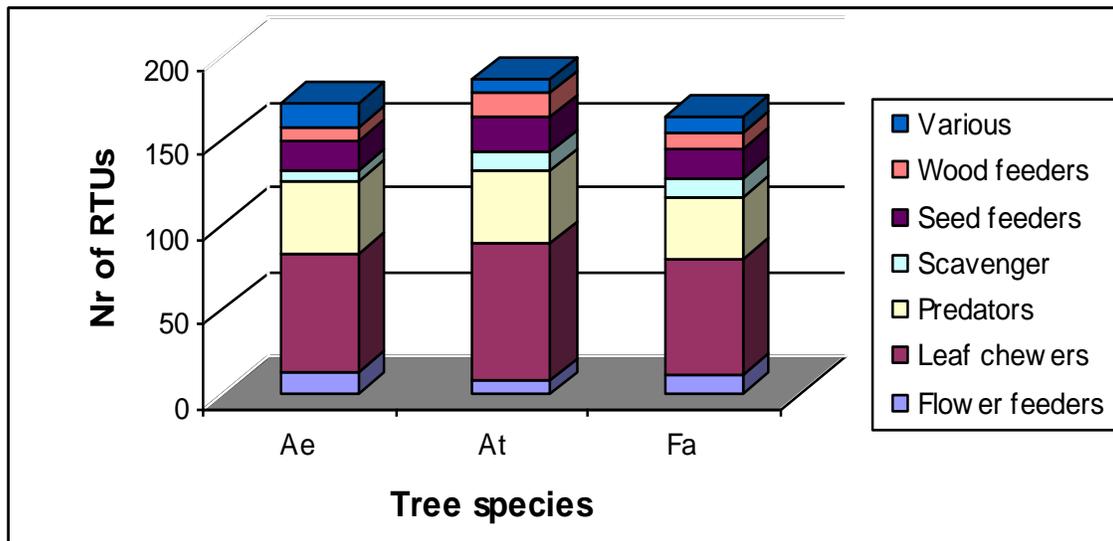


Figure 4. Distribution of the feeding guilds among the tree species for arboreal Coleoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

Considering the arboreal species commonality amongst the tree species, a QS value of 0 would indicate no species in common, and a value of 1.0 would indicate all species in common. Results from the survey indicated that the tree species are not only fairly similar regarding species richness, but they also share approximately 60% of the same RTUs among the pairs of tree species that were sampled (Table 2). This is similar to the 73% similarity for Hemiptera and the 65% similarity for Diptera, indicating that the Coleoptera species sampled represented more generalists than specialists.

Table 2. Sørensen's Quotient of Similarity (C_s) for the three selected tree species regarding arboreal Coleoptera RTUs, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

	<i>Ae-At</i>	<i>Ae-Fa</i>	<i>At-Fa</i>
Coleoptera	0.61	0.63	0.57

The results for phytophagy indicated that there is no difference by tree species (chi-square test: $\chi^2 = 5.681$, $df = 6$, $P = 0.4599$; log-linear analysis: $\chi^2 = 1.16$, $df = 2$, $P = 0.5609$), but the proportion of RTUs in each phagy group is different by insect order. Some orders are more likely to have tree-specific RTU groups than others. For Coleoptera, 22.4% of the RTUs sampled were monophagous (only found on one of the three sample tree species), 28.2% were oligophagous (found on two of the three sample tree species) and 49.4% were polyphagous (found on all three sample tree species). These results confirm that Coleoptera probably consists of more generalists than specialists.

4.3.2 Comparison between sampling sites regarding the effect of aridity

The five sampling sites, present in a transect along one of Namibia's ephemeral rivers, fall within five different rainfall regimes (Chapter 2, Table 1) and thus represent a gradient across aridity. Both the total number of RTUs (Figure 5 and Table 3), as well as the number of RTUs per feeding guild (Figure 6), showed a noticeable decrease in numbers from Otjikoko in the east (wetter) to Omdel (drier) in the west ($F = 14.25$, $df = 4.47$, $P = 0.0001$).

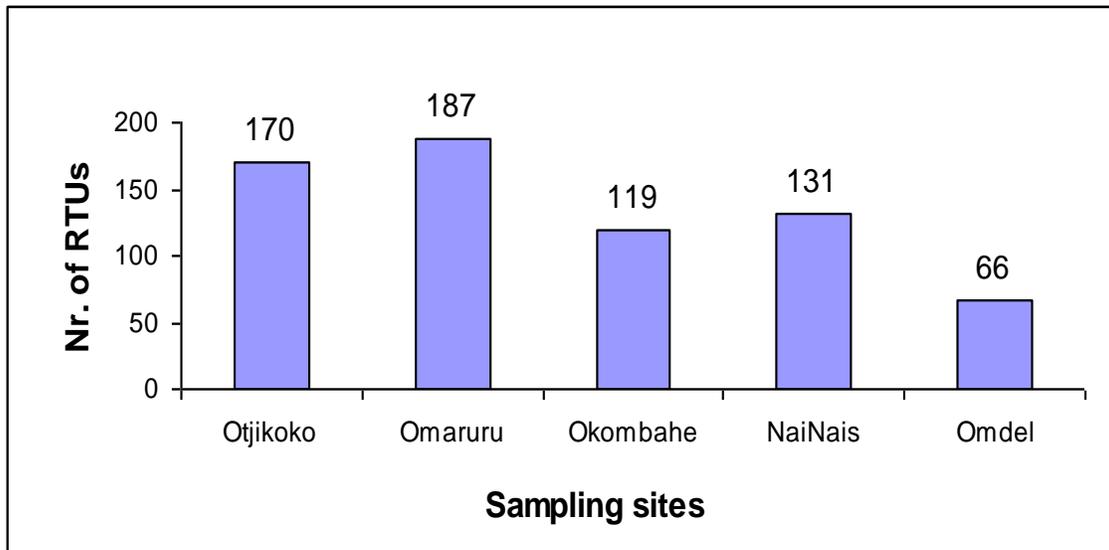


Figure 5. Species richness per sampling site (across aridity) for arboreal Coleoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

Table 3. Least square means and p-value (ANOVA; PROC MIXED (SAS Institute 2010)) for number of RTUs per sampling site in terms of arboreal Coleoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

	Least square means					
	Otjikoko	Omaruru	Okombahe	NaiNais	Omdel	p-value
Coleoptera	16.80	19.00	9.31	12.95	7.33	0.0001

Since insects are poikilothermic, it came as no surprise that the Coleoptera RTU numbers decreased as the sites became progressively drier and cooler towards the coast. If there was to be an increase in temperature, due to climate change, there might very well be a westward shift in species richness in the future along a river transect of this nature. The initial effect would probably be on the vegetation composition of such landscapes, followed by a knock-on effect regarding the insect composition of the areas. Sensitive trophic guilds are then

usually influenced first, which would imply that generalists might be favoured to the detriment of specialists (Haidekker & Hering, 2008). As for the economy of the country, should new insect species move into the changing present-day climatic zones, crop agriculture might be jeopardized. Insect life cycles are strongly linked to temperature, with an increase in temperature, for example, implying an increase in number of generations of certain insect species and subsequent consequences for crop agriculture (Dermody *et al.*, 2008).

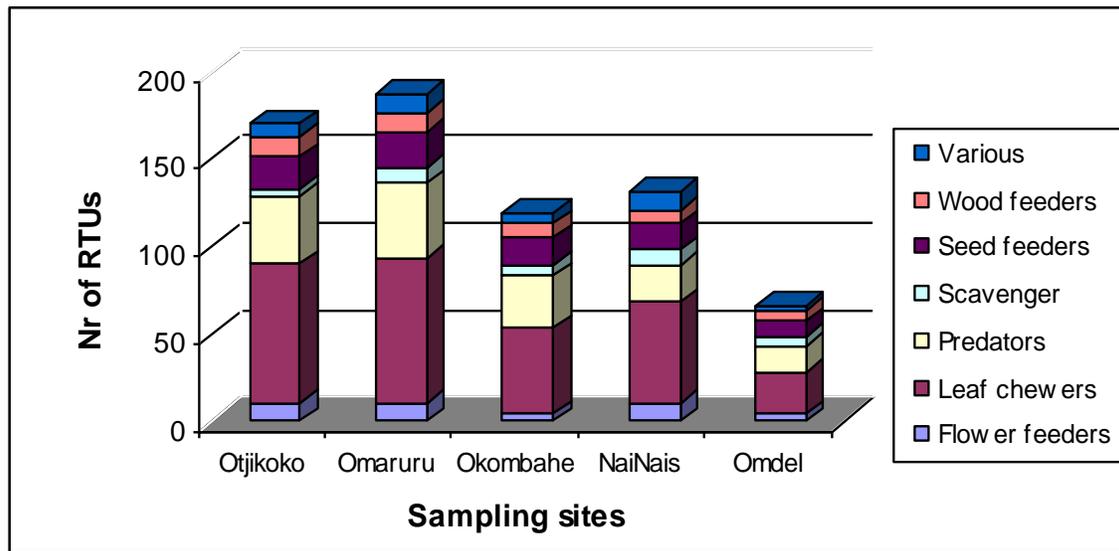


Figure 6. species richness per feeding guild per sampling site for arboreal Coleoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

Should the data in Figure 6 be expressed as percentages, it can however, be seen that, although the species richness per feeding guild decreased from east to west, the portion of each feeding guild relative to the sampling site remained within very narrow limits (Figure 7).

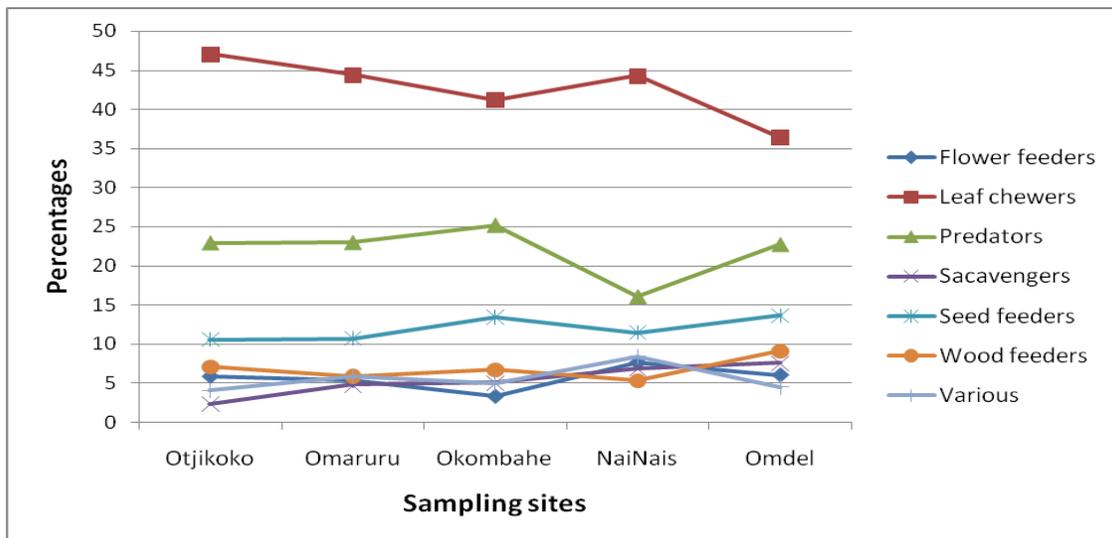


Figure 7. Proportion of each feeding guild (as a percentage of the total sample) relative to the sampling site regarding arboreal Coleoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

With the exception of the leaf choppers and predators, all other feeding guilds showed a proportional difference between the highest and lowest richness site of less than 5%. Leaf choppers showed a slight decline towards the west which corresponded with the decrease in RTUs already explained in Figure 5. The drop in predator numbers at NaiNais might possibly be explained by the severe windy conditions experienced during both the July as well as the November sampling trips. If this was in fact the case, it has to be asked why the other feeding guilds were not similarly affected. A possible explanation could be that the individuals in the other feeding guilds found refuge within the seeds, flowers, wood and leaves that make up the respective feeding niches, whilst free-moving predators were more exposed to the elements.

The similarity analyses (for RTU numbers) indicated that the further apart the sites are from each other, the lower the similarity index (Figure 8 and Table 4). For Coleoptera, Otjikoko and Omaruru (40km apart) were 72% similar; Otjikoko and Okombahe (100km apart) 58%; Otjikoko and NaiNais (170km apart) only 54% and Otjikoko and Omdel (260km apart) a mere 34%. It clearly indicated that the sites do differ from each other and the Mixed Procedure Analysis (ANOVA;

PROC MIXED (SAS Institute 2010)) indicated a marked decrease in RTU diversity from east to west. However, although the sites did differ from each other as far as the number of RTUs is concerned, their general composition remained very similar (Figure 7).

Table 4. Sørensen's similarity values with regard to site separation distances for five sites along the Omaruru River (Namibia) during 2004/5.

Sites	Distance apart (km)	Index value
Otjikoko – Omaruru	40	0.72
Otjikoko – Okombahe	100	0.58
Otjikoko – NaiNais	170	0.54
Otjikoko – Omdel	260	0.34
Omaruru – Okombahe	60	0.59
Omaruru – NaiNais	130	0.56
Omaruru – Omdel	220	0.34
Okombahe – NaiNais	70	0.62
Okombahe – Omdel	160	0.45
NaiNais - Omdel	90	0.48

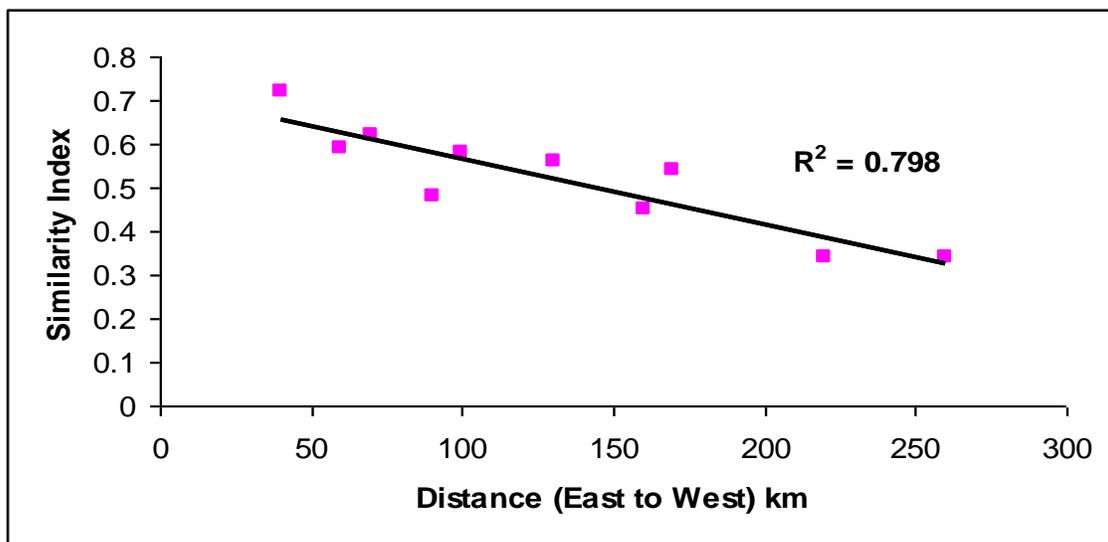


Figure 8. Coleoptera similarity index with regard to site separation distances along the Omaruru River (Namibia) during 2004/5.

4.3.3 Effect of seasonal changes

Both the total numbers of RTUs per sampling period (Figure 9), as well as the number of RTUs per feeding guild per sampling period (Figure 10), showed an increase in May (after the rainy season), then a decrease in July and September and then again a slow increase towards November (the pre-rainy season) and another increase towards January. From January to March there was a slight decrease as conditions became drier. Insects are poikilothermic animals and therefore more active during warmer conditions. Moisture is also important for their development, hence them being more active during wetter environmental conditions.

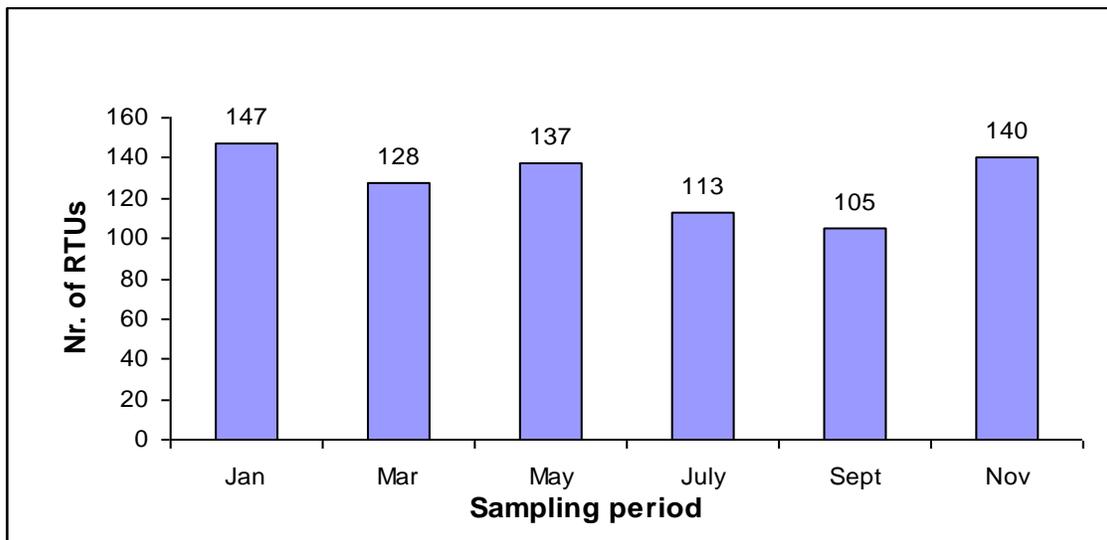


Figure 9. Species richness per sampling period (season) for arboreal Coleoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

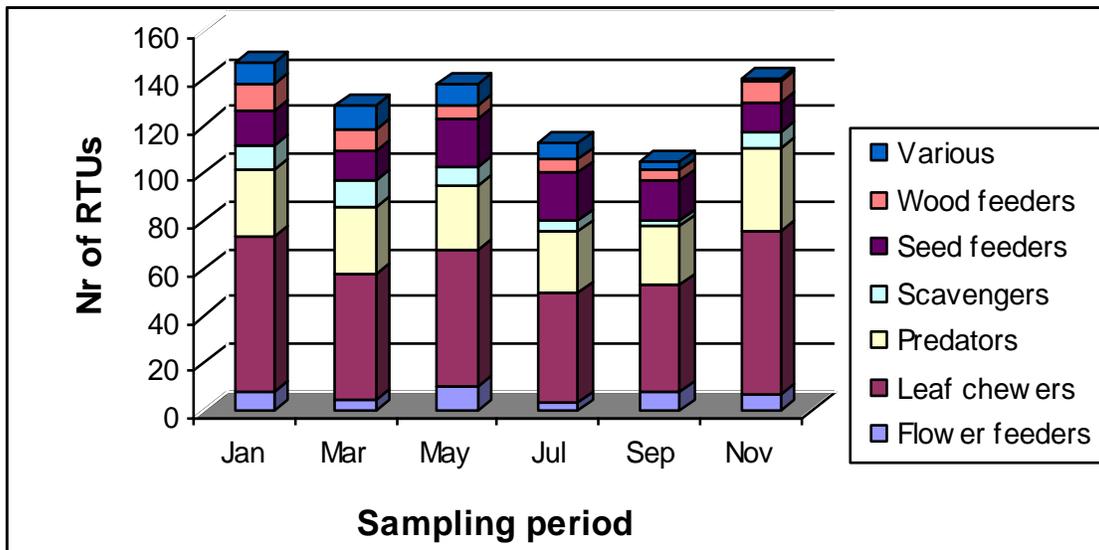


Figure 10. Species richness per feeding guild per sampling period (season) for arboreal Coleoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

Figure 11 provides insight in understanding the distribution of the different feeding guilds across the different seasons. Wood feeders showed the lowest variation in percentage (4.51%). This can possibly be explained by the fact that the bark of the tree is present throughout the year, unlike most of the other feeding components. Although a slight zigzag pattern was observed for the flower feeders, they expressed the second lowest variation in percentage (4.97%). Leaf feeders showed an increase from September towards November, which corresponds with new leaves forming on the deciduous trees from August/September (Curtis & Mannheimer, 2005). Subsequently predators and scavengers also showed an increase towards September and November. According to Curtis & Mannheimer, (2005) fruits (and therefore also seeds) are available all year round, although a steep increase in seed feeders was observed in July.

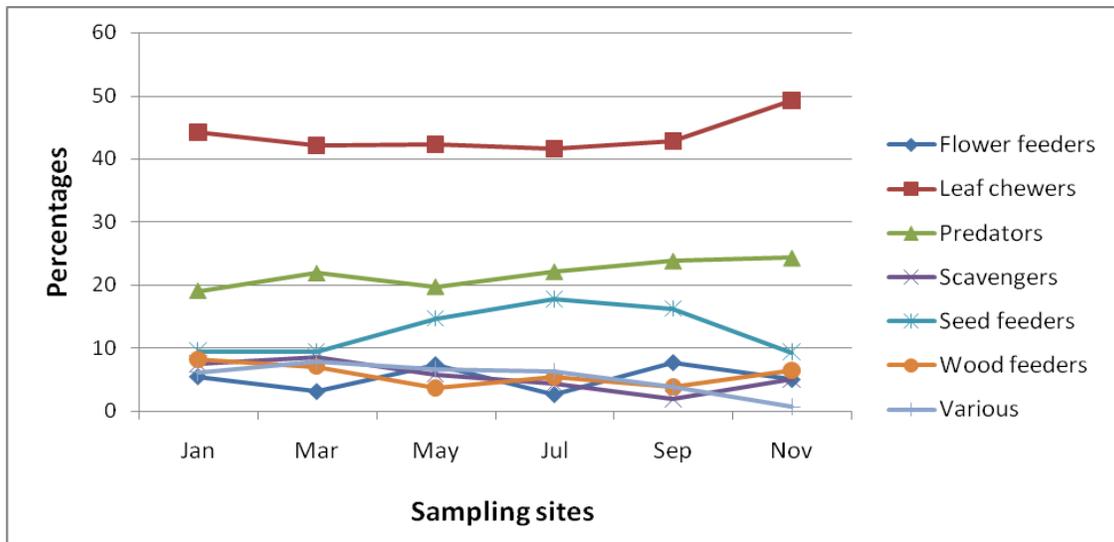


Figure 11. Proportion of each feeding guild (as a percentage of the total sample) per sampling period for arboreal Coleoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

4.4 Conclusion

For Coleoptera, the three selected tree species seemed to be fairly similar with regard to species richness and distribution of feeding guilds. Leaf choppers and predators were the two dominant guilds. Temperature and altitude played a definite role in the distribution of Coleoptera, with a noticeable decline from the warmer (eastern) sites to the cooler (western) sites. The composition of the feeding guilds however, remained fairly similar across aridity. The results indicated a decline in the similarity values between the different sites with an increase in distance between them. Species richness increased towards and after the rainy season, with a gradual decline towards the dry season. As for all animals, in fact all living organisms, insects also need water to survive and, being poikilothermic, their development and growth revolves around optimal temperatures. Changes in climate zones will thus have a definite affect on the distribution and abundance of Coleoptera, which in turn will change the structure and composition of various other animal and plant communities.

4.5 References

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CHAPTER 5

TEMPORAL AND SPATIAL COMPOSITION OF HEMIPTERA

5.1 Introduction

Members of the order Hemiptera, commonly known as bugs, exhibit a wide range of structural features and can be found in many different habitats. However, they all share one common characteristic. They all have long piercing-sucking mouthparts folded backwards underneath the head and between the legs. These mouthparts allow them to suck liquid from plants and animals. In the process they may act as vectors for viruses, bacteria and fungi, which can cause diseases in both plants and animals (Picker *et al.*, 2003).

Scholtz & Holm (1985), as well as Picker *et al.* (2003), divide the order Hemiptera into two suborders, namely the Heteroptera (with the apical half of the forewings thickened, forming the hemelytra) and the Homoptera (with both pairs of wings membranous). The Homoptera differ from the Heteroptera in that they hold their wings roof-like over their bodies, unlike the flat hemelytra of the Heteroptera. Storer *et al.* (1979) and Gullan & Cranston (2005), however, classify the Hemiptera and the Homoptera as two different insect orders. This study follows this classification.

For the purpose of this study, the majority of the Homoptera families were not identified to morphospecies (RTUs) level, but rather lumped together and labelled Homoptera. These lumped groups made up the minority within the order in terms of abundance. The only Homoptera families that were identified and grouped into RTUs together with the Hemiptera were the Fulgoridae (snout bugs); Dictyopharidae (planthoppers); Issidae (planthoppers); Flatidae (moth bugs) and Membracidae (treehoppers), which all belong to the suborder Auchenorrhyncha. The Homoptera were not included in any results dealing with RTUs, but were only considered in terms of overall Hemiptera and Homoptera

abundance, with the piercing-sucking mouthparts structured for feeding on liquids as the common denominator for the two groups.

The possible effects of climate change on Hemiptera have been studied by various scientists, for example Masters *et al.* (1998) and Andrew & Hughes (2005b). Being poikilothermic animals, as all insects are, Hemiptera are also very vulnerable to climate change because their basic physiological functions are influenced by the ambient temperature (Andrew & Hughes, 2005a and Deutsch *et al.*, 2008). Andrew & Hughes (2005b) raised the concern that our limited knowledge about what currently determines species abundance and distribution, will limit our ability to predict how future global climate change might affect species abundance and distribution. Plants are viewed as indicators of climate change, but are they necessarily the best indicators to use? Their inability to move and their slow rate of reproduction hampers their ability to respond to changes in climatic conditions. Insects, such as Hemiptera, on the other hand, have the ability to fly and exhibit short life cycles, and are therefore much more capable of adapting to changing environmental conditions. Changes in the distribution of plant-feeding insects should thus rather be used to indicate and measure rates of climate change (Hodkinson & Bird, 1998).

Namibia is an arid country with low rainfall and high temperatures. Drought outbreaks often occur with severe impact on the vegetation. According to Mattson & Haack (1987) drought conditions can lead to outbreaks in plant-feeding insect species that prefer the drought-stressed plants as feeding hosts. The reason being that the nutrient levels of drought-stressed plants are more concentrated and therefore leads to improved growth, survival and reproduction of various insect groups. Drought may also lower the defence systems of the plant, making it more susceptible to insect infestation. Overall, the warmer conditions of the environment favour the development of the poikilothermic insects. When all this is considered in crop agriculture context, it could have economical ramifications for a region.

5.2 Materials and Methods

The Materials and Methods for the complete survey are provided in Chapter 2.

5.3 Results and Discussion

A total of 57 234 individuals (55 760 adults and 1474 nymphs) were collected, representing 15.8% of the total sample. The collected adults were grouped into 91 morphospecies or Relative Taxonomic Units (RTUs). They were further also divided into four feeding guilds (Figure 1), namely sapsuckers (76 RTUs); predators (11 RTUs); seed suckers (1 RTU); and aquatic species (3 RTUs). The three aquatic species sampled were regarded as serendipitous. Adult Gerridae, Notonectidae and Naucoridae are aquatic predators. All three species are associated with permanent water and are not considered as being part of the canopy feeding guilds.

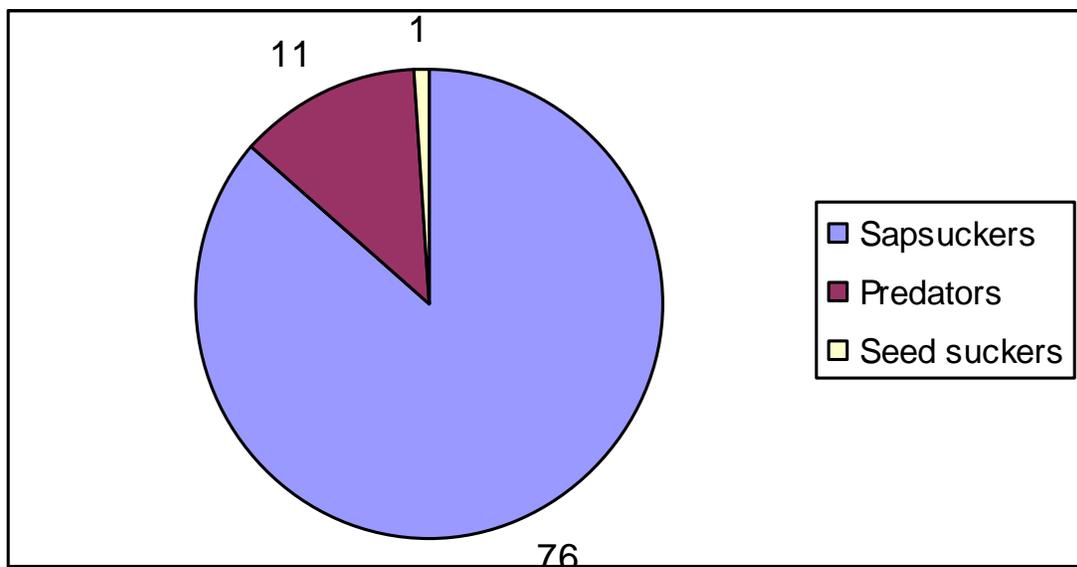


Figure 1. The feeding guild distribution of arboreal Hemiptera, sampled at five sites along the Omaruru River (Namibia) during 2004-2005.

5.3.1 RTU Comparison between three tree species

In declining order *Acacia tortilis* and *Faidherbia albida* showed the highest richness with 67 RTUs each, followed by *Acacia erioloba* with 63 RTUs (Figure 2). The abundance per tree species, however, varied slightly with *A. tortilis* having the greatest number (26 100) of individuals captured across all samples, followed by *A. erioloba* (17 790) and then *F. albida* with the lowest (13 344) (Figure 3). The three tree species, which are morphologically very similar, provide similar environments with a similar number of available niches, explaining the similarity in species richness. The differences in abundance probably indicate variable levels of food source availability in the canopies of the different tree species.

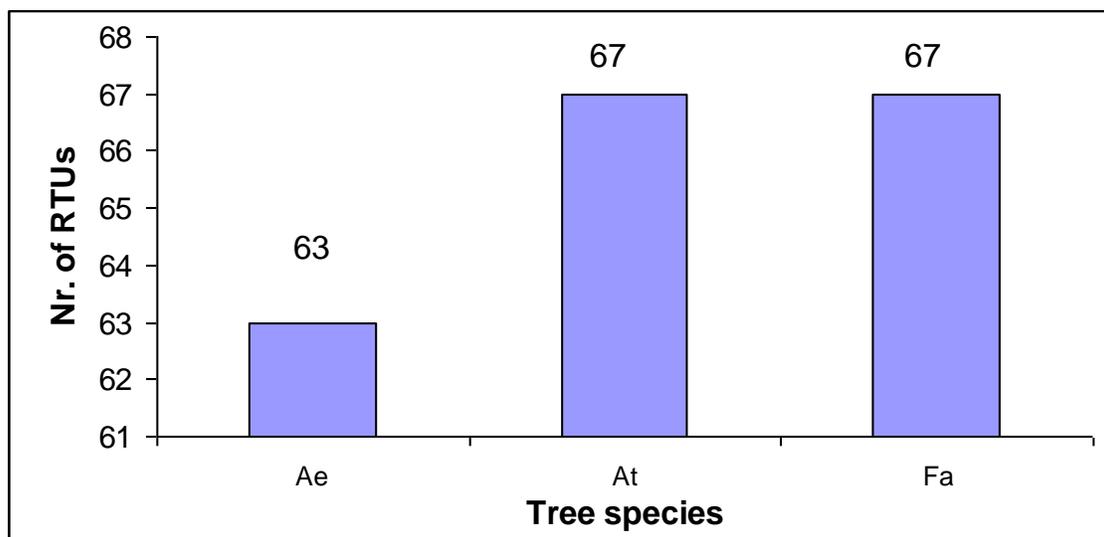


Figure 2. Species richness per tree species for arboreal Hemiptera, sampled at five sites along the Omaruru River (Namibia) during 2004-2005. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

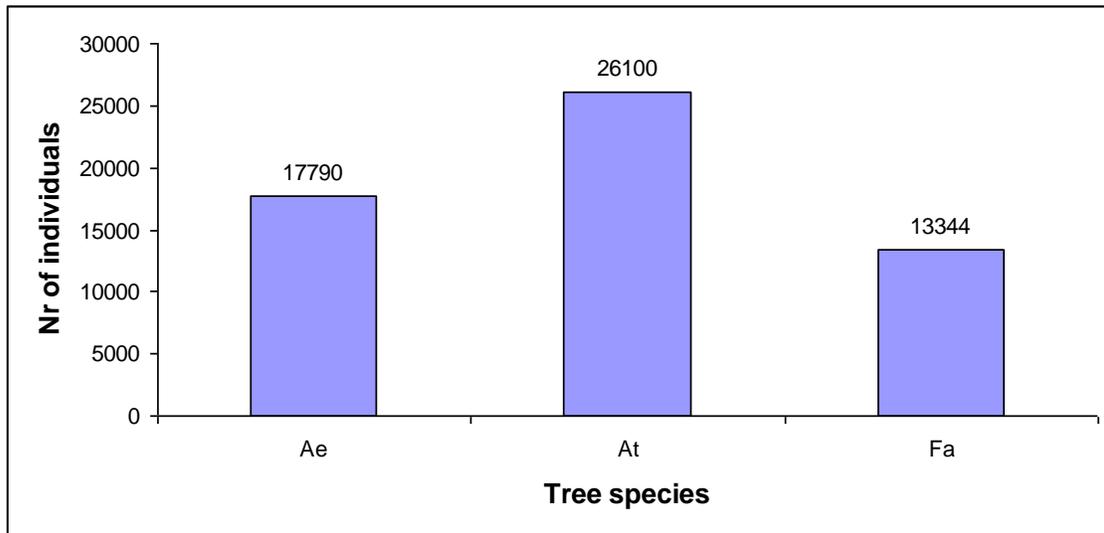


Figure 3. Specimen abundance per tree species for arboreal Hemiptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

The mean species richness, recorded for each sample (according to the mixed model analysis of variance (ANOVA PROC MIXED (SAS Institute 2010)), varied between the three tree species ($F = 3.58$, $df = 2.47$, $P = 0.036$), whilst the mean abundance recorded for each sample was markedly higher for *A. tortilis* than for *A. erioloba* or *F. albida* ($F = 1.65$, $df = 2.47$, $P = 0.203$) (Table 1). With regard to Hemiptera the three tree species sampled seemed to have less similar types or resources available and *A. tortilis* seemed to have richer resources available, compared to the other two tree species.

Table 1. Least square means (ANOVA; PROC MIXED (SAS Institute 2010)) for number of RTUs (species richness) and number of individuals (abundance) per tree species for arboreal Hemiptera, sampled at five sites along the Omaruru River (Namibia) during 2004-2005. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

	Least square means		
	Ae	At	Fa
Species richness	4.69	6.38	5.52
Abundance	142.63	316.27	126.45

Although the abundance per tree species varied greatly, the different tree species all harboured very similar feeding guilds with clear dominance regarding the sap suckers (Figure 4). Predators made up the next most abundant guild. The three tree species sampled are all morphologically very similar, thus providing similar niches to the insects. All three species have bipinnately compound leaves, as compared to single, broad-leaf trees. Being part of the riparian vegetation of the Omaruru River, they had leaves almost all year round which were available to the sap feeding Hemiptera.

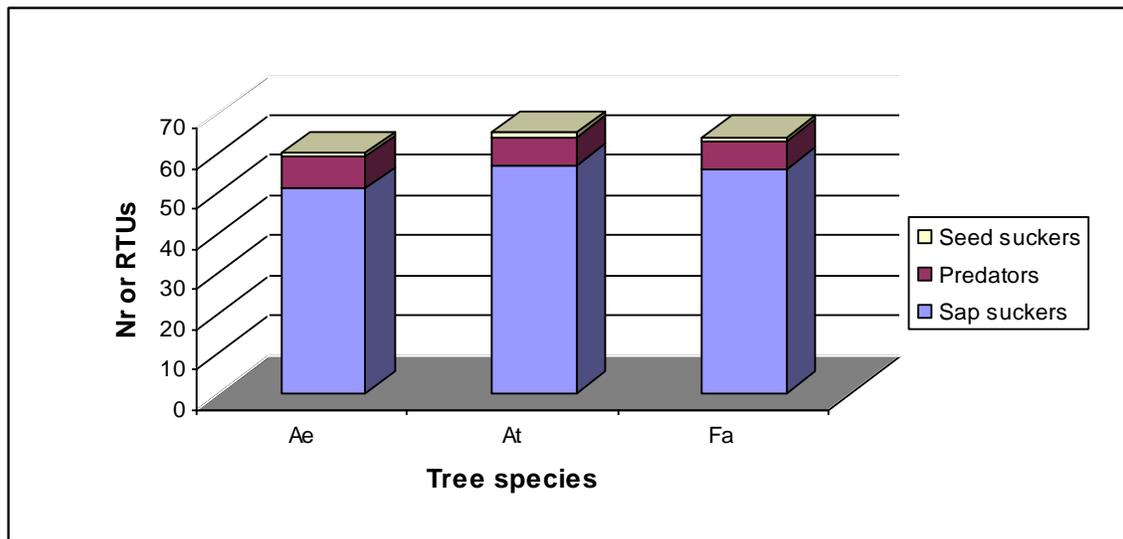


Figure 4. Distribution of the feeding guilds among the tree species for arboreal Hemiptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

In considering the arboreal species commonality amongst the tree species, a QS value of 0 would indicate no species in common, and a value of 1.0 would indicate all species in common. Results from the survey indicated that the tree species are not only fairly similar regarding number of RTUs, but they also share approximately 73% of the same RTUs among the pairs of tree species that were sampled (Table 2).

Table 2. Sørensen's Quotient of Similarity (C_s) for the three selected tree species regarding arboreal Hemiptera RTUs, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

	<i>Ae-At</i>	<i>Ae-Fa</i>	<i>At-Fa</i>
Hemiptera	0.70	0.76	0.74

The results for phytophagy indicated that there is no difference by tree species (chi-square test: $\chi^2 = 5.681$, $df = 6$, $P = 0.4599$; log-linear analysis: $\chi^2 = 1.16$, $df = 2$, $P = 0.5609$) but the proportion of RTUs in each phagy group is different by insect order. Some orders are more likely to have tree-specific RTU groups than others. For Hemiptera, 14.1% of the RTUs sampled were monophagous, (only found on one of the three sample tree species), 24.3% were oligophagous (found on two of the three sample tree species) and 60.2% were polyphagous (found on all three sample tree species). The remaining 1.4% was allocated to the 'various' group (those consisting of a conglomerate of species that could not be assigned to any specific phytophagous group). The low percentage of monophagous RTUs and the high percentage of polyphagous RTUs (much higher than that of Coleoptera and Diptera) indicate that the Hemiptera species sampled were mainly generalists.

5.3.2 Comparison between sampling sites regarding the effect of aridity

The five sampling sites, which run in a transect along one of Namibia's ephemeral rivers, fall within five different rainfall regimes (Chapter 2, Table 1) and thus represent a gradient across aridity. Both the total number of RTUs (Figure 5 and Table 3) as well as the number of RTUs per feeding guild (Figure 6) showed a noticeable decrease in numbers from Otjikoko in the east (wetter) to Omdel (drier) in the west ($F = 25.44$, $df = 4.47$, $P = 0.0001$).

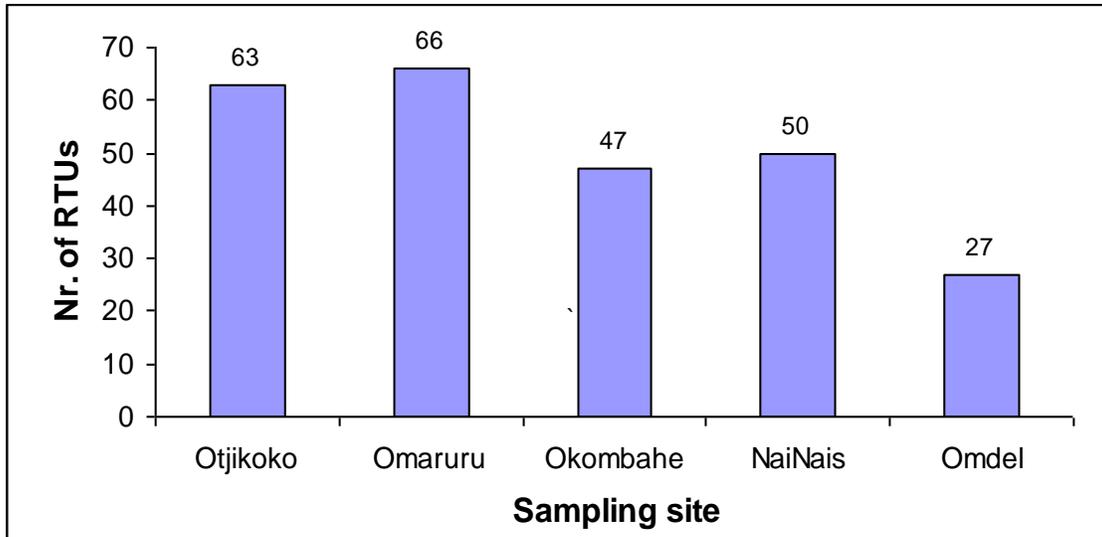


Figure 5. Species richness per sampling site (across aridity) for arboreal Hemiptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

Table 3. Least square means and p-value (ANOVA; PROC MIXED (SAS Institute 2010)) for number of RTUs per sampling site in terms of arboreal Hemiptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

	Least square means					
	Otjikoko	Omaruru	Okombahe	NaiNais	Omdel	p-value
Hemiptera	8.68	8.40	4.58	3.66	2.33	0.0001

The use of natural gradients (such as temperature, rainfall and altitude) has been a common ecological tool for understanding the influence of such factors on the structure and functioning of natural ecosystems (Devoto *et al.*, 2005). Deutsch *et al.* (2008) also found a decrease in species richness with a decrease in temperature.

Insects can react to environmental changes by acclimation, adaptation, dispersal or behavioural modifications. Their particular responses will have an impact on the ecosystem that they form part of. An increase in environmental temperature will have a greater influence on insects in warmer areas, because they are already living close to their optimal temperature level, whereas insects in cooler

areas might actually benefit from an increase in temperature (Deutsch *et al.*, 2008). Namibia is a country with fairly moderate temperatures (even during winter) and the resident insect communities are therefore particularly at risk in a 'greenhouse' future. Masters *et al.* (1998) is of the opinion that milder winters, due to climate change, will alter the reproductive behaviour of Auchenorrhyncha (Homoptera). They suspect that these insects will start to mature earlier, thus developing the ability to go through more generations per season, which in turn will have a major impact on the vegetation that they feed on. If these insects, over and above all this, can also move into new geographical regions, it will have major implications for their host plants. Climate change has already affected the distribution of many species and future changes are likely to have an even more severe impact (Schweiger *et al.*, 2008), especially an expansion in the distribution of agriculturally important species (Masters *et al.*, 1998). In agricultural countries, like Namibia, this can have a detrimental effect on the economy.

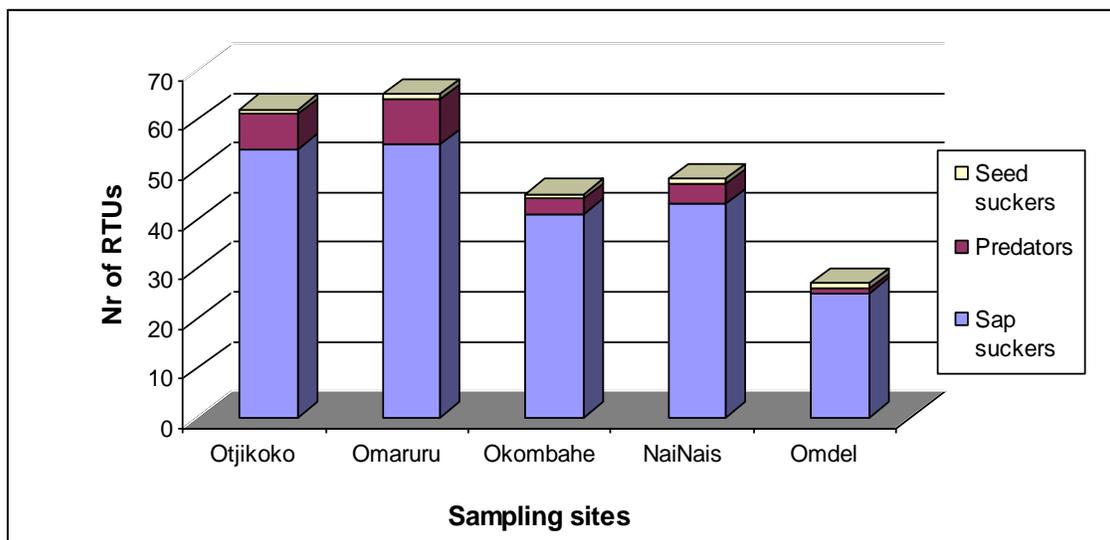


Figure 6. Species richness per feeding guild per sampling site for arboreal Hemiptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

Andrew & Hughes (2005a and b) also divided the species they studied into feeding guilds (similar to what was done in this study) and obtained similar results. They also came to the conclusion that species richness decreases towards the areas of lower temperature and predicted that global climate change

might lead to an increase in species richness towards the cooler areas in response to shifting climatic zones.

Should the data in Figure 6 be expressed as percentages, it can, however, be seen that although the number of RTUs per feeding guild decreases from east to west, the portion of each feeding guild relative to the sampling site remains within very narrow limits (Figure 7). The order Hemiptera consists mainly of phytophagous species, thereby the absolute dominance of sap suckers over predators and seed suckers.

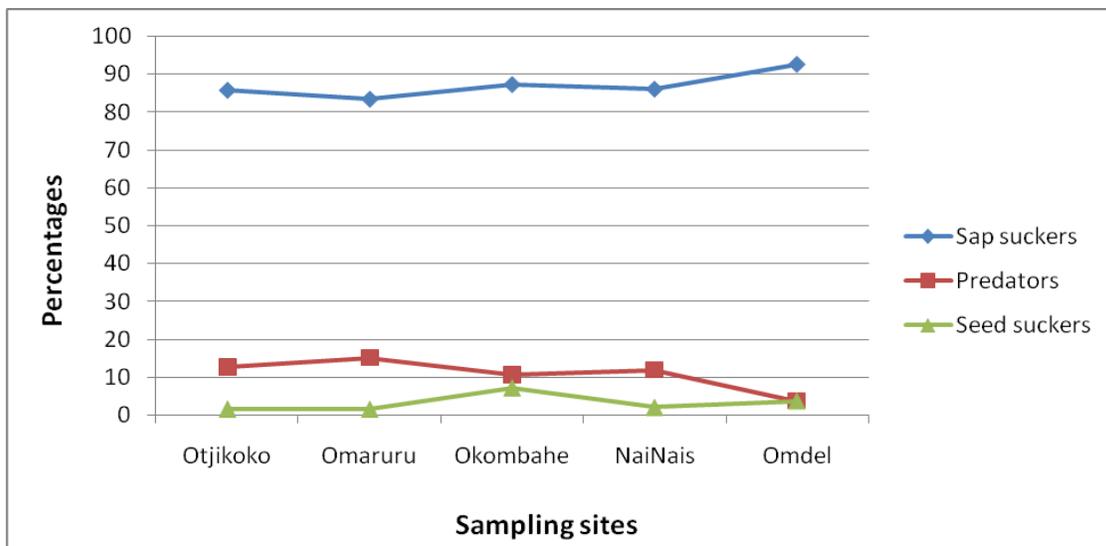


Figure 7. Proportion of each feeding guild (as a percentage of the total sample) relative to the sampling site regarding arboreal Hemiptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

Sap suckers slowly increased towards Omdel, albeit that there was still a less than 10% difference between the lowest and highest percentage across the sites. This unexpected phenomenon might be due to the fact that there are less other plant species available in the area and that the generalist sap sucker species as a result, congregated on the tree species selected for sampling purposes. As for the predators, they decreased towards Omdel, although also with a less than 10% difference. Taking into account the lower plant diversity, less prey species might be available for the predators. None of the feeding guilds showed major proportional changes to the total insect composition.

In this context, Voigt *et al.* (2003) reported that different species and different trophic levels (herbivores and predators) react differently to climate changes. The reaction of the herbivores towards climate change will have an influence on the resource availability of the predators above them. Communities are unlikely to respond as entities toward climate change and any climate change will disrupt the trophic relationship between organisms, leading to a cascading effect in trophic structure collapse.

The similarity analyses (for RTU numbers) indicated that the further apart the sites are from each other, the lower the similarity index (Figure 8 and Table 4). For Hemiptera the Otjikoko and Omaruru sites (40 km apart) were 75% similar; Otjikoko and Okombahe (100 km apart) 66% similar; Otjikoko and NaiNais (170 km apart) only 63% similar and Otjikoko and Omdel (260 km apart) a mere 46% similar. It clearly indicates that the sites do differ from each other and the Mixed Procedure Analysis (ANOVA; PROC MIXED (SAS Institute 2010)) indicated a marked decrease in RTU diversity from east to west. However, although the sites did differ from each other as far as the number of RTUs is concerned, their general composition remained very similar (Figure 7).

Table 4. Sørensen's similarity values with regard to site separation distances for five sites along the Omaruru River (Namibia) during 2004/5.

Sites	Distance apart (km)	Index value
Otjikoko – Omaruru	40	0.75
Otjikoko – Okombahe	100	0.66
Otjikoko – NaiNais	170	0.63
Otjikoko – Omdel	260	0.46
Omaruru – Okombahe	60	0.72
Omaruru – NaiNais	130	0.67
Omaruru – Omdel	220	0.47
Okombahe – NaiNais	70	0.61
Okombahe – Omdel	160	0.53
NaiNais - Omdel	90	0.59

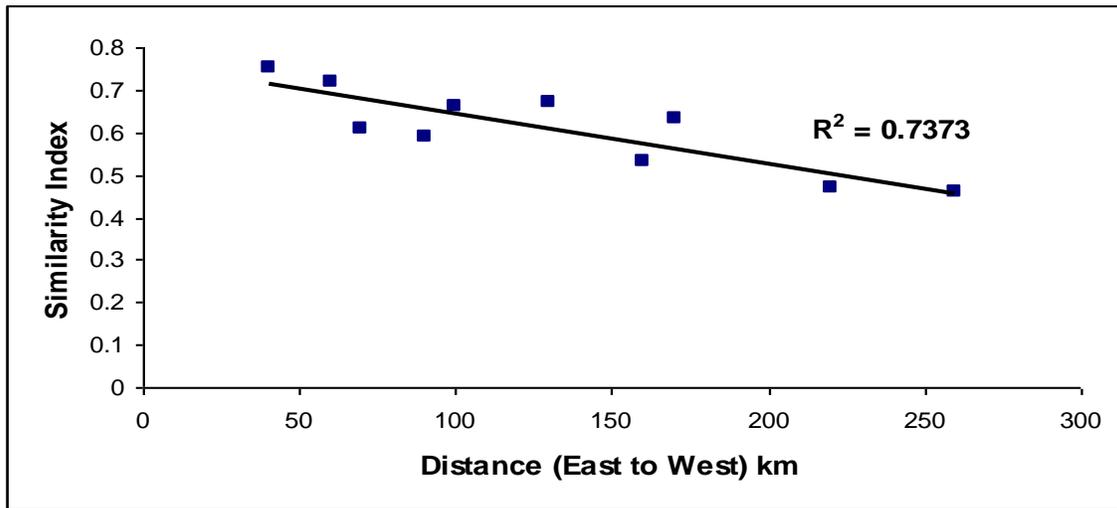


Figure 8. Hemiptera similarity index with regard to site separation distances, along the Omaruru River (Namibia) during 2004/5.

5.3.3 Effect of seasonal changes

Both the total numbers of RTUs per sampling period (Figure 9), as well as the number of RTUs per feeding guild per sampling period (Figure 10), showed an increase in May (after the rainy season), then a decrease in July and September and then again a slow increase towards November (the pre-rainy season) and another increase towards January. From January to March there was a slight decrease as conditions became drier.

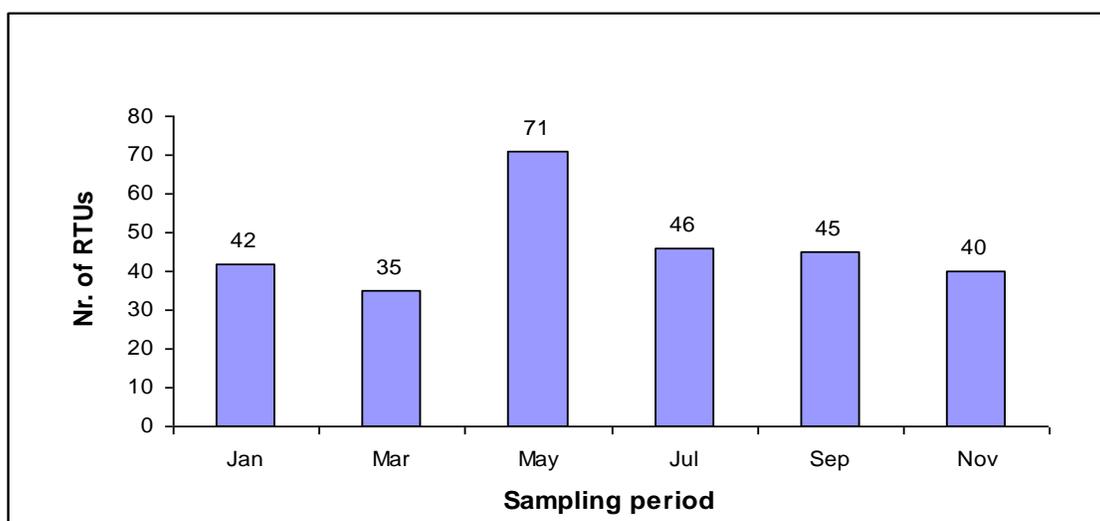


Figure 9. Species richness per sampling period (season) for arboreal Hemiptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

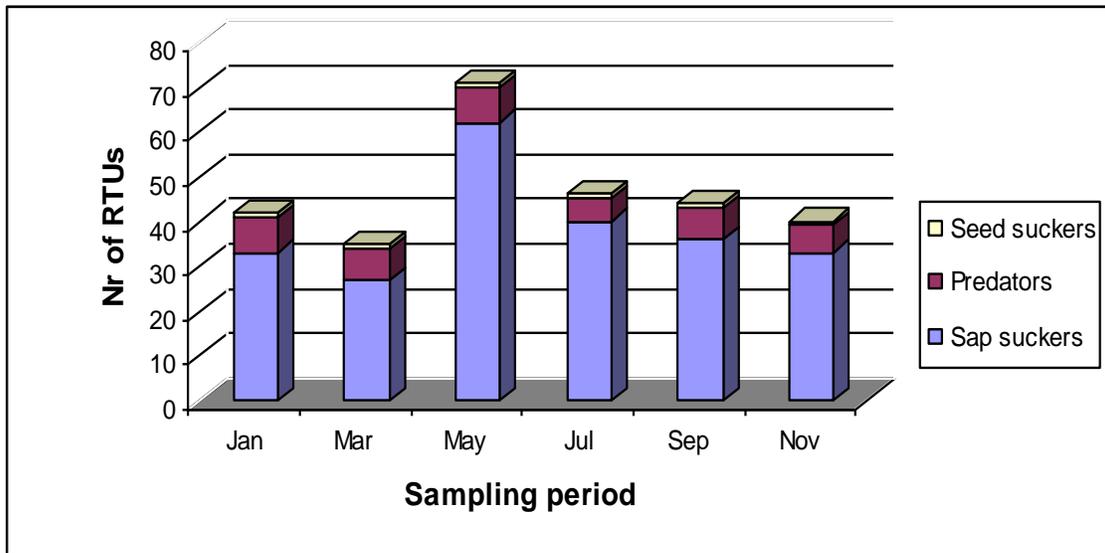


Figure 10. Species richness per feeding guild per sampling period (season) for arboreal Hemiptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

Figure 11 provides insight in understanding the distribution of the different feeding guilds across the different seasons. Seed suckers showed the lowest variation in percentage (1.45%). According to Curtis & Mannheimer (2005), fruit is available on the trees studied for most of the year, thus explaining the low variation regarding seed suckers. It must, however, be mentioned that only a single (and the same) species was collected at all sites. The reason for this low figure might be that the fogging method is not successful for species secluded within seeds. Predators showed a 7.97% difference with a steady decrease from January to July and then an increase towards September. Aquatic insects were also collected in extremely low numbers (zero, one, and a maximum of 2), which is quite understandable in the context of the arboreal insects that were targeted. These insects were serendipitous visitors and not canopy residents. The sap suckers showed a gradual increase from March onwards, with the peak in May to July. According to Curtis & Mannheimer (2005) the study trees have leaves available all year round, with new leaf growth sprouting in July for *F. albida*, whilst new growth develops in August to September/October for the two *Acacia* species.

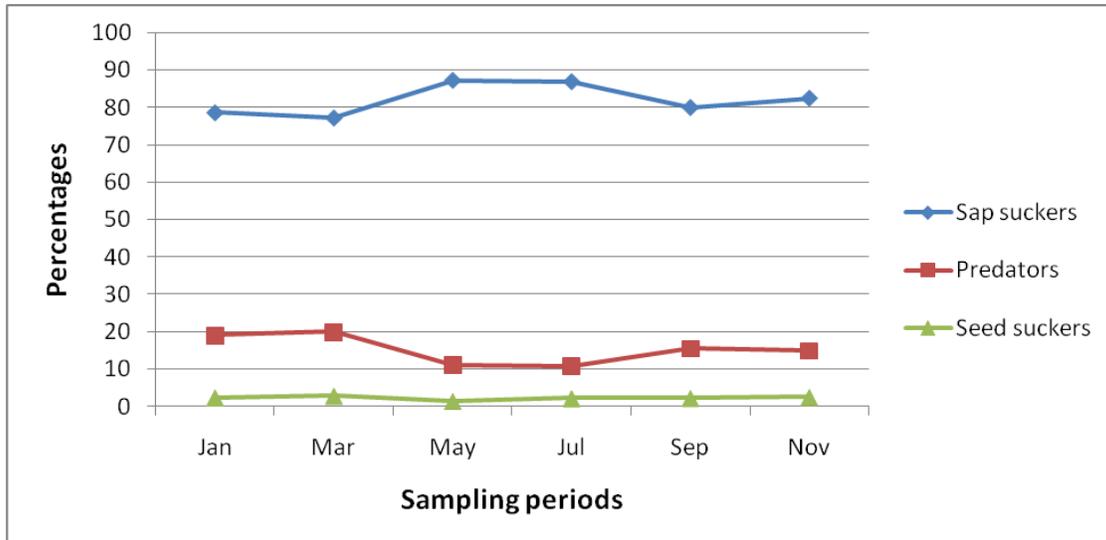


Figure 11. Proportion of each feeding guild (as a percentage of the total sample) per sampling period for arboreal Hemiptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

5.4 Conclusion

Species richness of the three study tree species turned out to be fairly similar with slight differences in abundance. Because they are morphologically very similar these species probably provide similar niches for the arboreal species to occupy. Across the aridity gradients both species richness and abundance gradually declined from east (wetter and hotter) to west (drier and cooler). Sap suckers were dominant at all five sampling sites with a slight increase in dominance towards the west. Predators slowly declined towards the more arid sites. Results also indicated that the further apart the sites are from each other, the less similar they become. The different sites vary from each other with regard to environmental conditions and vegetation composition and therefore differ from each other with regard to suitability for insect occurrence. On account of poikilothermy the presence and abundance of this fauna waxes and wanes through the seasons, in spite of their arboreal habits.

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CHAPTER 6

TEMPORAL AND SPATIAL COMPOSITION OF HYMENOPTERA

6.1 Introduction

The order Hymenoptera is one of the largest and most specialized insect orders in the insect world (Scholtz & Holm, 1985) and includes sawflies, wasps, bees and ants that are diverse in structure and function. The Hymenoptera are divided into two sub-orders, *i.e.* Symphyta and Apocrita (e.g. Scholtz & Holm, 1985, Picker *et al.* 2003, Gullan & Cranston, 2005). The Symphyta (woodwasps, horntails and sawflies) include the more primitive Hymenoptera and can be identified by the absence of the narrow connection between the thorax and abdomen, typical of all other Hymenoptera. All other Hymenoptera belong to the Apocrita. With the exception of bees and a few wasps, who feed their offspring pollen and nectar, all the other species are predators, or parasites of primary or secondary phytophagous insects, or spiders, or plants and their products (Picker *et al.*, 2003). In this study all Hymenoptera species, with the exception of four (2 flower feeders and 2 nectar feeders) were placed in either the predator or the parasitic feeding guild (Chapter 3, Table 2). Ants were treated separately (see below). All the Hymenoptera species sampled during the study belong to the Apocrita. Phytophagous Symphyta, which according to Scholtz & Holm (1985), are not abundant in the Afrotropical region, were not recorded.

Ants (Formicidae) are very important role players in terrestrial ecosystems (Neves *et al.*, 2010), mainly because they are such fierce predators (Corbara *et al.*, 2009), serve as important ecosystem engineers in soil (e.g. Ettema & Wardle, 2002) and play a potential role as bio-indicators of habitat disturbance (Neves *et al.*, 2010). All ant species are social, with a typical matriarchal society structure. Unlike most other Hymenoptera, ants are generally wingless, with only the males and reproductive females bearing wings. After mating reproductive females

discard their wings. Ants can also be distinguished from other Hymenoptera by the fact that their antennae have a characteristic elbow at the first joint (Picker *et al.*, 2003).

The Hymenoptera is an economically important group. Bees are pollinators, the parasitic and predatory wasps help in controlling insect pest species and some ant species are pests themselves (Scholtz & Holm, 1985). The need to consider the potential influence of climate change on this insect group can therefore not be under-estimated. Many parasitic wasps are currently deployed as biological control agents and changes in climatic conditions could lessen their effect on pest species, which might lead to an increase in the use of pesticides (Stireman *et al.*, 2005). Honey bees have a noteworthy economic value because not only do they pollinate our crops and therefore contribute to food security, but they are also crucial in maintaining biodiversity (which determines ecosystem function) because they pollinate plant species in general (Le Conte & Navajas, 2008).

Since 1995 heavy mortality and the subsequent collapse of populations of *Apis mellifera*, the most economically valuable pollinator of agricultural crops worldwide, has been experienced. Researchers agree that a combination of factors is responsible for this, but that the influence of variable climate conditions has been the decisive factor (Le Conte & Navajas, 2008). It is general knowledge how important pollinators, not only *Apis mellifera*, are in order to continue plant pollination, which in turn maintains ecological equilibrium, which in turns influences the economy of countries. Namibia is not excluded from this equation and also relies on crop agriculture (and therefore pollinators) to ensure sustainable food security.

6.2 Materials and Methods

The Materials and Methods for the complete survey are provided in Chapter 2.

6.3 Results and Discussion

A total of 171 561 specimens (144 657 ants and 26 904 bees and wasps) were collected, representing 45% of the total sample. Of the ant sample 85.5% (123 735 specimens) belongs to the genus *Pheidole*. The ants were grouped into 24 RTUs. The rest of the Hymenoptera were grouped into 71 RTUs. Low abundance parasitoid groups were lumped as 'Other Parasitica', were not identified to morphospecies and not included in RTU analysis. Based on the above, the Hymenoptera were divided into four feeding guilds (Figure 1), namely flower feeders (2 RTUs); nectar feeders (2 RTUs); predators (23 RTU's) and parasitoids (43 RTUs).

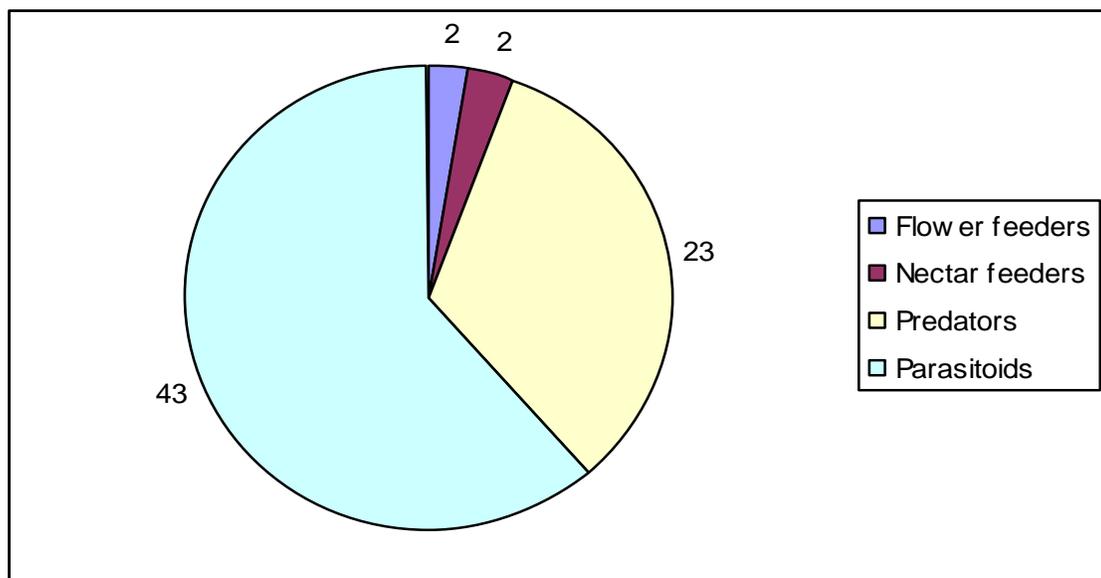


Figure 1. The feeding guild distribution of arboreal Hymenoptera sampled at five sites along the Omaruru River (Namibia) during 2004/5.

6.3.1 RTU comparison between three tree species

In declining order *Acacia erioloba* showed the highest species richness with 46 RTUs, followed by *Acacia tortilis* with 37 RTUs and *Faidherbia albida* with 31 RTUs (Figure 2a). The species richness for Formicidae showed an almost even distribution between the three tree species with 13 RTUs for *A. erioloba* and 14 each for *A. tortilis* and *F. albida* (Figure 2b).

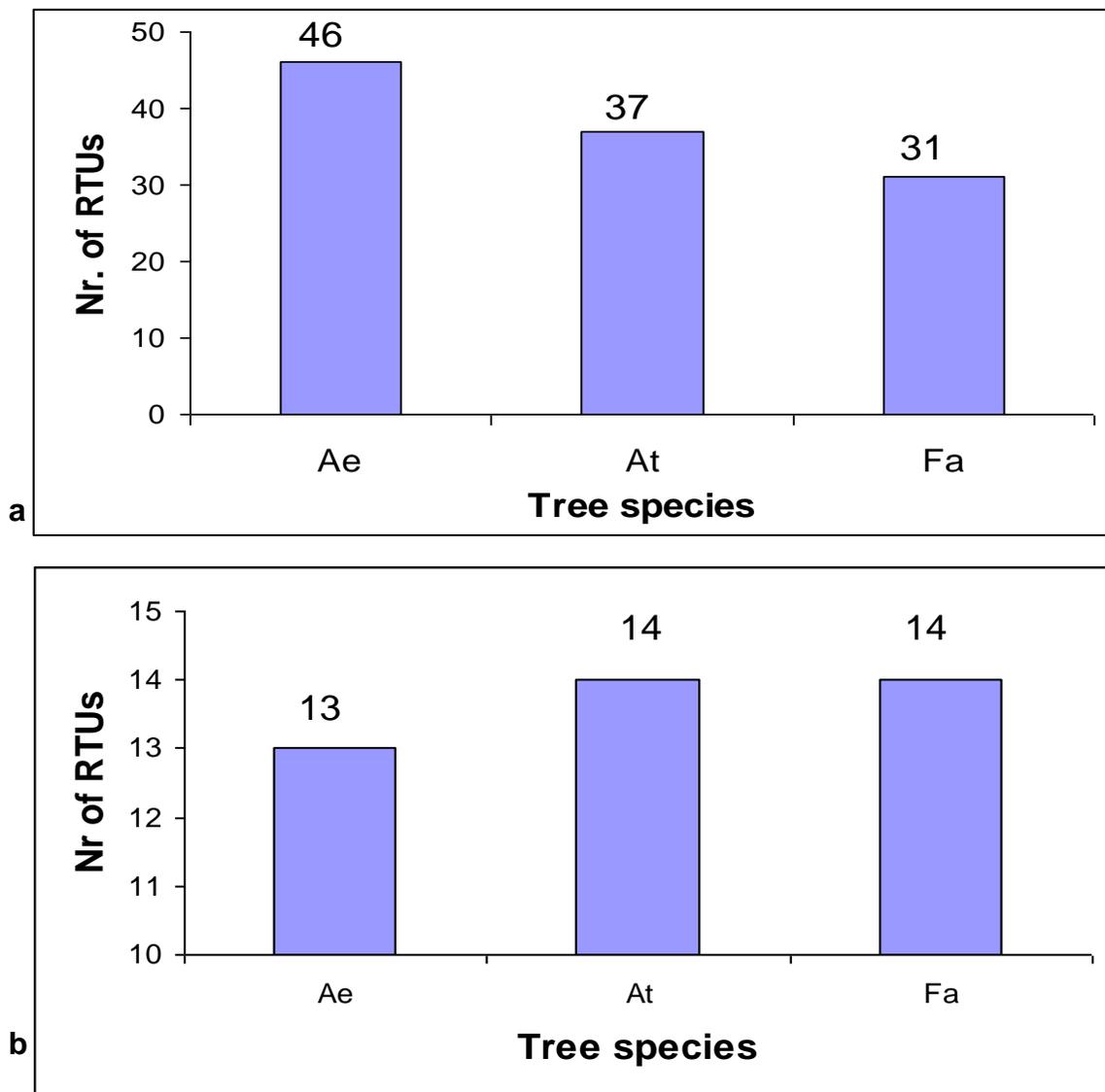


Figure 2. Species richness per tree species for arboreal Hymenoptera (a) and Formicidae (b), sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

The high species richness of the *A. erioloba* arboreal insect fauna, amongst others, probably indicates a larger qualitative and quantitative supply of prey animals for the parasitoid Hymenoptera, compared to *F. albida*, for example, which allows for more species packing. This is partially explained by assuming that *A. erioloba* provides a larger number of ecological niches that can be occupied by the prey species, which in turn is based on a different, more complex, canopy structure than in the case of the other tree species. This corresponds with the other orders, especially Coleoptera and Diptera, where

A. erioloba and *A. tortilis* also showed higher species richness than *F. albida*. *A. erioloba* also had the greatest abundance of specimens (15 000) sampled across all samples, followed by *F. albida* (7720) and then *A. tortilis* (4184) (Figure 3a). For Coleoptera and Hemiptera, prey animals for Hymenoptera, *A. erioloba* also had the greatest abundance. Thus, the more prey animals, the more predators/parasitoids. Formicidae, however, showed a clear preference for *F. albida* with 96 740 individuals compared to the 31 869 of *A. tortilis* and the 16 048 for *A. erioloba* (Figure 3b). (Field observations revealed high ant activity along the trunks of the *F. albida* trees.)

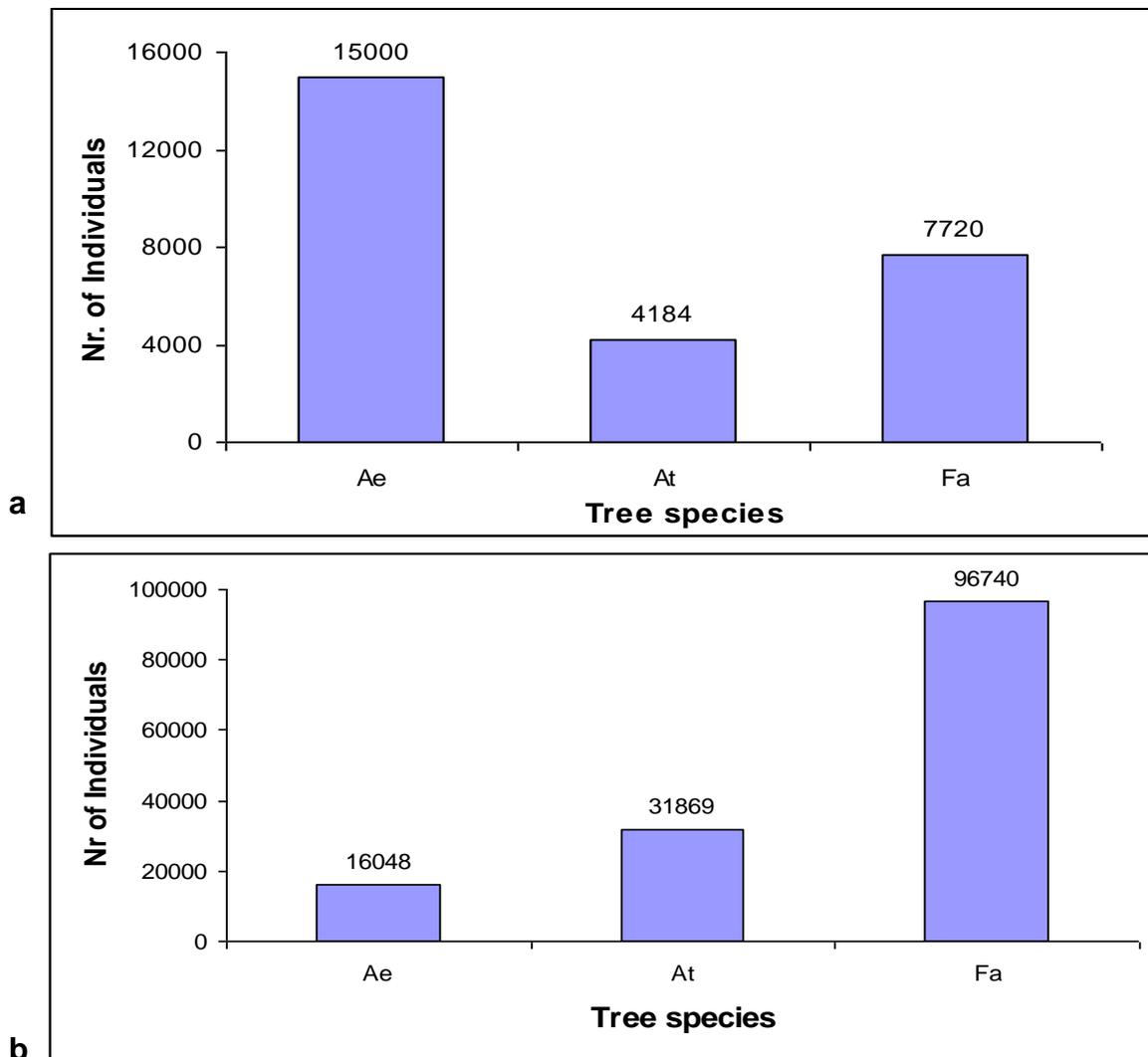


Figure 3. Specimen abundance per tree species for arboreal Hymenoptera (a) and Formicidae (b), sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

Pheidole species are aphidicolous, *i.e.* they tend aphids and coccids (Scholtz & Holm, 1985). The bark of *F. albida* is smoother than the bark of the acacia species, and is probably more suitable for aphids and coccids. This means that *F. albida* probably provides a better food source for the ants compare to the other two tree species.

Results of the mixed model analysis of variance (ANOVA PROC MIXED (SAS Institute 2010)) indicated that the mean species richness recorded (Formicidae excluded), for each sample varied among the three tree species ($F = 5.75$, $df = 2.47$, $P = 0.006$), similar to those of Hemiptera (their prey). The mean abundance recorded in each sample, was higher in *A. erioloba* than *F. albida* or *A. tortilis* ($F = 2.93$, $df = 2.47$, $P = 0.063$; Table 1).

Table 1. Least square means (ANOVA; PROC MIXED (SAS Institute 2010)) for number of non-Formicidae arboreal Hymenoptera RTUs (species richness) and number of individuals (abundance) per tree species, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

	Least squares means		
	<i>Ae</i>	<i>At</i>	<i>Fa</i>
Species richness	3.28	2.77	2.24
Abundance	161.31	39.02	77.64

Although the abundance per tree species varied greatly, the different tree species all harboured very similar feeding guilds with dominance in terms of parasitoids and larval predators (Figure 4). Although the *A. erioloba* trees sampled harboured considerably more individuals than the other two tree species, it had similar proportions of the different feeding guilds and therefore similar number and types of niches available to the arboreal insects. The deeply fissured bark of *A. erioloba* might provide more hiding or nesting space for insects than the smoother bark of the other two species.

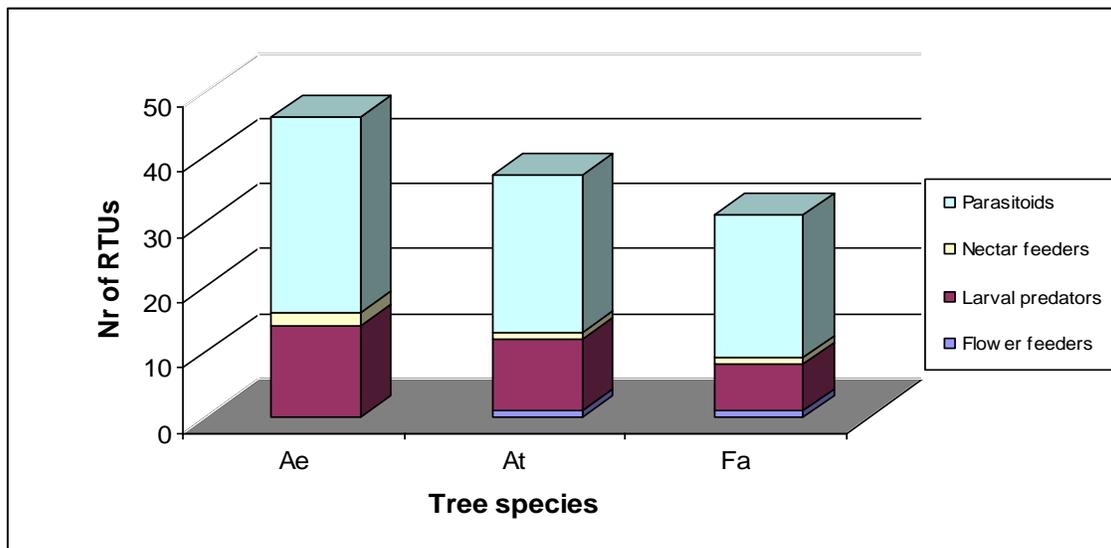


Figure 4. Distribution of feeding guilds among the three tree species for non-Formicidae arboreal Hymenoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

Considering the arboreal species commonality amongst the tree species, a QS value of 0 would indicate no species in common, and a value of 1.0 would indicate all species in common. Results from the survey indicated that the tree species are not only fairly similar regarding number of RTUs, but also share approximately 49% of the same RTUs among the pairs of tree species that were sampled (Table 2). This is, however, much lower than the 60% similarity for Coleoptera and the 73% similarity for Hemiptera. This phenomenon is explained on the basis that a larger proportion of the Hymenoptera species exhibit a specialist life-style (especially regarding the parasitoid guild) than is the case for the Coleoptera and Hemiptera species, which are more generalist in their activities. For Formicidae, however, the situation is quite different. Although the species are fairly similar regarding the number of RTUs found on each tree species, they do not share many species. The sampled ant species therefore seemed to be more tree species-specific than the rest of the Hymenoptera (Table 2).

Table 2. Sørensen's Quotient of Similarity (C_s) for the three selected tree species regarding arboreal Hymenoptera and Formicidae, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

	Ae-At	Ae-Fa	At-Fa
Hymenoptera	0.54	0.46	0.48
Formicidae	0.52	0.52	0.57

6.3.2 Comparison between sampling sites regarding the effect of aridity

The five sampling sites, present in a transect along one of Namibia's ephemeral rivers, fall within five different rainfall regimes (Chapter 2, Table 1) and thus represent a gradient across aridity. Both the total number of RTUs (Figure 5 and Table 3), as well as the number of RTUs per feeding guild (Figure 6) showed a noticeable decrease in numbers from Otjikoko in the east (wetter) to Omdel (drier) in the west ($F = 13.97$, $df = 4.47$, $P = 0.0001$). This corresponds with the decrease in numbers for the Hemiptera and Coleoptera. Apart from Lepidoptera, Hymenoptera also feeds on Hemiptera and Coleoptera. A decrease in numbers for the latter will thus also result in a decrease of Hymenoptera numbers.

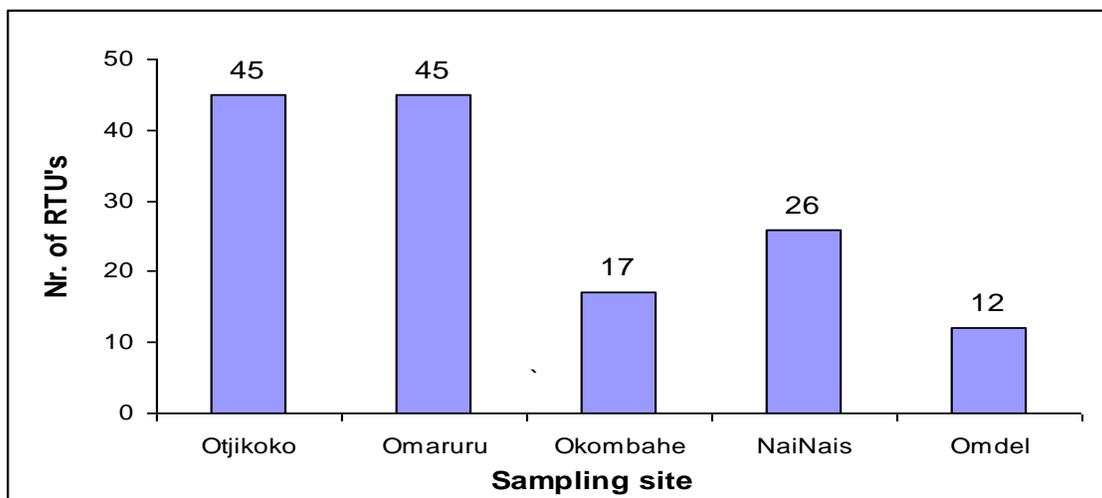


Figure 5. Species richness per sampling site across aridity for non-Formicidae arboreal Hymenoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

Table 3. Least square means and p-value (ANOVA; PROC MIXED (SAS Institute 2010)) for number of non-Formicidae arboreal Hymenoptera RTUs

per sampling site, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

	Least squares means					
	Otjikoko	Omaruru	Okombahe	NaiNais	Omdel	p-value
Hymenoptera	3.47	4.04	1.94	2.88	1.49	0.0001

A decrease in species diversity due to a decrease in ambient temperature has been reported for a wide range of organisms and there is evidence that many species have already extended their range towards the poles in response to recent global warming (Andrew & Hughes, 2005). As colder areas gradually become warmer the herbivores, which are more mobile than their hosts, are able to move into areas previously unavailable to them and exert enormous pressure on the climatically stressed plants. It is then that the role of predators (and parasitoids) becomes vitally important in controlling the herbivore populations (Andrew & Hughes, 2005). Temperature increase is also potentially harmful to bees. A case in point is a beetle species (*Aethina tumida* (Coleoptera, Nitidulidae)) from South Africa that was accidentally translocated to the USA, which caused large hive husbandry problems for beekeepers in the hot and humid regions of the country. These beetles are, however, excluded from colder areas. A rise in global temperature will allow this species to move into new areas, which will negatively influence the local bee populations, which in turn will have a huge negative impact on the USA economy (Le Conte & Navajas, 2008).

Apart from the predator problem bees face, they also have to deal with the possibility of mismatch of trophically interacting species, as predicted by Schweiger *et al.*, 2008). Changes in temperature will not only affect the reproductive biology of pollinators, but also the flowering of their host plants. Because different species react differently to climate changes (Voight *et al.*, 2003) the changes in plant phenology and the life-cycle of the respective plant pollinators might not synchronize properly, resulting in a mismatch. In other

words, plants might produce flowers ready for pollination before the pollinators have hatched, or vice versa.

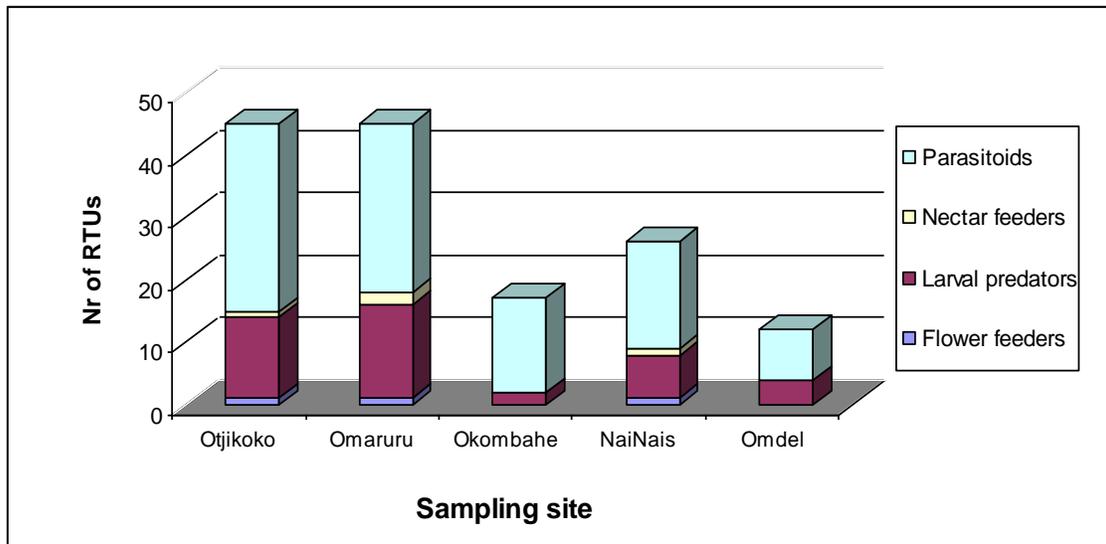


Figure 6. Species richness per feeding guild per sampling site for non-Formicidae arboreal Hymenoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

Should the data in Figure 6 be expressed as percentages, it can, however, be seen that although the species richness per feeding guild decreased from east to west, the proportional presence of each feeding guild relative to the sampling site remained within very narrow limits, with the exception of Okombahe where there was a considerable increase in parasitoids and a decrease in larval predators. (Figure 7). The results for Coleoptera (Chapter 4) and Hemiptera (Chapter 5) also indicate some degree of increase for various feeding guilds at Okombahe. Them being potential prey species for Hymenoptera, it is then understandable that the parasitoids would also show an increase at Okombahe.

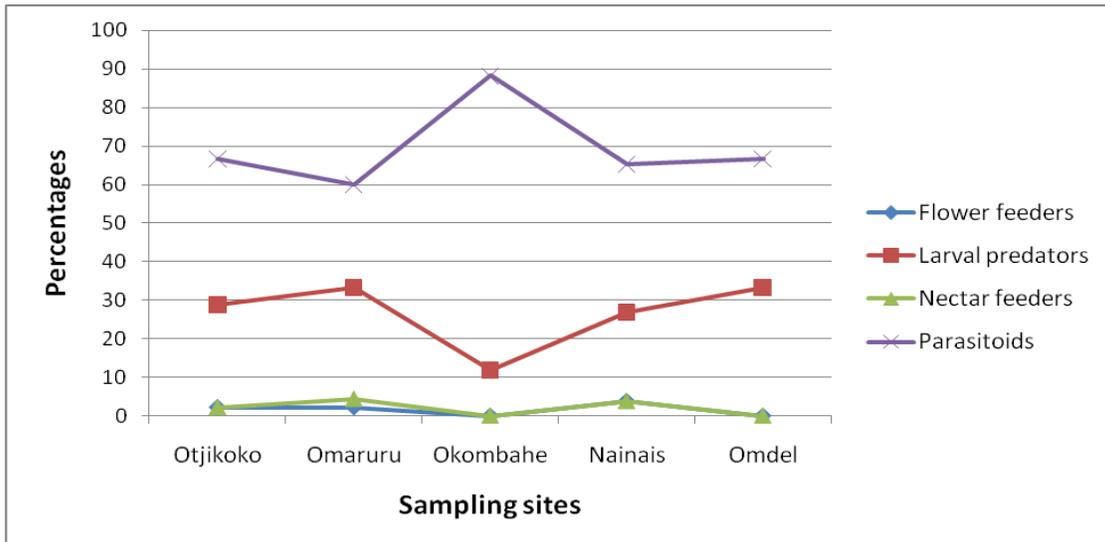


Figure 7. Proportion of each feeding guild (as a percentage of the total sample) relative to the sampling site, for non-Formicidae arboreal Hymenoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

The number of RTUs for Formicidae also showed the highest number at Otjikoko (east) and the lowest number at Omdel (west), with very little difference between the other three sites (Figure 8). Neves *et al.* (2010), studying the diversity of arboreal ants in Brazil, indicated that habitat heterogeneity and resource availability are important factors for ant species richness and composition. At the sample sites along the Omaruru River the more eastern sites showed more diverse and abundant vegetation than the more western sites.

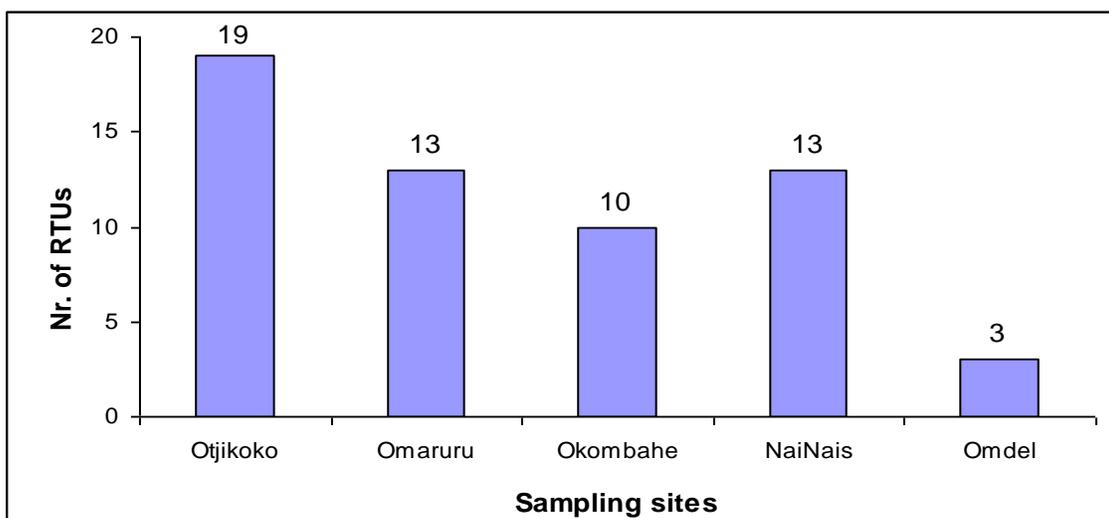


Figure 8. Species richness per sampling site for arboreal Formicidae, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

Both Neves *et al.* (2010) and Kaspari & Weiser (2000) found an increase in ant activity along a moisture gradient. The results of this survey thus correlate with their results. At Omdel all the ants sampled, with the exception of some *Crematogaster* individuals who was sampled in May, belonged to the *Pheidole* spp RTU.

The similarity analyses (for RTU numbers) indicated that the further apart the sites are from each other, the lower the similarity index (Figure 9 and Table 4). For Hymenoptera, (excluding Formicidae) Otjikoko and Omaruru (40 km apart) were 60% similar, Otjikoko and Okombahe (100 km apart) were 50% similar, Otjikoko and NaiNais (170 km apart) only 58% similar and Otjikoko and Omdel (260 km apart) a mere 24% similar. It clearly indicates that the sites do differ from each other with the Mixed Procedure (ANOVA; PROC MIXED (SAS Institute 2010)) indicating a marked decrease in RTU numbers from east to west ($F = 13.97$, $df = 4.47$, $P = <0.001$). Although there was a decline regarding the similarity index from east to west, it was, however, much lower (48% on average) than that for Coleoptera (55% on average) and Hemiptera (63% on average). This probably reiterates the specialist composition of the Hymenoptera. The same trend is also present for the between pairs of tree species index.

Table 4. Sørensen's similarity values with regard to site separation distances for five sites along the Omaruru River (Namibia) during 2004/5.

Sites	Distance apart (km)	Index value
Otjikoko – Omaruru	40	0.60
Otjikoko – Okombahe	100	0.50
Otjikoko – NaiNais	170	0.58
Otjikoko – Omdel	260	0.24
Omaruru – Okombahe	60	0.46
Omaruru – NaiNais	130	0.60
Omaruru – Omdel	220	0.30
Okombahe – NaiNais	70	0.69
Okombahe – Omdel	160	0.41
NaiNais - Omdel	90	0.36

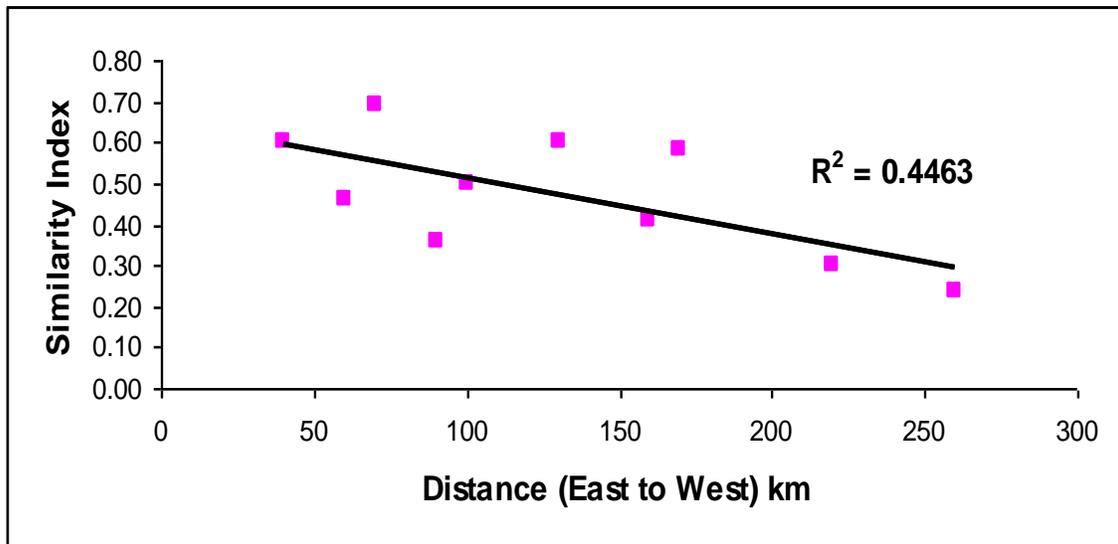


Figure 9. Hymenoptera similarity Index with regard to site separation distances along the Omaruru River (Namibia) during 2004/5.

6.3.3 Effect of seasonal changes

Both the total numbers of RTUs per sampling period (Figure 10), as well as the number of RTUs per feeding guild per sampling period (Figure 11), showed an increase in May (after the rainy season), then a decrease in July and September and then again a slow increase towards November (the pre-rainy season) and another increase towards January. From January to March there was a slight decrease as conditions became drier. This again correlates with the results from Coleoptera (Chapter 4) and Hemiptera (Chapter 5), the prey species for the Hymenoptera. In Namibia the rainy season falls within the warmer months of the year and thus also the more favourable months for the poikilothermic insects. June to August are the colder months when most insects prefer to be in a dormant or larval stage, often in more protected microhabitats, and then more difficult to sample.

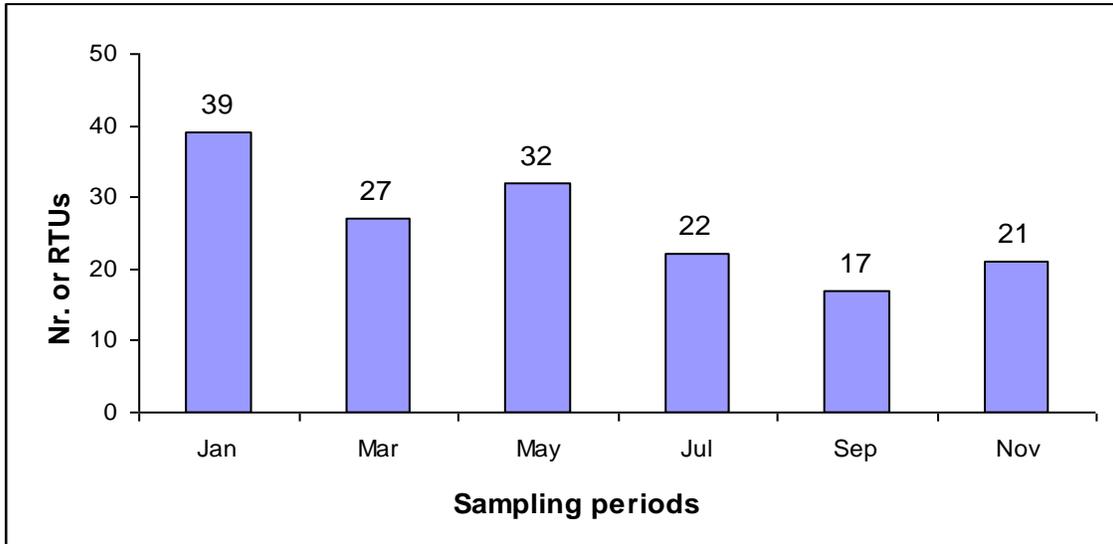


Figure 10. Species richness per sampling period (season) for non-Formicidae arboreal Hymenoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

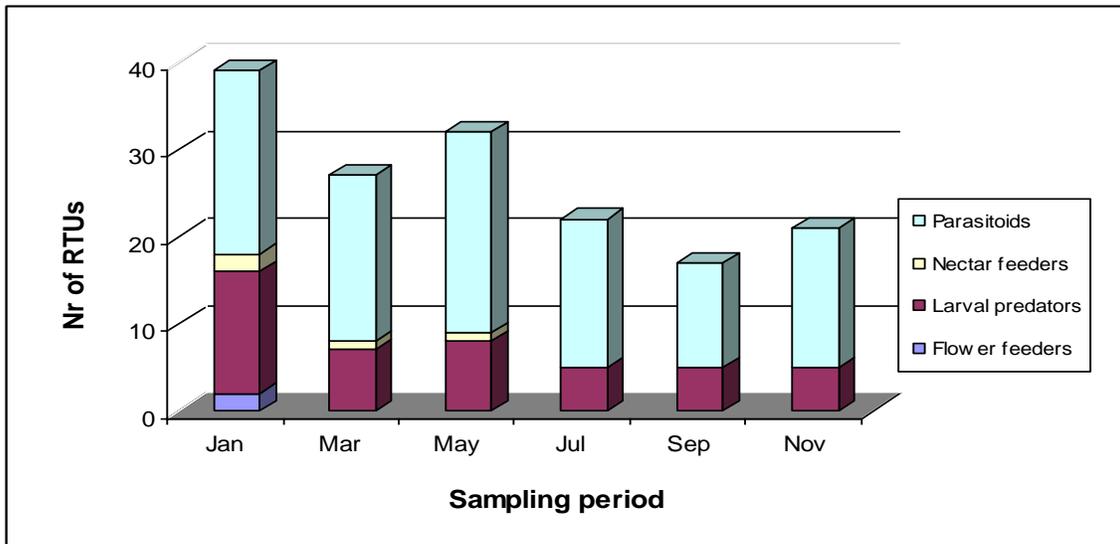


Figure 11. Species richness per feeding guild per sampling period (season) for non-Formicidae arboreal Hymenoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

Figure 12 provides insight towards understanding the distribution of the different feeding guilds across the different seasons. Flower feeders and nectar feeders were found in very low numbers (2 RTUs for each). Parasitoids showed a steady increase after the rainy season as more host insects, such as sap suckers and others with piercing-sucking mouthparts (Hemiptera, Chapter 5) and leaf chewers

(Coleoptera, Chapter 4) became available. Larval predators, on the other hand, showed a decline because most of their host insects (Hemiptera and Coleoptera), amongst others, have then moulted to adulthood.

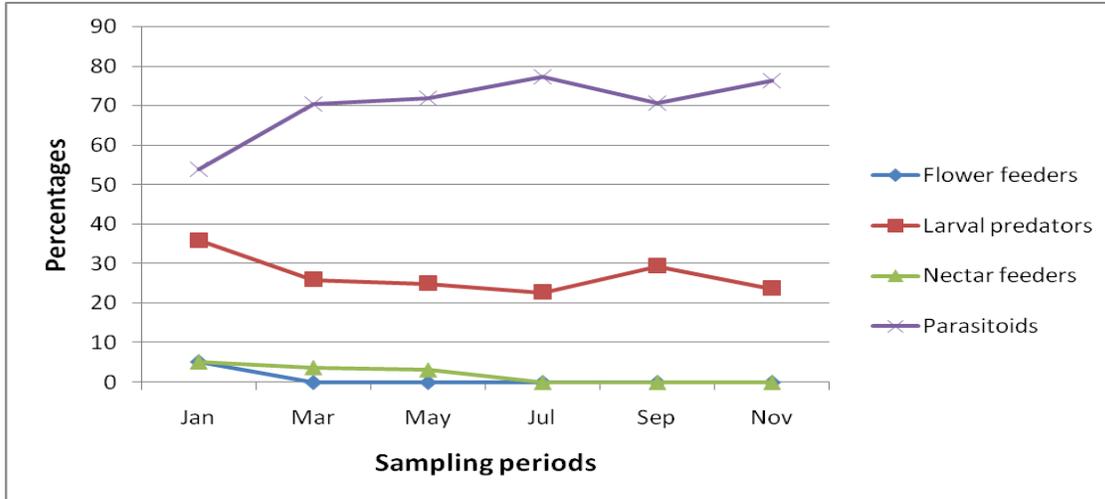


Figure 12. Proportion of each feeding guild (as a percentage of the total sample) per sampling period for non-Formicidae arboreal Hymenoptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

The number of RTUs sampled per sampling period for Formicidae also indicated a decrease in the dry season and an increase again towards the rainy season (Figure 13). Grove *et al.* (2005) and Neves *et al.* (2010) also reported on the importance of seasonality for ants.

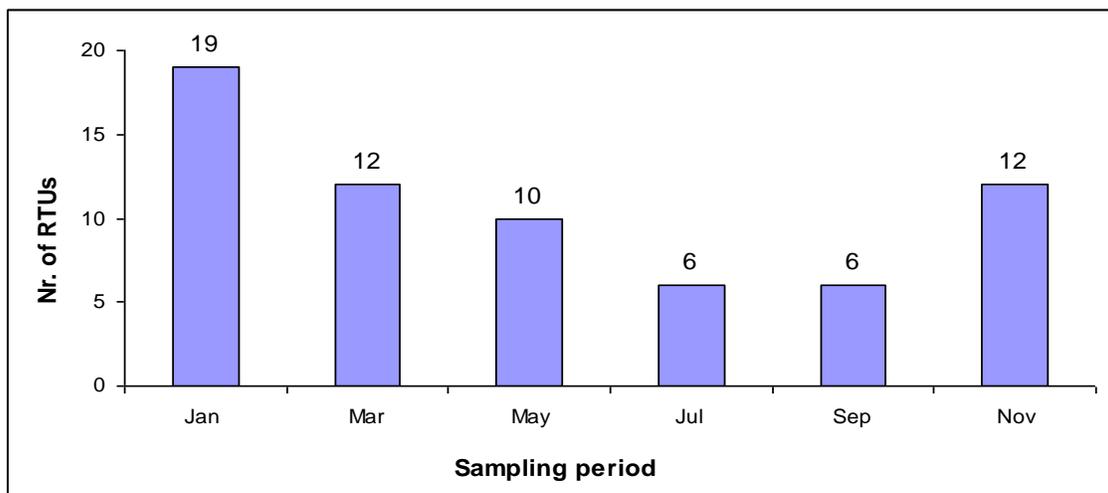


Figure 13. Species richness per sampling period (season) for arboreal Formicidae, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

6.4 Conclusion

For Hymenoptera, as for Coleoptera and Hemiptera, results from the survey indicated that the three tree species are not only fairly similar regarding the number of RTUs, but also share approximately 49% of the same RTUs among the pairs of tree species that were sampled. This, however, is much lower than for the latter two orders, indicating that Hymenoptera might have more specialist species and less generalists species than Coleoptera and Hemiptera. For Formicidae the three tree species had almost similar species richness, but a very low similarity index, indicating a species-specific tendency. As for abundance, Hymenoptera (excluding Formicidae) showed a preference for *A. erioloba* and Formicidae a preference for *F. albida*. The effect of aridity showed a decrease in species richness from the wetter sites to the drier sites. Although species richness declined from east to west the distribution of feeding guilds within each sample site remained fairly constant. The similarity index again indicated a lower value for Hymenoptera than for Coleoptera and Hemiptera, which again might support the notion of more specialist species than generalist species. The species richness of Hymenoptera, as well as Formicidae, showed a pattern somewhat similar to Coleoptera and Hemiptera, with an increase after the rainy season and a gradual decline towards and after the dry season.

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CHAPTER 7

TEMPORAL AND SPATIAL COMPOSITION OF DIPTERA

7.1 Introduction

The order Diptera (flies) is one of the largest insect orders. They can be distinguished from all other insects in that their second pair of wings is reduced to club-shaped structures, referred to as halteres. Flies occur in almost every habitat and have very diverse feeding habits. Diptera are holometabolous insects, with the larvae (referred to as maggots) differing in appearance, feeding strategies and niche occupation preferences from the adults (Picker *et al.*, 2003).

A number of Diptera families are important to humans because they act as vectors for various diseases, *e.g.* malaria (caused by the *Plasmodium* protozoan parasite and transmitted by the *Anopheles gambiae* complex of mosquitoes) and African sleeping sickness (caused by the *Trypanosoma* protozoan parasite and transmitted by *Glossina* spp. (tsetse)). Terblanche *et al.* (2008) stated that in East Africa, climate change will allow tsetse flies to move into areas currently unfavourable to them due to low temperatures. This will have enormous health and financial implications for the region. Flies are also of veterinary importance since they transmit diseases to game and livestock, wide-ranging health problems and even mortality. Diseases such as African horse sickness and bluetongue are directly linked to fly vectors (Wittmann *et al.*, 2001). Some flies are also destructive towards crops *e.g.* *Atherigona* spp (Muscidae) which attack graminaceous crops. Furthermore, the development of insecticide resistance by house flies and many other agricultural and medical important species causes major problems (Akiner & Çağlar, 2006).

However, there are also numerous beneficial species. Some help with the pollination of plants and other are useful as biological control agents, since they parasitize insect pest species (Scholtz & Holm, 1985). The housefly, *Musca domestica* (Diptera: Muscidae) and the blowfly, *Chrysomya megacephala* (Diptera: Muscidae) are both regarded as forensically-important species. Their presence on a corpse or at a death scene can provide the investigators with valuable evidence (Siriwattananarungsee *et al.*, 2005).

Climate change poses a threat to vector-borne diseases and with regard to Diptera this is a very pertinent issue. Arthropod vectors of these diseases are poikilothermic and their development, reproduction and behaviour are subjected to temperature fluctuation (Gage *et al.*, 2008). The influence of climate change on vector species has been widely studied (e.g. Martens *et al.*, 1995, Lindsay & Martens, 1998, Carcavallo, 1999, Githeko *et al.*, 2000 and Gage *et al.*, 2008). For Namibia, as for the rest of Africa, the potential role of climate change on the occurrence and spread of malaria is of real importance. The African continent has a high diversity of vector-species that have the potential to expand their habitat into new areas should temperature increases occur (Githeko *et al.*, 2000). Climate change will, for instance, affect the behaviour and distribution of malaria-transmitting mosquitoes, thereby changing and mostly increasing the incidence of malaria. Rainfall provides the aquatic medium needed for the development of mosquito larvae and temperature regulates the development and growth of both the malaria mosquito, as well as the *Plasmodium* protozoan, the causal parasite (Martens *et al.*, 1995). Increased risk of malaria due to climate change may become a real problem for a developing country such as Namibia.

7.2 Materials and Methods

The Materials and Methods for the complete survey are provided in Chapter 2.

7.3 Results and Discussion

A total of 10 376 individuals were sampled, representing 2.7% of the total sample. 175 Individuals were identified as predators and grouped into nine different morphospecies or Relative Taxonomic Units (RTUs). Only five maggots, all belonging to the same RTU, were sampled. Of the remaining 10 196 individuals, 8421 were generally referred to as flower feeders, with no distinction made between nectar feeders, pollen feeders or fruit flies. They were grouped into 143 RTUs (Figure 1). The rest of this overall total (1775 specimens) constituted Diptera that were relatively scarce. These were lumped and referred to as 'General Diptera' and were not assigned morphospecies status.

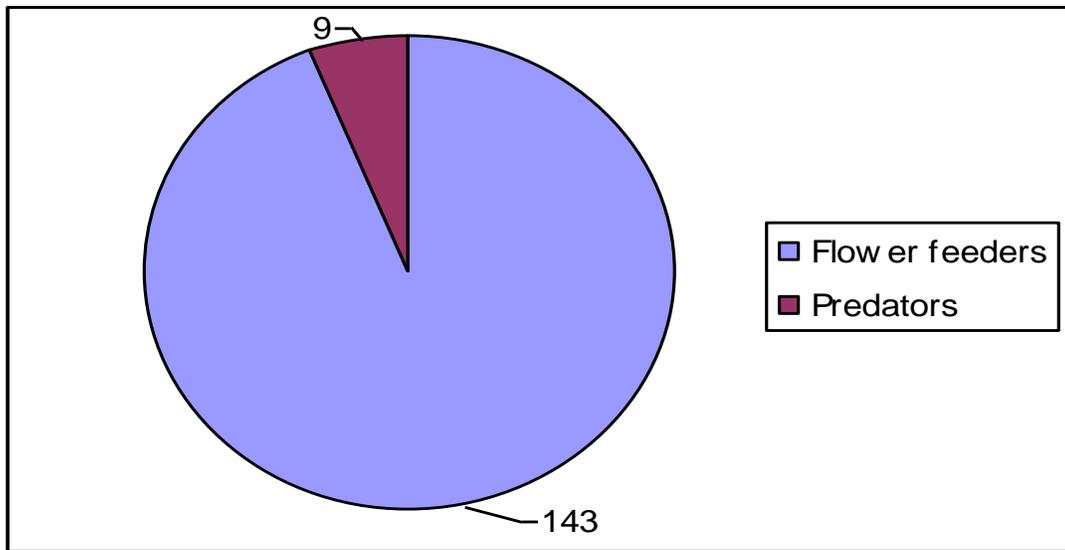


Figure 1. The feeding guild distribution of arboreal Diptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

7.3.1 Comparison between three tree species

In declining order *Acacia erioloba* showed the highest richness with 103 RTUs, followed by *Acacia tortilis* with 99 RTUs and *Faidherbia albida* with 90 RTUs (Figure 2). *A. erioloba* also had the greatest abundance (5715) across all

samples, followed by *A. tortilis* (2440) and *F. albida* (2216) (Figure 3). Species richness thus followed the same trend as abundance. The reason for this breakdown is based on *A. erioloba* providing more space in terms of niches, as well as richer nutritional resources. With its deeply fissured bark this tree species provides abundant shelter.

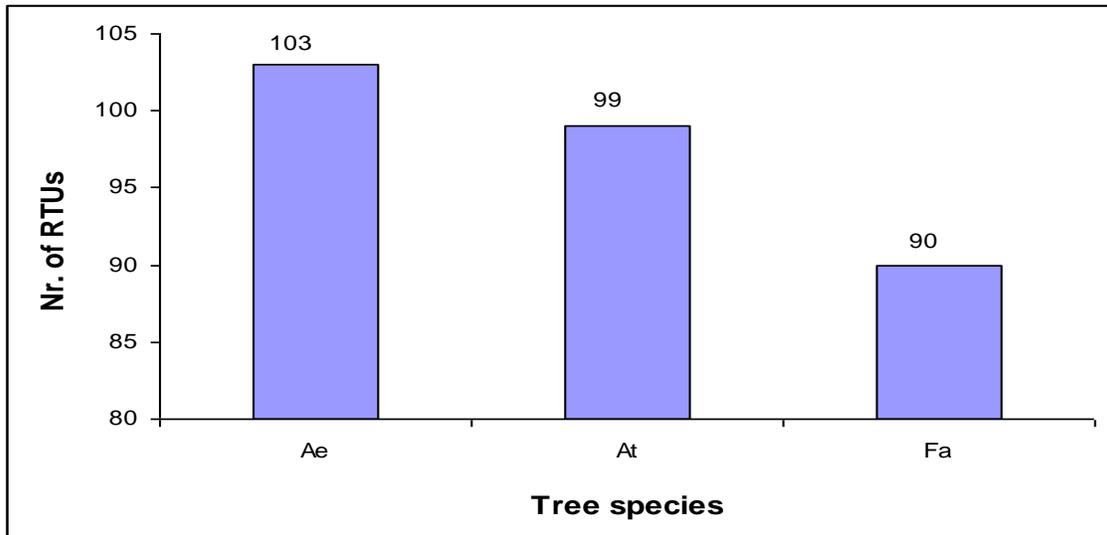


Figure 2. Species richness per tree species for arboreal Diptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

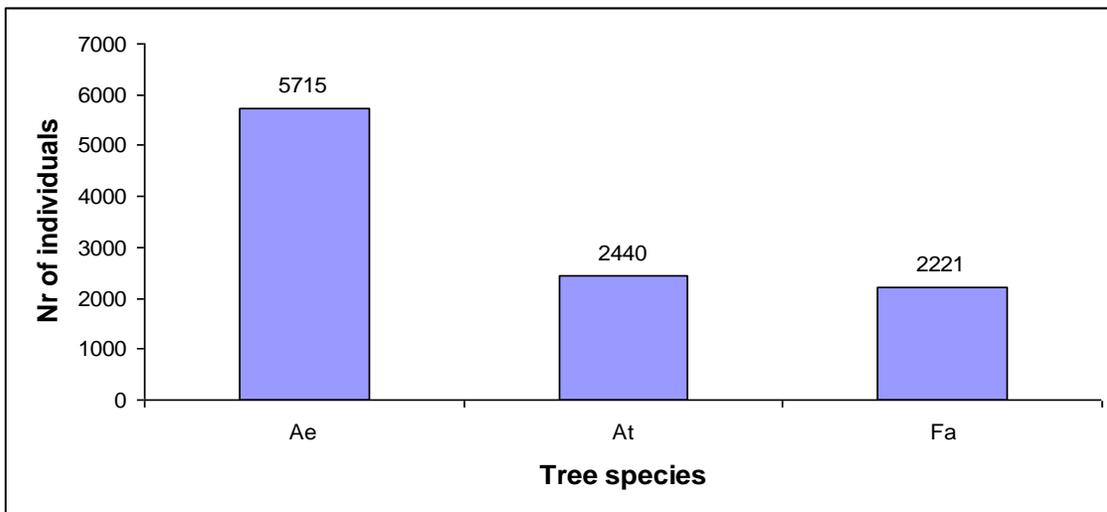


Figure 3. Specimen abundance per tree species for arboreal Diptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

The mean species richness, recorded for each sample, (according to the mixed model analysis of variance (ANOVA PROC MIXED (SAS Institute 2010)) did not vary among the three tree species ($F = 1.02$, $df = 2.47$, $P = 0.370$) and is largely similar to the results obtained for Coleoptera. However, the mean abundance recorded in each sample, was much higher in *A. erioloba* than *A. tortilis* or *F. albida* ($F = 4.12$, $df = 2.47$, $P = 0.022$, Table 1).

Table 1. Least square means (ANOVA; PROC MIXED (SAS Institute 2010)) for number of RTUs (species richness) and number of individuals (abundance) per tree species for arboreal Diptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

	Least square means		
	<i>Ae</i>	<i>At</i>	<i>Fa</i>
Species richness	5.90	4.94	5.29
Abundance	56.30	20.84	20.72

Although the abundance per tree species varied greatly, the different tree species all harboured very similar feeding guilds, with complete dominance regarding flower feeders (Figure 4). Although *A. erioloba* harboured more than double the number of individuals than was recorded on *A. tortilis* and *F. albida*, the proportion of each feeding guild, with regard to the total sample, were quite similar for each tree species. All three tree species therefore have similar number of niches available to harbour similar feeding guilds of insect species. *A. erioloba*, however, harboured many more individuals per species than the other two tree species.

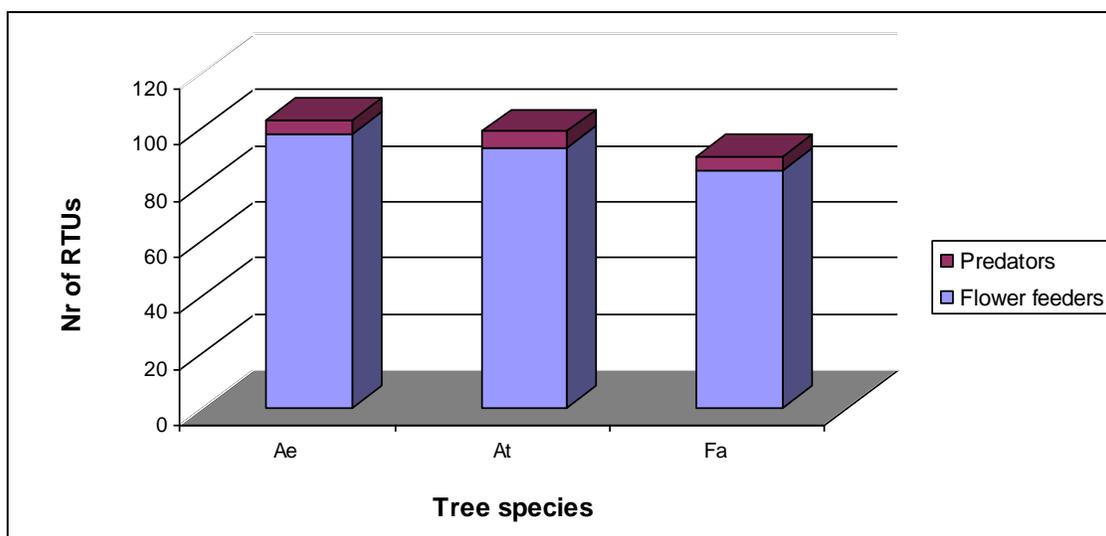


Figure 4. Distribution of the feeding guilds among the tree species for arboreal Diptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

When analyzing the arboreal species commonality amongst the tree species, a QS value of 0 would indicate no species in common, whilst a value of 1.0 would indicate all species in common. Results from the survey indicated that the tree species are not only fairly similar regarding number of RTUs, but they also share approximately 65% of the same RTUs among the pairs of tree species that were sampled (Table 2). These results compare well with the 60% similarity for Coleoptera and the 73% similarity for Hemiptera, possibly indicating that the Diptera samples also consisted of more generalists than specialists.

Table 2. Sørensen's Quotient of Similarity (C_s) for the three selected tree species regarding arboreal Diptera RTUs, sampled at five sites along the Omaruru River (Namibia) during 2004/5. (Ae = *Acacia erioloba*, At = *Acacia tortilis* and Fa = *Faidherbia albida*).

	<i>Ae-At</i>	<i>Ae-Fa</i>	<i>At-Fa</i>
Diptera	0.69	0.65	0.61

The results for phytophagy indicated that there is no difference across the different tree species (chi-square test: $\chi^2 = 5.681$, $df = 6$, $P = 0.4599$; log-linear analysis: $\chi^2 = 1.16$, $df = 2$, $P = 0.5609$). However, the proportion of RTUs in each phagy group is different for each insect order with some orders more likely to have tree-specific RTU groups than others. Based on this tree specificity, phytophagy specificity was assumed. For Diptera, 20.0% of the RTUs sampled were considered monophagous, 28.1% were considered oligophagous and 50.9% were considered polyphagous. The remaining 1% was allocated to a 'various' group consisting of a conglomerate of species that couldn't be assigned to any specific phytophagous group. This breakdown again indicates that the Diptera consisted of more generalist than specialist RTUs.

7.3.2 Comparison between sampling sites regarding the effect of aridity

The five sampling sites, present in a transect along one of Namibia's ephemeral rivers, fall within five different rainfall isohyets (Chapter 2, Table 1) and thus represent a gradient across aridity. Both the total number of RTUs (Figure 5 and Table 3), as well as the number of RTUs per feeding guild (Figure 6) revealed a noticeable decrease in numbers from Otjikoko in the east (warmer and wetter) to Omdel (cooler and drier) in the west ($F = 18.62$, $df = 4.47$, $P = 0.0001$). Again these results correspond with what was recorded for the other three orders.

Table 3. Least square means and p-value (ANOVA; PROC MIXED (SAS Institute 2010)) for number of RTUs per sampling site for arboreal Diptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

	Least square means					
	Otjikoko	Omaruru	Okombahe	NaiNais	Omdel	p-value
Diptera	7.14	8.99	2.94	4.10	3.72	0.0001

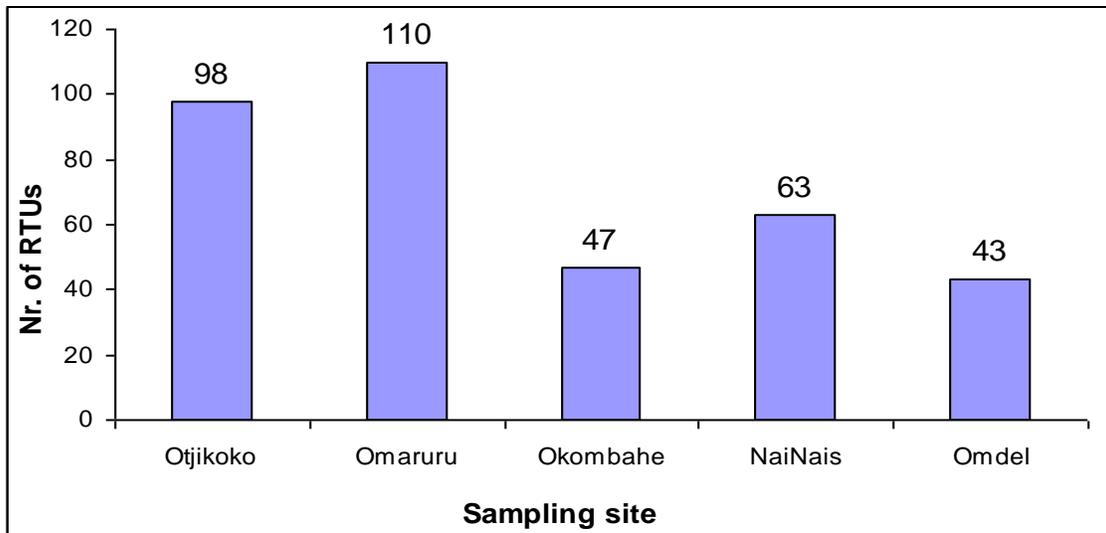


Figure 5. Species richness per sampling site (across aridity) for arboreal Diptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

In the last decade investigations regarding the monitoring of the impacts of climate change on ecological communities and processes have increased (Hodkinson & Bird, 1998). Dipterans, such as flies and mosquitoes, include numerous species that are disease vectors and have a high nuisance value, notably *Musca domestica* (housefly) and *Anopheles* spp (malaria mosquito). Many of these species are closely linked with human populations and a potential increase in their abundance, as a result of climate change, are a matter of concern (Goulson *et al.*, 2005). Patitucci *et al.* (2010) reported on the activities of the false stable fly (*Muscina stabulans* (Diptera: Muscidae)) along an urban-rural gradient in Argentina and indicated a marked increase towards the cities. According to them the temperature in urban areas tends to be higher than that of rural areas. The results of this study thus reported higher Diptera activity towards areas of higher temperature. Goulson *et al.* (2005) predicted a quantitative increase in calyprate fly populations up to 244% by 2080. Wittmann *et al.* (2001) presented evidence that the distribution range of *Culicoides imicola*, the vector of bluetongue virus and African horse sickness virus, already appears to be expanding in Europe, whilst Terblanche *et al.* (2008) predicted that the

abundance and distribution of *Glossina* spp, the vectors for human and animal trypanosomiasis (sleeping sickness), would be substantially influenced by changes in temperature ranges and moisture levels.

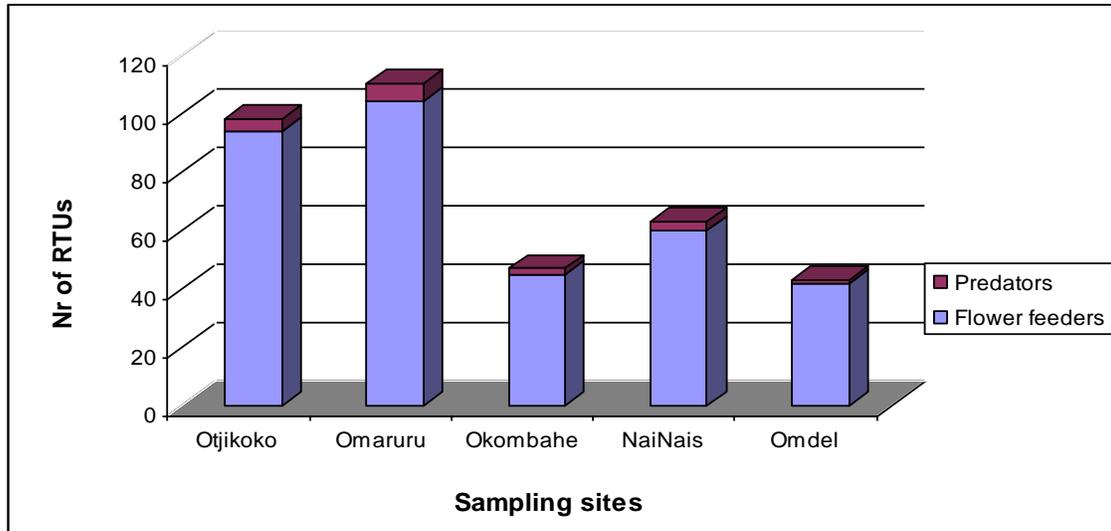


Figure 6. Species richness per feeding guild per sampling site for arboreal Diptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

As conditions across the Omaruru River transect become more and more arid, vegetation diversity decreases resulting in fewer phytophagous insects. In the case of Diptera, this equates to fewer flower feeders. Predators also decrease due to fewer host insects. This corresponds with Devoto *et al.* (2005) who stated that insect abundance patterns are directly dependent on plant diversity and abundance. Their results also indicated that flies are dominant towards the wetter end of the gradient (In this study that would be the Otjikoko and Omaruru sites). Smith *et al.* (2000) clearly stated that changes in temperature, as was the case along the sampling gradient in Namibia, will influence the population dynamics of insects. However, it is not only temperature that is relevant in this context, since competition and resource availability also influence insect development. Pinto *et al.* (2009) listed light, temperature and humidity as the primary environmental factors determining the distribution of mosquitoes and

reported a positive correlation between the abundance of culicid mosquitoes and variations in temperature and relative humidity.

Should the data in Figure 6 be expressed as percentages, it can, however, be observed that although the number of RTUs per feeding guild decreased from east to west, the proportion of each feeding guild, as a percentage of the total sample, remained within very narrow limits at each of the sample sites (Figure 7). Changes in the proportion of both flower feeders and predators remained within a 10% range across all five sampling stations. The species richness for all feeding guilds decreased in an equal sense.

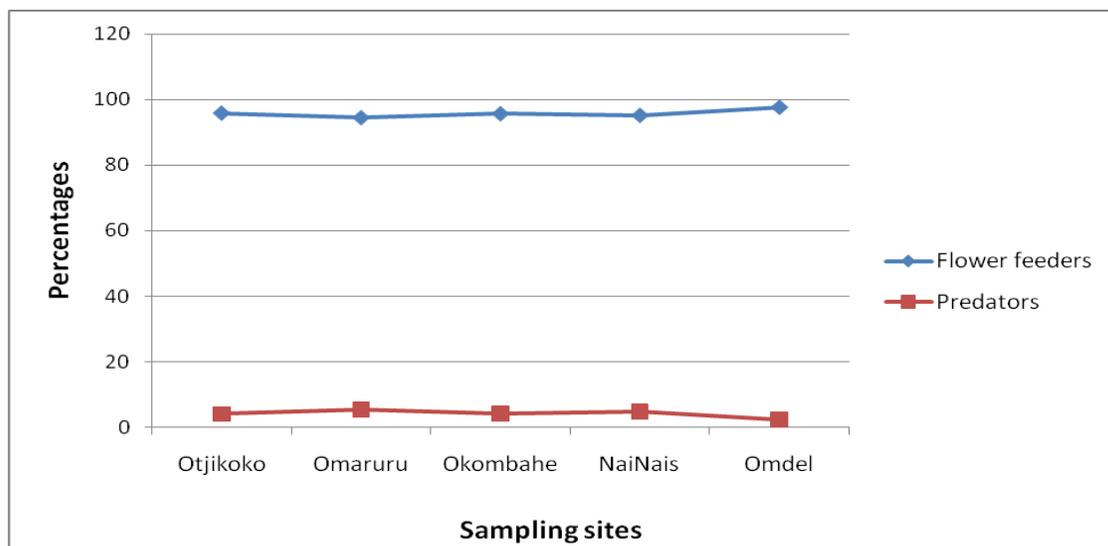


Figure 7. Proportion of each feeding guild (as a percentage of the total sample) relative to the sampling site regarding arboreal Diptera sampled at five sites along the Omaruru River (Namibia) during 2004/5.

The similarity analyses also indicated that the further apart the sites are from each other, the lower the similarity index (Figure 8 and Table 4). For Diptera Otjikoko and Omaruru (40 km apart) were 73% similar, Otjikoko and Okombahe (100 km apart) 51% similar, Otjikoko and NaiNais (170 km apart) only 59% similar and Otjikoko and Omdel (260 km apart) a mere 46% similar. Although there still was a declining trend (as for Coleoptera, Hemiptera and Hymenoptera)

it was less steep. It appears as if the similarity index for Diptera was less affected by distance, possibly indicating that the Diptera sampled during this survey in general comprised more generalist species. The Mixed Procedure analysis (ANOVA; PROC MIXED (SAS Institute 2010)) also indicated a marked decrease in RTU numbers from east to west ($F = 18.62$, $df = 4.47$, $P = <0.001$). However, although the sites did differ from each other as far as the number of RTUs is concerned, their general composition remained very similar (Figure 6).

Table 4. Sørensen's similarity values with regard to site separation distances for five sites along the Omaruru River (Namibia) during 2004/5.

Sites	Distance apart (km)	Index value
Otjikoko – Omaruru	40	0.73
Otjikoko – Okombahe	100	0.51
Otjikoko – NaiNais	170	0.59
Otjikoko – Omdel	260	0.46
Omaruru – Okombahe	60	0.49
Omaruru – NaiNais	130	0.56
Omaruru – Omdel	220	0.42
Okombahe – NaiNais	70	0.61
Okombahe – Omdel	160	0.46
NaiNais - Omdel	90	0.50

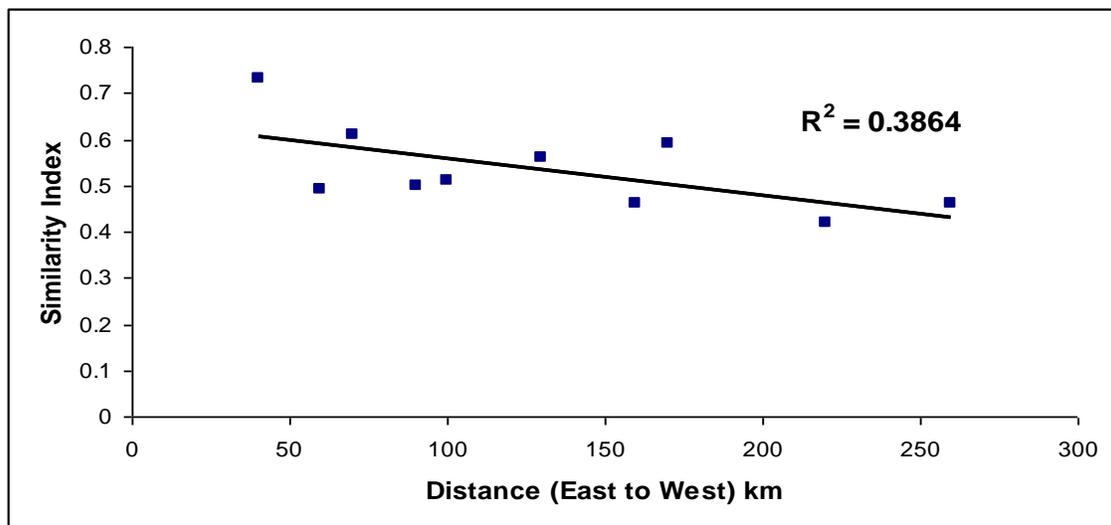


Figure 8. Diptera similarity index with regard to site separation distances along the Omaruru River (Namibia) during 2004/5.

7.3.3 Effect of seasonal changes

Both the total numbers of RTUs per sampling period (Figure 9), as well as the number of RTUs per feeding guild per sampling period (Figure 10), showed a sharp increase in May (after the rainy season), then a decrease in July to January with a slight increase again in March. Patitucci *et al.* (2010) also recorded the lowest activity of the false stable fly (*Muscina stabulans* (Diptera: Muscidae)) during winter months and Loetti *et al.* (2007) reported a clear seasonal pattern with higher values in summer than in winter for human-biting mosquitoes. According to Curtis & Mannheimer (2005) *Faidherbia albida* mostly flowers between March and September, reaching peaks in April/May and again in July to September. *Acacia erioloba* also has a flowering peak around April with *A. tortilis* flowering from November to April. Various other plant species along the river might also have had flowers after the rainy season, around April/May, which could explain the spike in Diptera (primarily flower feeders) during May.

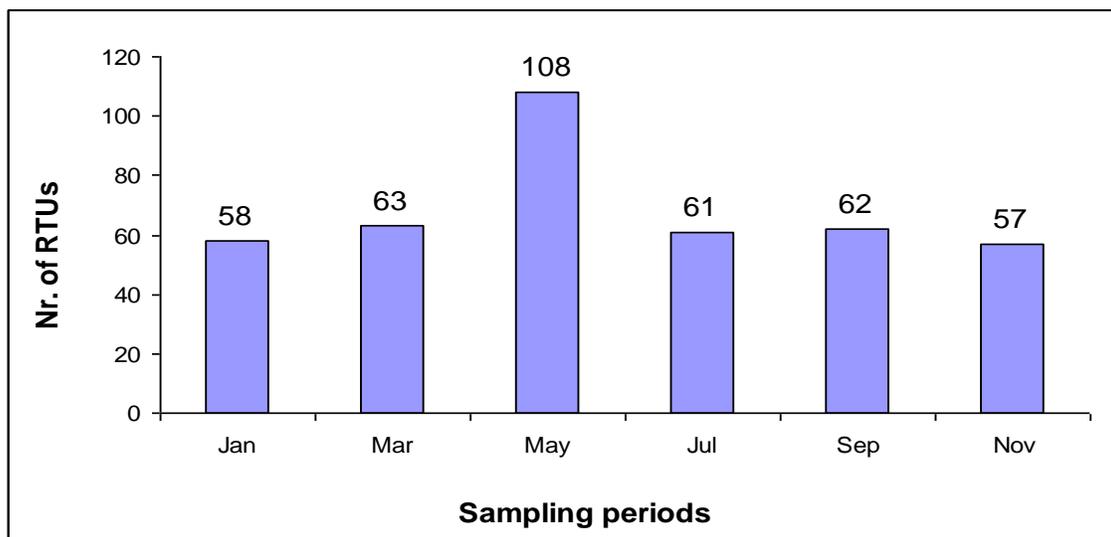


Figure 9. Species richness per sampling period (season) for arboreal Diptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

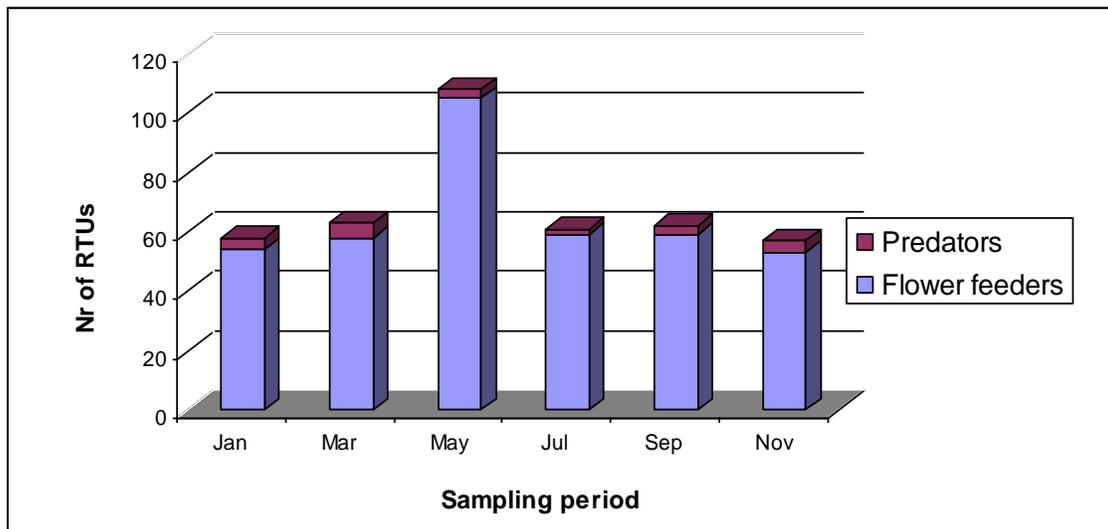


Figure 10. Species richness per feeding guild per sampling period (season) for arboreal Diptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

Figure 11 provides insight in understanding the proportion of each feeding guild as a percentage of the total sample per sampling period. Although there was a steep increase in RTUs in May, the proportion of each feeding group remained within very narrow limits across the sampling periods. Both the flower feeders and the predators proportionally remained the same. Similar trends were recorded in Coleoptera, Hemiptera and Hymenoptera.

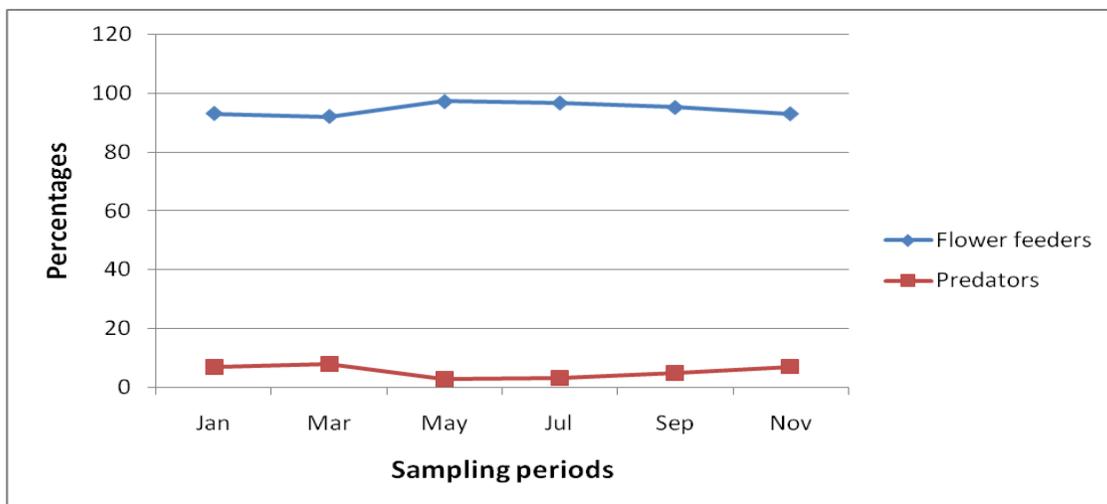


Figure 11. Proportion of each feeding guild (as a percentage of the total sample) per sampling period for arboreal Diptera, sampled at five sites along the Omaruru River (Namibia) during 2004/5.

7.4 Conclusion

As for the other three orders, the three species of sample trees turned out to be fairly similar to one another regarding Diptera species richness, with some degree of differences in abundance. Because the tree species are morphologically very similar, they provide a similar range of niches for the canopy insects. As the sites become drier and cooler from east to west the species richness and abundance gradually decline. This order was totally dominated by the generalized feeding guild referred to as flower feeders. Although the species richness declined from east to west, the proportional contribution of each species guild remained fairly stable. Results indicated a lowering in the similarity values between sites as the distances between them became larger. The different sites differ from each other with regard to environmental conditions and vegetation composition and therefore differ from each other with regard to suitability for insect occurrence. Species richness increased after the rainy season with a gradual decline towards the dry season.

Epidemic malaria is a serious problem of the semi-arid and highland areas in Africa (Thomson *et al.*, 2005). A study, conducted in Botswana, reported a methodology for assessing the importance of climate, and in particular rainfall, as a driver of malaria early warning system. According to them, excessive rainfall is an important predictor of epidemics in the warm semi-arid lowland areas in Africa.

Due to the fact that many Diptera are vectors for various diseases, climate change will not only affect the population dynamics of those particular insects, but will also have a huge impact on human and animal health. As a consequence this could also affect the economic development of the region.

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CHAPTER 8

GENERAL DISCUSSION

8.1 Introduction

- Of the estimated 35 000 insect species occurring in Namibia, only about 18% are described. About 24% are endemic, occurring mostly in western Namibia.
- There is a need for more entomological research in Namibian landscapes in order to understand and manage natural resources sustainably.
- Namibia is an arid country with low rainfall, low relative humidity and relatively high temperatures. Rainfall distribution is variable and unpredictable. The isohyets lie northwest to southeast, with rainfall decreasing from northeast to southwest.
- Arboreal insect diversity along an east-west gradient was conducted along the Omaruru River, one of Namibia's ephemeral rivers. Three tree species commonly occurring along dry river courses in Namibia were used as focus species.
- Arboreal insect communities of lowland savannahs are poorly studied and very few studies have been conducted in the African savannah habitat.
- Climate change poses a real threat to biodiversity worldwide. Increase in temperature has already caused the movement of many insect species into previously unoccupied areas. The impact of such a scenario has multiple consequences regarding plant pollination, disease transmission and general human and animal well-being.

- Namibia provides a unique opportunity to study plant and animal distribution patterns related to rainfall gradients, since the country has a strong east-west climatic gradient. Most rivers in Namibia are ephemeral and only flow after strong rains have fallen in their catchments. These rivers support approximately 20% of the Namibian human population and are important sources of water and fodder for man and domestic and wild animals respectively.
- Trees are ideal for studying insect community dynamics, since they exhibit a large niche diversification, especially in their canopies. Large trees growing along the ephemeral rivers courses in Namibia do not directly depend on rainfall for their survival, but obtain their water and nutrients requirements from an edaphic environment that is more or less uniform across the rainfall gradient. This results in more or less fixed flowering and new growth patterns each year. To a certain extent this synchronization limits the scope of ecological function (especially food web complexity), which in turn determines species diversity. Environmental constraints are temperature and humidity and to a lesser extent altitude.

8.2 RTU comparison between three tree species

- The results for the four major orders (Coleoptera, Hemiptera, Hymenoptera and Diptera) all indicated that there are not many differences between the three sample tree species with regards to their associated arboreal insect diversity. For Coleoptera, Hymenoptera and Diptera the two *Acacia* species showed the highest species richness. For Hemiptera, *A. tortilis* and *Faidherbia albida* showed the highest and exactly identical richness, with *A. erioloba* the lowest, but with only four RTUs less than the other two.

- The abundance per tree species did vary with regard to the different insect orders, with *A. erioloba* having the highest abundance for Coleoptera, Hymenoptera and Diptera. For Hemiptera *A. tortilis* had a higher abundance than *A. erioloba*. *Faidherbia albida* had the lowest abundance for Hemiptera and Diptera and the second lowest for Coleoptera and Hymenoptera.
- The Sørensen's Similarity Index indicated that the three tree species not only showed relative similar species richness, but also share a high percentage of the same species (*i.e.* high species similarity index). This was the case for Coleoptera, Hemiptera and Diptera, whereas Hymenoptera showed a less than 50% similarity index. This probably indicates that the Hymenoptera arboreal RTUs that were sampled consisted mainly of specialists, while the arboreal RTUs sampled for Coleoptera, Hemiptera and Diptera were primarily generalists.
- Although the number of individuals per tree species varied within each order, all four orders showed that the proportion of each feeding guild towards the total sample were very similar between the three tree species.
- The Chi-square tests indicated that there was no statistical difference between the proportions of phytophagy on each of the host species. In this regard the recorded percentage of monophagy across the Coleoptera, Diptera and Hemiptera was very similar between the three tree species. (Hymenoptera was not included in the phagy analysis due to the fact that no phytophagous individuals were sampled). The same situation applies with regard to oligophagous and polyphagous species. Therefore, a certain tree species was not more likely to have tree-specific RTU groups than another. The proportion of RTUs in each phagy group did, however, show a difference by insect order and some orders turned out to be more likely to have tree-specific RTU groups than others.

- The results of this study indicated that the proportion of mono- and oligophagy is not as common as polyphagy. For all the orders the percentage of polyphagous species was almost equal to that of the mono- and oligophagous species combined. For Hemiptera polyphagy contributed to more than 60% of the total sample.
- Phylogenetically the three sample tree species are closely related and as a result they exhibit high morphological similarity in canopy architecture, as well as, amongst other, leaf and flower characteristics. As a result all three tree species provide more or less similar niches and resources for the canopy insects to occupy and utilize.
- These results emphasized the potential impact of climate change on insect and general landscape ecology. A dramatic westward shift in climatic conditions in Namibia would affect both insect composition and vegetation composition and species richness which would affect underlying trophic interaction structures. Specialists, for instance, are the most sensitive trophic guilds and would probably be influenced first. Should new species move into a previously unoccupied region, as changing climatic conditions open up new niches, the total landscape ecology can be altered, resulting in positive or negative economic consequences for the country.

8.3 Comparison between sampling sites regarding effect of aridity

- For all four the orders that were analyzed both the total number of RTUs, as well as the number of RTUs per feeding guild, showed a noticeable decrease in numbers from east to west (Otjikoko to Omdel) across the gradient. The Mixed Procedure analysis also indicated a considerable difference in RTU numbers between the different sampling sites. Sørensen's Quotient of Similarity showed that the further apart the sampling sites are from each other, the less similar they are in terms of arboreal insect composition, which clearly indicates that the sites differ

from each other. The similarity index for Hymenoptera was, however, much lower than those of the other three orders, indicating that the canopy RTUs sampled for Hymenoptera consisted of more specialists than generalists, unlike the other three orders where generalists dominated.

- Once again, although the species richness decreased across the aridity gradient, the proportion of each feeding guild towards the total sample remained very similar for all four orders.

8.4 Effect of seasonal changes

- Both the total numbers of RTUs per sampling period, as well as the number of RTUs per feeding guild per sampling period, showed an increase in May (after the rainy season), then a decrease in July and September with a slow increase towards November (the pre-rainy season) and another increase towards January. Although the results for Diptera differed slightly from the other three orders, the trend remained the same.
- Another reason for the drop in numbers during the dry season might be due to of the different stages in the life cycle of insects. Certain insects, such as certain Chrysomelidae and Curculionidae have endophytic larvae, which results in these species not being sampled during certain times of the year. This leads to the misconception that those species are absent during certain months, whilst they are actually present but do not make out part of the arboreal fauna at that point of time.
- On account of poikilothermy, the presence and abundance of the canopy insects waxes and wanes through the seasons, in spite of the refugium effect of the tree canopies and the arboreal habits of the insects.

8.5 Conclusion

- When analyzing the temporal and spatial composition of arboreal insects along a gradient (as was conducted along the Omaruru River in Namibia), seasonality seems to be the most important determining factor, followed by the specific locality (site), with host (tree) species as the least important.
- All in all, short-term (seasonal) faunistic analyses across a landscape transect of increasing aridity can provide insight into long-term climate induced environmental changes.