Department of Environmental Biology

Assessing factors influencing the spatial distribution of species diversity in ground dwelling ant assemblages in lowland, wet forest of southwest Sri Lanka

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This thesis is presented for the Degree of
Doctor of Philosophy
of
Curtin University of Technology

March 2008

Declaration

To the best of my knowledge and belief this thesis contains no material previously published by any other person except where due acknowledgment has been made.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

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Abstract

Tropical forests of the world are fast disappearing and there is a race to understand patterns of species distribution in space and time. Studying species distributions can provide better frameworks for conservation of these ecologically important patches of floral and faunal diversity. The island of Sri Lanka is a well known harbour of unique and highly threatened biodiversity. Tropical lowland forest is remnant in the south-west of the island now mainly existing in small patches. While most are small disturbed fragments, Sinharaja Forest Reserve represents one of the largest remaining patches of this important ecosystem. As a UNESCO World Heritage Site and a Man and Biosphere Reserve, it has a dual role as a conservation area and a historically important resource forest. While the distribution of vegetation diversity has been well documented, analyses of invertebrate species distributions are lacking.

This thesis investigated a key arthropod group, ground dwelling ants, in relation to environmental gradients within the forest. Cumulative results demonstrate the high diversity of the forest patch. In an area representing less than half the reserve, over 173 ground dwelling ant species were found in distinct assemblages throughout the forest. Since the forest is located upon a series of parallel ridges, ant species distribution was first analysed in terms of this small elevation change. Species richness declined over a vertical incline from 430 m to 660 m, highlighting a possible small-scale, mountain mass effect. This section of the reserve is also characterised by a patch of once-logged forest (30 years previously). A study was undertaken to investigate whether there were residual effects of selective logging on the reserve. Significant differences between species assemblages in once-logged forest and unlogged forest add to growing evidence that selectively logged forests continue to remain distinct from unlogged forest even after decades of regeneration. Ant distribution was then analysed for their relationship with habitat heterogeneity and tree species distribution. Long-term research on tree species in the SFR has demonstrated a close relationship to habitat complexity. Ant species appear to respond more to the structural heterogeneity of the vegetation than to actual topographic variation within the forest. From a conservation perspective, maintaining the integrity of this highly diverse forest is imperative. The impact of anthropogenic land uses surrounding the forest was investigated in terms of ant assemblages along the forest edges. Significant differences were found between assemblages within the edges bordered by different matrix types. Even relatively large forest remnants can be affected by the surrounding matrix land uses and encouraging the growth of structurally similar vegetation and maintaining low disturbance along the borders should attenuate the effect of the edge.

Overall, the highly heterogeneous distribution of ant assemblages within the SFR demonstrates the potential for other small patches to be harbours of further species diversity. Future research should be undertaken to assess the diversity and distribution of ant species within this region and encourage the protection of this remnant diversity.

Acknowledgements

Doing the research for my Ph.D. in Sri Lanka had always been a pipe dream of mine, I never thought that I would get the opportunity to do any work there, let alone study a fantastic taxon like ants. For this great opportunity, I would like to express my deepest appreciation to Professor Jonathan Majer, my supervisor, for taking a leap of faith and supporting me in my bid to do research in a country he had never been to.

Due to my own inexperience with working in Sri Lanka, the research would not have been possible without the expert advice of Professor Jayanthi Edirisinghe, my co-supervisor. Her influence and great understanding of working in the field in Sri Lanka made my research experience that much more fulfilling. I would like to thank the Professors Savitri and Nimal Gunatilleke for their invaluable advice and long experience of working in the forests of south-west Sri Lanka. Thank you for supporting my work in the Sinharaja Forest Dynamics Plot and for generously providing the tree species data. I greatly appreciate all the fantastic opportunities they gave me during my time in Sri lanka.

The research would not have been possible without the sponsorship of Curtin University of Technology, Australia, in my application for an Endeavour International Postgraduate Research Scholarship. I would like to thank all those at the Scholarships Office who supported my candidature. I would also like to thank the Post Graduate Institute of Science, Peradeniya University, Sri Lanka, in their support of my application for and administration of an International Foundation for Science research grant (Grant No. D/3929). Part of this research would not have been possible without the support of the International Foundation for Science, Sweden. I would also like to thank the Centre for Tropical Forest Science-Arnold Arboretum (CTFS-AA) Asia Program for supporting my work in the Sinharaja Forest Dynamics Plot and for administration of the T.L. Higginson, Jr. Fund. I extend a personal thank you to Mr. Tom Higginson for taking an interest in ants, my studies and for being a generous and kind patron.

I am very grateful to the Sri Lankan Forest Department for permitting access to the reserve (Permit no. FRC/8) and to the Sri Lankan Wildlife Deparment for allowing the collection and export of specimens from the reserve (Permit no. WL/3/2/1/7).
I would like to thank all my various field assistants for their patience and hardwork- Sanjeeva, Masitha, Mahinda, Pradeep, Kirthi, Piasena and Prabath. Also, a thank you to all the Forest Dept. staff who helped me and the residents of Sinharaja Adaviya who took care of me while I was there.

I would like to thank Drs. Gary Alpert, Marek Borowiec, Kazuo Eguchi, Brian Fisher, Brian Heterick, Shingo Hosoishi, Kazuo Ogata, Seiki Yamane, and Thresiamma Varghese for their generosity in accepting my ant specimens for identification.

To all my friends in Australia, Sri Lanka and scattered elsewhere around the globe, thank you for liking ants (even if it was only for my benefit), and for always asking questions about them. And especially, to Joe Grove, my wonderful Sinharaja buddy.

To my family, I dedicate this entire thesis.

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1. General Introduction

1.1 Protecting tropical forests

Tropical rain forest harbours at least 50% of global biodiversity (Primack 2002), a large proportion of which is restricted to particular regions of the world (Collins *et al.* 1991; Primack & Corlett 2005). Unfortunately these forests are among the most threatened ecosystems in the world today. Across the tropics, annual deforestation was estimated at 9.2 million hectares per year for the decade between 1990 and 2000. Of that area, 6 million hectares was considered “tropical rain forest” (FAO 2001). Of the 63 nations in the tropics with forested areas, 29 have been classified as having disturbed greater than 80% of their forests (Soulé & Sanjayan 1998). These forests have been reduced in area and fragmented as land is continuously being modified by human population pressures (Whitmore 1997). Currently, tropical wet forests cover 6 - 7% of the Earth’s land surface, most of which is under human management, either as resource forests or as protected reserves (Gómez-Pompa & Burley 1991; Primack & Corlett 2005). However, with the majority of these forests located in developing nations, macro-economic factors often determine the degree of protection of these reserves (Kahn & McDonald 1997).

Protected reserves often represent a very small percentage of the land surface of the countries that harbour tropical forests (Laurance 1997). As of 1990, only 8.7% of tropical forests were under some degree of legal protection (Grieser Johns 1997). There is a widespread opinion that most of these parks are merely documented on paper and are not physically protected (Soulé & Sanjayan 1998; Norton 1999). Most represent land that was inaccessible due to topography and therefore escaped conversion or disturbance by humans (Norton 1999). Hence, while there may be a degree of legal and/or physical protection, many of these forests still face pressure from surrounding land users (Olupot & Chapman 2006); and a vast number have already been disturbed to an extent that exceeds natural disturbance levels (Palik & Engstrom 1999). The processes of disturbance in these areas tend to be more gradual and subtle, unlike large scale deforestation and selective logging, therefore the changes in biodiversity in these forests are often more difficult to detect (Pethiyagoda 2005).

The high biological diversity of these tropical forest remnants is still relatively understudied (Hubbell 1995). There is an urgent need to gain a firmer understanding of their ecology so that they can be managed into posterity. Those that are relatively undisturbed require careful monitoring, as they are important as seed banks and sources of organisms for re-colonising adjacent, disturbed land (Thebaud & Strasberg 1997; Chazdon 1998). One of the difficult issues of protected area management is the adequate maintenance of genetic diversity of organisms in a restricted space (Jennings *et al.* 2001). If a forest is to become a sustainable source of maintainable genetic diversity, we must first assess the diversity of flora and fauna that inhabits the forest and continue to assess it even after it has been designated as a protected area.

Global biodiversity is on the decline, and there is a need for rapid assessments to be made, especially in areas where little work has been done. Biological inventories are an important part of environmental management, as they allow those involved to make responsible decisions regarding areas that have high biodiversity and are harbours of complex ecosystems (Stork & Samways 1995). Thus, it is imperative that biodiversity is documented in these forests before further degradation occurs and significant species have disappeared completely.

1.2 Ant diversity in tropical forests

Ants can constitute up to 20% of the animal biomass in tropical forest and play essential roles in ecosystem functioning (Kaspari 2000; Primack & Corlett 2005; Wilson & Holldobler 2005). They inhabit all levels of forest structure, from the canopy to the soil layer and, while most are opportunist foragers, some are the major predators of many invertebrate groups (Kaspari 2000; Primack & Corlett 2005). In lowland wet forest of Malaysia, up to 524 species of ants have been recorded in 4 km^2 (Brühl *et al.* 1998) and over 400 species have been collected in 1500 ha of neotropical wet forest in Costa Rica (Longino *et al.* 2002b).

In recent decades, ant species have been used as bioindicators of environmental change in a variety of situations such as: soil quality assessment (Lobry De Bruyn 1999); fire effects (Friend 1994); plantation management (Majer 1988); logging and mining (Jackson & Fox 1996); and mine site rehabilitation

(Wallis *et al.* 2001). Long-term community studies have shown them to be good indicators of regeneration of plant communities after large-scale disturbances such as logging and mining (Neumann 1991; Majer & Nichols 1998).

Ants are species rich, easily collected and play a major role in the functioning of ecosystems (Folgarait 1998). Many ant species have long-lived colonies and semi-permanent foraging ranges, which makes them amenable to comparisons with physical and climatological variables of an area (Alonso 2000). With the publication of Bolton's (1994) key to the ant genera of the world, identification to genus has been made relatively simple and species information is becoming increasingly available via websites such as [antbase.org], [antbase.de] and [antweb.org]. For these reasons and more, ants have become an accepted part of biological inventorying, and a handbook which describes a sampling protocol has now become available (Agosti *et al.* 2000).

1.3 Sri Lanka - a biodiversity hotspot

The island of Sri Lanka has had a long history of human colonisation. It covers an area of 64,740 sq km and has had a recorded history dating back more than 2500 years. (Ashton & Gunatilleke 1987; Collins *et al.* 1991). Though separated by a narrow sea passage, the island is part of the Gondwanan tectonic unit known as the Deccan Plate, which includes the Indian subcontinent. Lowered sea levels at various times during the last ice age exposed the land bridge between the two countries thus connecting them both floristically and faunistically (Ashton & Gunatilleke 1987; Naggs & Raheem 2005).

The rise in population density over the last few centuries, as evidenced by the presence of numerous ancient irrigation canals, has resulted in high rates of deforestation in the lowlands of the country (Ashton & Gunatilleke 1987). During the 19th century, colonialists introduced plantation crops, such as tea and coffee, that could be grown on hillsides, resulting in further deforestation along forested slopes (Erdelen 1996; Gunatilleke *et al.* 2005). Natural forest covered 44% of the country in 1956, this dropped to 27% by 1980 and during the last decade 1.5% of that was further lost to land conversion (IUCN 1993; FAO 2001). Total forest cover in Sri Lanka remains at about 25% of its land area (Figure 1.1).

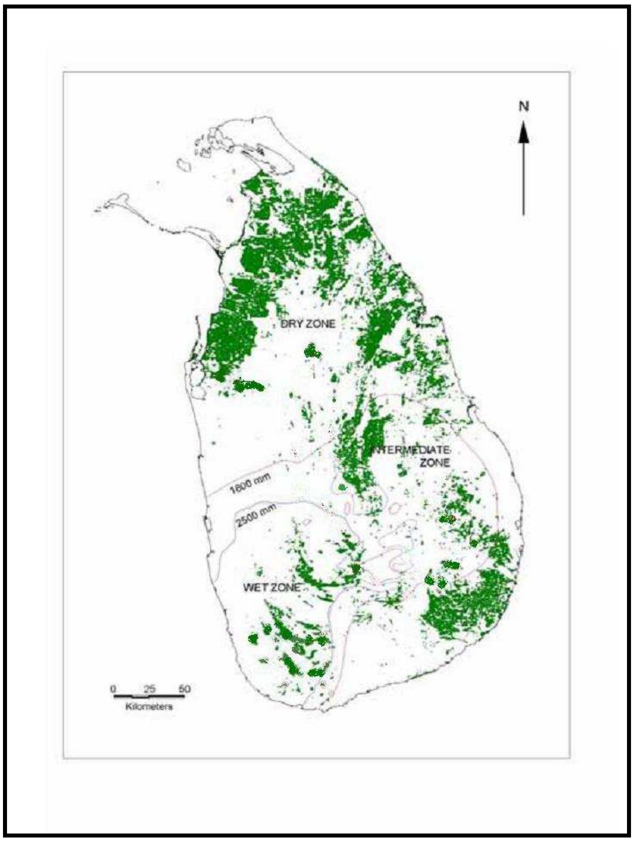


Figure 1.1. Forested areas of Sri Lanka showing the main rainfall zones. Source of forest cover data: 1:50,000-scale forest map by Legg and Jewell (1995).

Research on Sri Lanka's unique biodiversity has flourished in recent years, with numerous publications appearing on different floral and faunal groups. These studies have found that previous estimates of species richness and endemism were too low and that the relatedness of species across the Palk Strait (between India and Sri Lanka) is much more limited than previously assumed (Bossuyt *et al.* 2004; Pethiyagoda 2005). Species continue to be discovered, including a new owl species in 2005, more than 100 new rhacophorine frog species since 1993, five new species of mosses and 10 new fresh water crabs (Pethiyagoda & Manamendra-Arachchi 1998; Warakagoda & Rasmussen 2004; Bahir & Ng 2005; Tan 2005). The status of many vertebrates and aquatic invertebrates has been presented in a recent publication of the Raffles Bulletin of Zoology by Yeo *et al.* (2005).

The Western Ghats in India plus the whole island of Sri Lanka is considered one of 34 world biodiversity hotspots (Figure 1.2) (Myers *et al.* 2000; Mittermeier *et* *al.* 2004). The term biodiversity hotspot indicates an area that supports at least 0.5% of global plant and animal species and where more than 70% of the primary vegetation has been lost. Sri Lanka harbours 1.6% of global plant species, almost half of which are endemic to the island, and 3.9% of global animal species (Myers *et al.* 2000). Another component that further emphasizes Sri Lanka's designation as a hotspot is that it is also considered one of three hotspots with the most elevated risks of biodiversity loss due to high population densities (Cincotta *et al.* 2000).

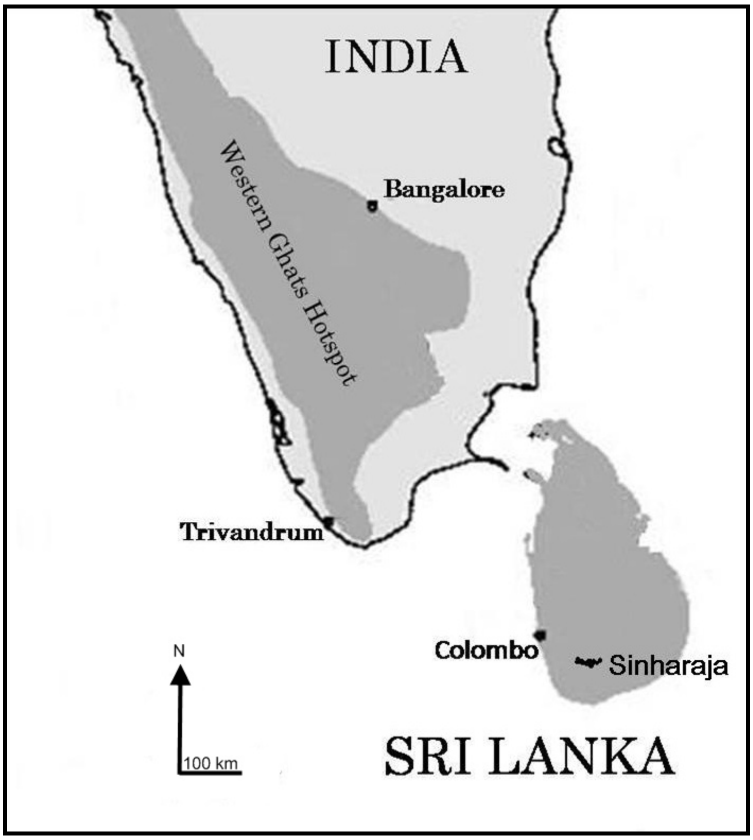


Figure 1.2. The Sri Lankan and Western Ghats biodiversity hotspot shown in dark grey. The Sinharaja Forest Reserve in the south-west of the island is also shown.

The degree of endemism in Sri Lanka has also been widely recognised. Endemic species, both floral and faunal, are concentrated in the Wet Zone of Sri Lanka (Ashton & Gunatilleke 1987; Meegaskumbura *et al.* 2002; Bossuyt *et al.* 2004), so this region can be considered a 'hotspot within a hotspot' (Pethiyagoda 2005). Rainfall patterns divide the country into two main hygroclimatic zones and one intermediate zone of rainfall (see Figure 1.1), these are also associated with the forest types that are found in these areas (Erdelen 1996). The Wet Zone (mean annual rainfall >1904 mm), found in the south-west of the country, covers 23% of the land area of Sri Lanka and is the only zone that contains tropical wet forest. In the last few decades, increasing population density in the south-west has caused further fragmentation and degradation of these forests. It is estimated that 67% of the island's 19 million inhabitants live in this part of the country (Anon 2003). Less than 5% of the Wet Zone is still covered by tropical rain forest and most of this in the form of about 140 fragments (Bahir *et al.* 2005; Pethiyagoda 2005).

These fragments are home to large proportion of the endemism in the country. Up to 80% of freshwater crab species occur in these fragments, all of which are endemic to Sri Lanka (Bahir *et al.* 2005). Similar degrees of endemism are found in other small-ranging animal groups, such as land snails and tree frogs (Meegaskumbura *et al.* 2002; Naggs & Raheem 2005). All new species discoveries mentioned in previous paragraphs were made in these fragments. In terms of angiosperm flora, all 11 endemic genera (845 species) are confined to the Wet Zone, contributing a third of plant species diversity in the country (Gunatilleke & Ashton 1987). Gunatilleke *et al.* (1987) reported from studies in nine sites within the Wet Zone that more than half of the woody subcanopy and understorey plant species are endemic and almost all are considered rare, vulnerable or endangered under the IUCN Red Data Categories.

Ant species of Sri Lanka have been poorly documented, with the degree of endemicity within the family unknown (Dias 2002b). The first comprehensive survey of ants in Sri Lanka was published by C.T. Bingham in 1903, as part of a larger body of work documenting the fauna of British India (Bingham 1903). To myrmecologists, Sri Lanka is of special interest as it is the home to the Relict Ant, *Aneuretus simoni* Emery. It is the only remaining living representative of the subfamily (genus and species) of an extinct tribe (Aneuretinii) whose fossil remains are found in the Baltics, Russia and the USA (Bolton 2003). Phylogenetically, it has been placed between the primitive and the modern lineages of ants, and it has generated interest as to its exact placement within the ant subfamily tree. Recent analyses by Brady *et al.* (2006) place it within a suprasubfamilial clade of 'dolichoderomorphs' which includes the Dolichoderinae subfamily. Once thought to be rare due to its absence from museum collections (Wilson *et al.* 1956), it was found to be quite abundant in disturbed forests in the Wet Zone (Jayasuriya & Traniello 1986; Dias & Perera 2003). So far, it is the only ant species in Sri Lanka that has received attention and is on the IUCN Red Data List (IUCN 1996).

The forest fragments scattered across the Wet Zone come under varying degrees of protection and usage, but most are small (<10 sq km), degraded and under-managed (Ashton *et al.* 2001a) (Figure 1.3). There may be other species more enigmatic than the Relict Ant in Sri Lanka, so research should be undertaken not only to assess the viability of ants as indicators of forest disturbance but also to record the ant species diversity in this unique area. The largest patches of forest are found in three areas: the Peak Wilderness (250 sq km); the Knuckles Hills (175 sq km); and the Sinharaja Forest Reserve (90 sq km) (Bahir *et al.* 2005). The research carried out in this thesis has been centred on this last forest reserve as it is by far the least disturbed and contiguous patch of lowland rain forest left in Sri Lanka.

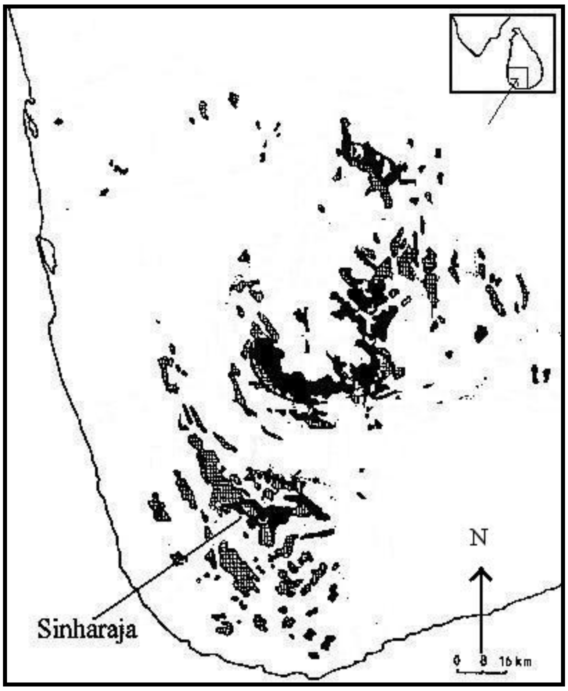


Figure 1.3. South-western Sri Lanka showing the distribution of disturbed tropical forest (stipple areas) and undisturbed tropical forest (dark shaded areas) (modified from Ashton and Gunatilleke 1987). The position of Sinharaja Forest Reserve is shown in the southern ranges and a detailed map is shown in Figure 1.4.

Figure 1.4. Composite of Sri Lanka Survey Department 1: 50,000 topographical maps of Sinharaja Forest Reserve

1.4 Sinharaja Forest Reserve

In 1875, a Ceylon Government Gazette designated the hills of Sinharaja as a forest reserve, with further forested areas being added later in the 20th century. Sinharaja Forest Reserve (hereafter SFR) currently spans 11,187 ha (6° 21-26’ N, 80° 21-34’ E) in three administrative districts in the south-west of Sri Lanka (Figure 1.4) (Gunatilleke *et al.* 2004b). Prior to the early 70’s, it was relatively inaccessible due to its topography and was utilised mostly by the surrounding villages. Floristic studies initiated by Merritt and Ranatunga (1959) used ground and aerial sampling for determining the timber potential of the area. This led to the opening up of the western part of the forest for selective logging between 1972 and 1977 (Gunatilleke & Gunatilleke 1980). After considerable public outcry from the scientific as well as the local community, logging was terminated in 1978 (IUCN 1993) and the Sri Lankan Government designated the area as a strict forest reserve and submitted it for consideration as a UNESCO Man and Biosphere Reserve. Further land conservation legislation was developed in 1988 and Sinharaja Forest Reserve was established as a National Wilderness Area. This culminated in UNESCO inscribing Sinharaja as a Natural World Heritage Site in 1990 (UNEP 2001).

1.4.1 Biodiversity of Sinharaja Forest Reserve

Flora - Studies on the plant species diversity of the SFR started with surveys of the timber content of the forest (Merrit & Ranatunga 1959) leading to more extensive studies carried out by I.A.U.N. Gunatilleke and C.V.S. Gunatilleke in the 1970’s. Since then, comprehensive studies of plant diversity and distribution have been carried out in many areas of the forest. In 1993, a long-term Forest Dynamics Plot (25 ha) was laid out in unlogged forest within the reserve and the species and location of every single plant with a stem diameter at breast height (d.b.h.) greater than 1 cm diameter was recorded (Gunatilleke *et al.* 2004a). A total of 206,501 stems represent 215 species of tree and liana in 25 ha of undisturbed forest (Gunatilleke *et al.* 2004a). This has led to a very thorough understanding of the floristics of the forest and a greater appreciation of its unique diversity.

The main forest type in the SFR is mixed dipterocarp forest, ubiquitous throughout the Asian tropics. De Rosaryo (1954) divided the vegetation into three main categories according to elevation. Low slopes and valleys (150 m - 600 m) are dominated by *Dipterocarpus zeylanicus* (a very tall canopy emergent), midslopes (600 - 1000 m) are characterised by *Mesua-Shorea* (Dipterocarpaceae) dominated canopy, and the upper slopes (>1000 m) are dominated by a mix of transitional species as the vegetation moves towards that typical of tropical montane areas found in the highlands of the country. This forest type is found mainly in eastern SFR and is sometimes dominated by monotypic stands of *Shorea gardneri* (IUCN 1993). Out of the 217 endemic tree species of the island, SFR harbours 125, many of which are found in low densities throughout the forest (Gunatilleke *et al.* 2004b).

Fauna - Comprehensive studies have been carried out on most of the vertebrate groups of animals found within the forest. While distribution and density is still not clearly documented, 262 vertebrate species have been recorded in the reserve (IUCN 1993). These include large animals such as the Asian elephant (*Elephas maximas*) and the leopard (*Panthera pardus kotiya*), both of which are considered endemic subspecies (Pethiyagoda 2005), and small mammals such as rodents and bats. Almost all endemic bird species found in Sri Lanka (19 out of 20) have been recorded in the reserve, including the new species of owl mentioned earlier. Invertebrate fauna has been less well documented, however butterfly, mosquito and arachnid studies also demonstrate the importance of this forest reserve as a centre of high biodiversity (Abeywickrama 2003).

1.4.2 Sinharaja as a Man and Biosphere Reserve

The area of forest designated as a Man and Biosphere (MAB) Reserve in 1978 comprised 8500 ha of high forest, fernlands and secondary forest. This included a 1400 ha area of selectively logged forest within the western portion of the reserve (Figure 1.5). Contiguous lower montane forest towards the east was added to this mosaic in the 80’s, bringing it to the current total of roughly 11,000 ha (Gunatilleke *et al.* 2004b). In effect, discounting the disturbed forest within the reserve, undisturbed forest comprises about 7000 ha, just under two thirds of the reserve (Gunatilleke & Gunatilleke 1980; de Zoysa & Raheem 1990).

The reserve is administrated by the Sri Lankan Forest Department under the Ministry of Lands and Land Development. Despite its high level of legal protection the SFR is still being encroached upon today. Since monitoring began in the 1988, a total of 312 encroachments have been recorded, mostly from the more heavily populated southern border of the reserve (Figure 1.6). The issue of reserve boundaries has been dealt with to some degree, starting with the planting of Caribbean pine (*Pinus caribaea)* rows in the 1990's by the Forest Department to establish a distinct border for the forest (de Zoysa *et al.* 1991; Abeywickrama 2003). There are an estimated 30 villages (most are over 100 years in existence) located around the fringe of the forest, as well as numerous small private land owners and eight large tea plantations. It is also bordered by State Forest and proposed forest reserves, as well as natural forest on private land. All this land together constitutes the 'Sinharaja Adaviya' group of forests of about 47,350 ha in extent (IUCN 1993).

Since the designation of SFR as a MAB Reserve, all harvesting activity within the forest became illegal. The only activity licensed by the Forest Department is kithul palm (*Caryota urens*) tapping - the sap collected is made into palm sugar and is sold by the villagers as a source of income (McDermott 1986). Villagers still collect fuel wood, medicinal plants and seasonal fruits from the forest, as enforcement is difficult due to the unpredictability of the resource use. Poaching of wild boar and deer also occurs. The Forest Department has tried to encourage the cultivation of exploitable plants and fuel wood trees within the 'buffer zone' around SFR but, as the zone is not adequately defined, it is difficult for villagers to recognise where the forest begins and the buffer zone ends. There has also been an effort to reafforest degraded or abandoned land within the buffer zone, and research has shown the potential of using the rows of *Pinus* trees as nurse trees for growing shade tolerant late-successional rain forest tree species (Ashton *et al.* 1997).

As a result of media publicity, increased education programmes and information dissemination, villagers and other stakeholders around the reserve are aware of the conservation value of the SFR. Land owners adjacent to the reserve are encouraged to practice traditional agroforestry, as studies have shown that plantings of timber and non-timber forest products are as financially lucrative as the more popular tea plantations (Ashton *et al.* 2001b). However, while the boundaries of the forest and the buffer zone are not defined, encroachment and other disturbance causing activities continue within the boundaries of the reserve.

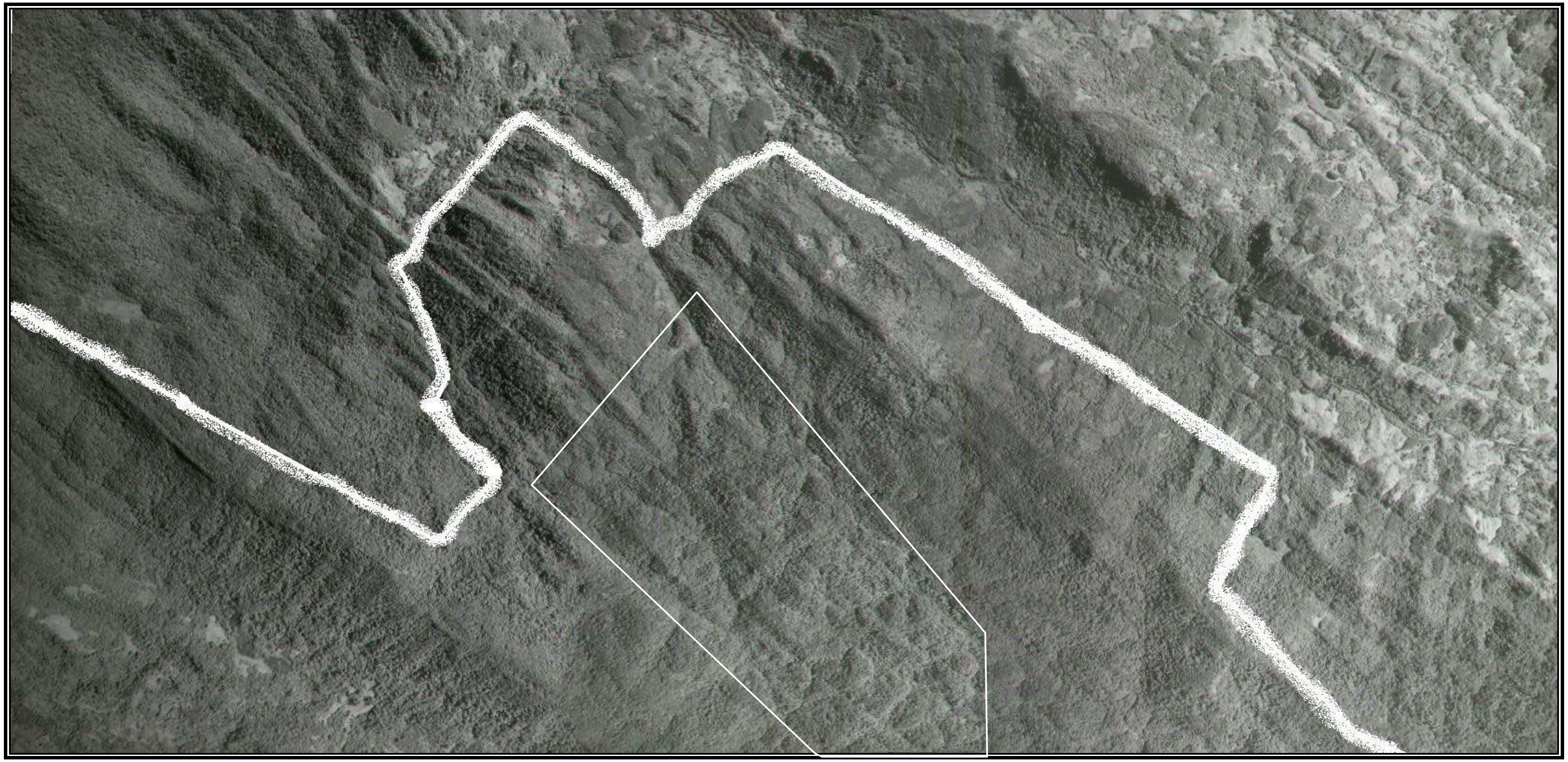


Figure 1.5. Composite of Survey Department aerial photos of western Sinharaja showing the forest boundary line. Evident in the image is visible clearance of forest outside the boundary and also within the boundary as a result of historical land use. Most of the intact forest is remnant on steep slopes. The rectangular box shows where logging occurred 30 years previously; this extends just below the extent of the image.

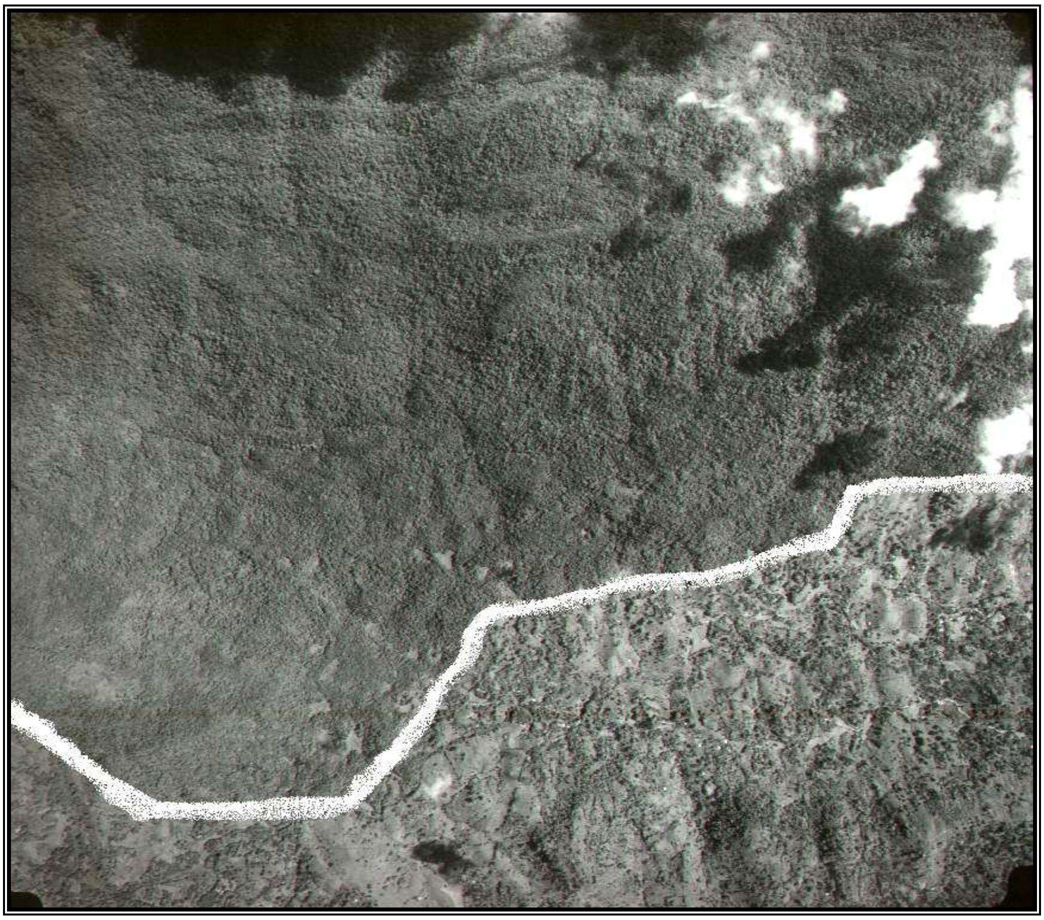
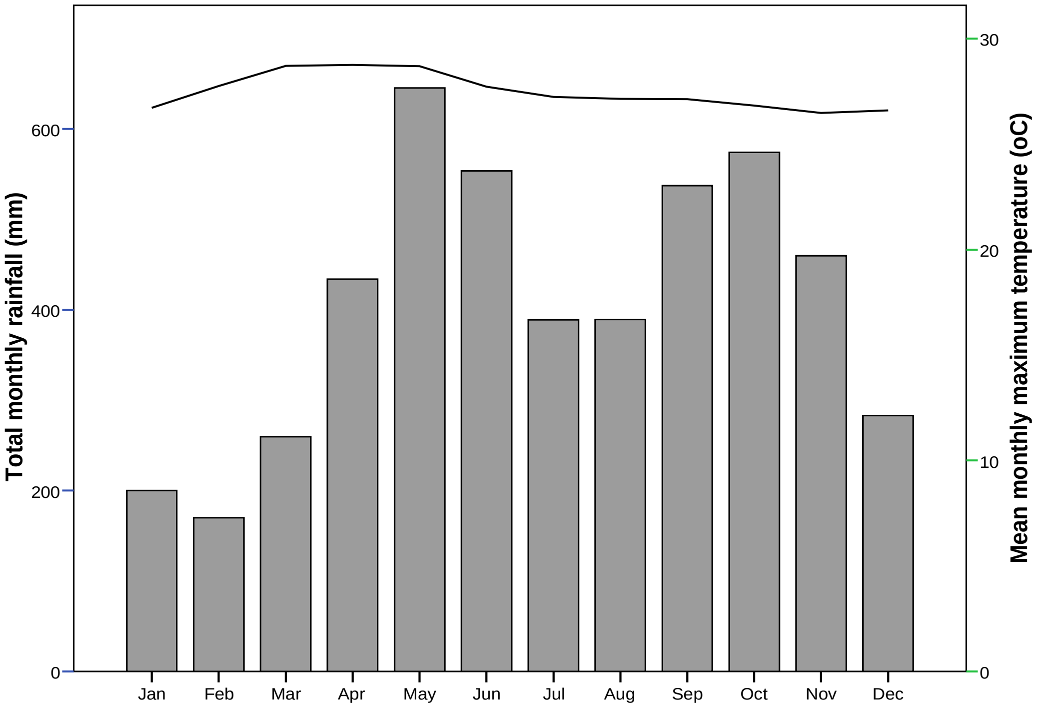


Figure 1.6. Survey Department aerial photograph showing the more heavily populated eastern Sinharaja where there is a greater proportion of intact forest. Here, the forest slopes rise to over 1000 m, making the area historically more inaccessible. There is some forest degradation in the lower slopes near the populated area. Note that there is some low cloud cover on the top edge and in the right hand corner of the photograph which is throwing a shadow on the forest below making the forest appear darker.

1.5 Study site

The SFR traverses a series of parallel ridges that are oriented east to west with a northerly bend along the western half of the forest. The hills range in altitude from about 300 m to 1170 m, the highest peak being Hinipitigala West in the eastern half of the reserve (Gunatilleke & Gunatilleke 1980; IUCN 1993). On average, the hills in the eastern portion of the SFR are higher than those in the western portion. The forest is underlain with red-yellow podzolic soils that sit on granite gneisses found throughout the south-west region (Panabokke 1996; Gunatilleke *et al.* 2005).

Climatically, the area is characterised as a lower montane aseasonal climatic region. Sri Lanka experiences two monsoon seasons during May to July (south-west monsoon) and during October to December (north-east monsoon) (IUCN 1993). Although SFR falls within an ‘aseasonal’ climatic region (rainfall does not drop below 60 mm for any month of the year), there are two observable peaks in rainfall during the monsoonal events (Figure 1.7). The monthly rainfall for the duration of the collection period for this study is shown in Figure 1.8. The rainfall patterns follow the 22 year trends but with more rainfall in the late wet season rather than the early wet season.



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igure 1.7. Rainfall and temperature patterns for an average year, based on daily rainfall and temperature data from 1984 to 2006 provided by the Sri Lankan Forest Department. Despite the two peaks in rainfall during the year, a dry season is only indicated when monthly rainfall drops below 60 mm.

The SFR receives between 4000 and 5000 mm of rain annually, which feed the ephemeral and permanent streams draining forest, making it an important watershed system for the south-west. One large river, the Gin Ganga, borders the southern edge of the forest and flows westward towards the coast. Another important river bordering the reserve to the north is the Kuduwa Ganga, which is a tributary of the Kalu Ganga, a major river in the south-west. Temperature variability throughout the year is minimal (Figure 1.7) with the mean daily temperatures ranging between 25 and 27 °C (Ashton 1992).

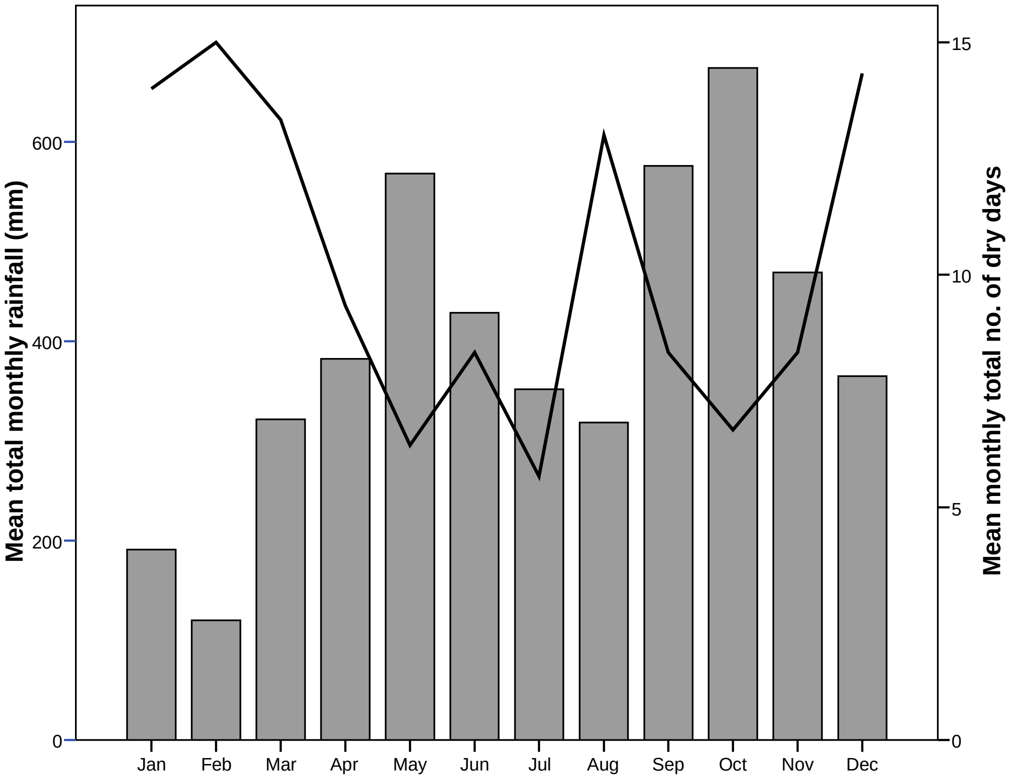

Figure 1.8. Mean monthly rainfall for the entire collection period (2004-2006) showing the two rainy seasons in May-June and September-November and the corresponding number of days without rain. Average total annual rainfall for this period was 4766 mm.

All ant collections were made within the western half of Sinharaja Forest Reserve where road and path access was possible (Figure 1.9), hence collections were limited to hills ranging between 200 m and 700 m altitude. All sites were located with a west/south-west facing aspect so as to reduce variability in insolation and moisture availability. Research was conducted between 2004 and 2006 to take into account possible seasonal variation in ant distribution.

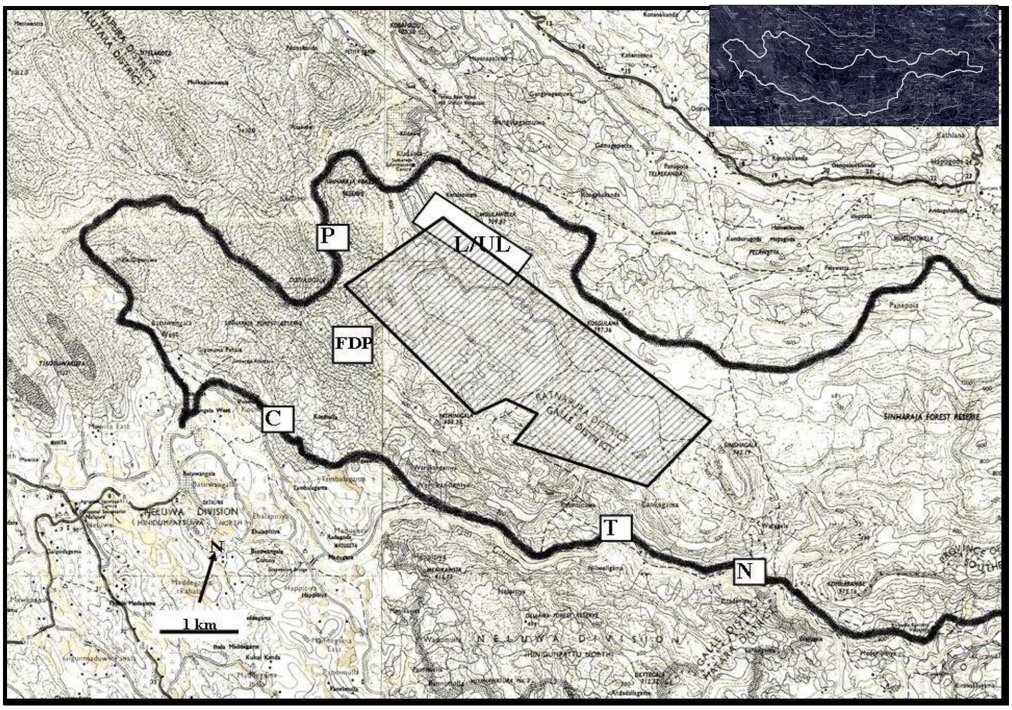

Figure 1.9. Distribution of collection sites within western Sinharaja Forest Reserve (whole reserve is indicated in inset). The stippled area represents forest that was selectively logged between 1972 and 1977. Collection sites are indicated by the white boxes: 'L/UL' is where the logged sites and unlogged sites were located; 'FDP' shows the location of the long-term Forest Dynamics Plot; 'P' respresents the pine/forest edge sites; 'C' represents the chena/forest sites; 'T' locates the tea/forest edge; and 'N' shows the location of the natural edge sites.

1.6 Overview of chapters

The objective of this thesis was to quantitatively assess the diversity of litter dwelling ants in the SFR and to provide a baseline analysis of distributional influences on their assemblages. My aim was to provide future researchers a comprehensive reference collection of these ants and an understanding of their organisation within the forest. The chapters were prepared for submission as individual articles to peer-reviewed journals; this necessitated a degree of repetition in their respective texts.

As this was the first comprehensive collection of ant species in the SFR, Chapter 2 presents an analysis of the efficacy of the **collection methods** carried out to assess their appropriateness and complementarity. Winkler extraction, pitfall trapping and baiting are established collection methods for tropical forest ants, though each has their advantages and disadvantages in the field (Figures 1.10 and 1.11). In this chapter, as well as capture rates of species richness, species composition was also taken into account. As the objective of the study was not complete inventorying, methods were applied in terms of an ecological context.

Figure 1.10. Litter collecting for the Winkler sacks using a 1 m^2 PVC pipe quadrat, a trowel and a litter sifter (a); and the 1 m^2 after it had been cleared of litter (b).

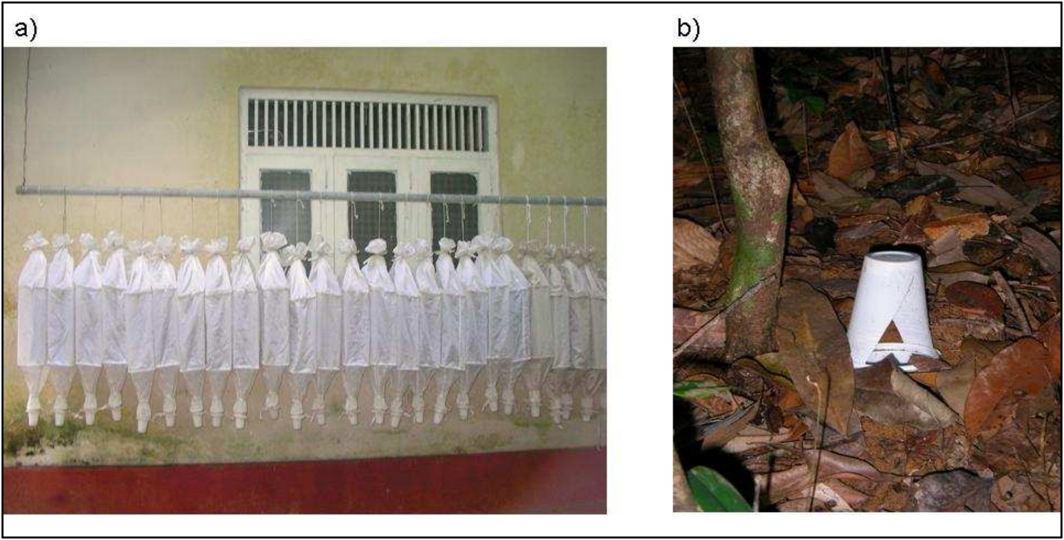

Figure 1.11. a) Mini-Winkler sacks hanging outside under shade at the SFR field station, b) Plastic cups used as pitfall traps were filled with methylated spirits and left for 3 days. An inverted cup with large triangles cut from the sides was used to prevent rainfall from entering the cup.

The following three chapters are primarily analyses of spatial distribution of ant species assemblages in the SFR. Although the SFR is considered a large patch of primary tropical forest, the internal composition of the forest is highly heterogeneous. Understanding the species distributions within this forest patch can allow for extrapolation to other forest patches in the region and can provide baseline information for the protection of other such reserves.

Chapter 3 considers the effects of small altitudinal or **elevation change** on ant species richness and composition. As most of the remnant forest in the south-west of Sri Lanka is restricted to slopes and hills, an analysis of biotic and abiotic factors influencing species distribution is carried out. Previous studies on altitudinal distribution of ants in tropical forests looked at ranges spanning over 1000 m. In this chapter, I analysed ant species distribution over an altitudinal range of 250 m. Different forest types were also taken into account as part of the study site was located within old logged forest.

Differences between old-logged forest and unlogged forest were hence analysed in Chapter 4. Analysis of the **residual effects of logging** was carried out by comparing ant species assemblages in logged forest and adjacent unlogged forest in order to assess forest regeneration more than 30 years after the disturbance (Figure 1.12). Selective logging is widespread across the Asian tropics and is seen as a low impact forest management practice. Current studies have shown that even after many decades of regeneration, structural differences still persist between logged forest and unlogged forest. Structural differences were quantified and assessed in terms of their influence on ant species composition. Naturally occurring topographic heterogeneity and tree species patchiness in the SFR may also have contributed to differentiating faunal assemblages.

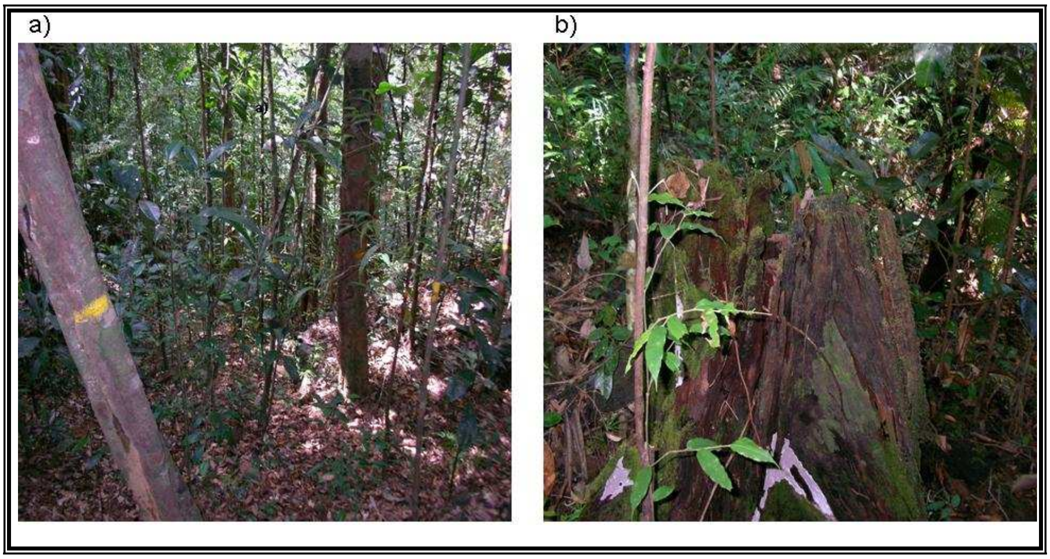

Figure 1.12. a) The forest understorey of unlogged forest is fairly open and well shaded; there are a number of saplings which is a characteristic of this type of forest. b) shows an old stump of a large tree that was logged 30 years previously. These can be differentiated from naturally formed stumps due to the absence of the tree trunk in the surrounding area.

In Chapter 5, ant species distribution across an unlogged, undisturbed forest landscape was analysed in relation to **habitat heterogeneity** (Figure 1.13) and tree species composition. The influence of tree species and their contribution to structural heterogeneity is looked at to gain an insight into the degree of influence vegetation structure has on the ant species assemblage.

The final chapter is an analysis of external influences on the forest. The SFR is surrounded by a variety of land uses; Chapter 6 looks at ant assemblages within forest edges bordered by matrix habitat of varying structure and disturbance (Figure 1.14). This ‘buffer zone’ of matrix habitats can protect a forest against external abiotic and biotic influences and improve its long term conservation potential. Investigating how different **matrix habitats impact upon forest edges** of the SFR in terms of differences in ant species assemblages can provide information on how to enhance conservation management in the region.

Figure 1.13. Views from different areas in the Sinharaja Forest Dynamics Plot: a) spur top; b) gully bottom; and c) central stream valley.

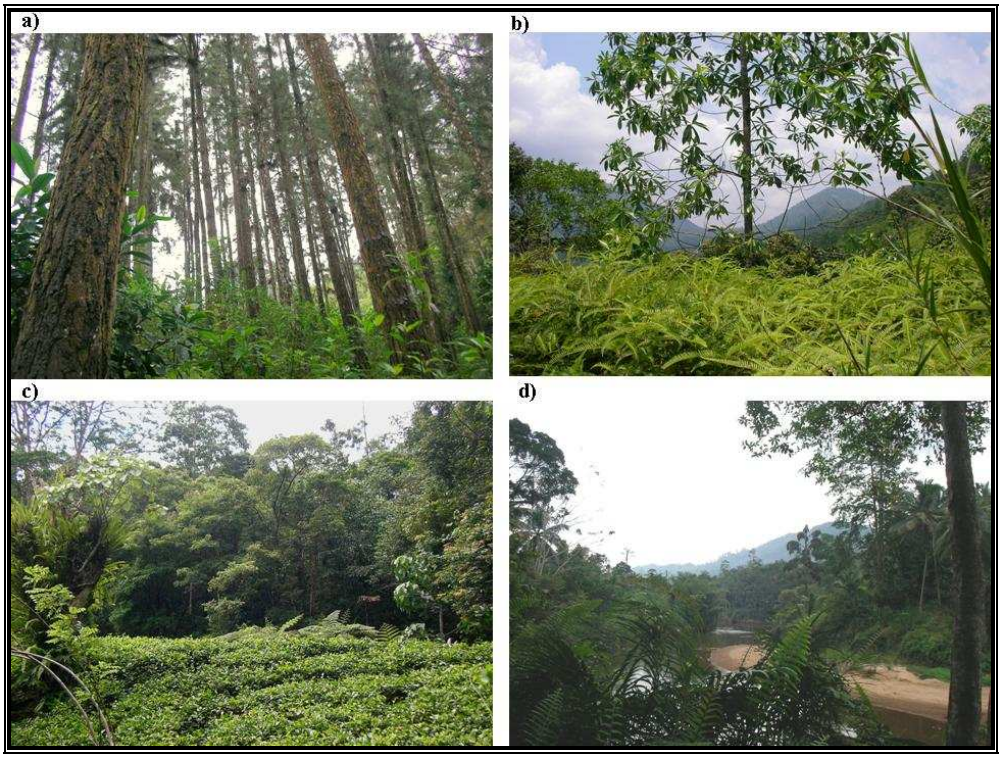

Figure 1.14. Collections occurred in pine/forest edge (a), chena/forest edge (b), tea/forest edge (c) and natural river/forest edge (d).

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2. Evaluation of methods for collecting ground dwelling ant species in Sinharaja Forest Reserve, Sri Lanka

Abstract

Ants were collected in the Sinharaja Forest Reserve using three methods; leaf litter extraction with Winkler sacks, pitfall trapping and baiting. A total of 146 species were captured, with Winkler extraction providing the highest number of species and pitfall traps contributing a complementary set of species. Baiting did not attract additional unique species. Species richness estimates extrapolated from the specimens collected by each method showed that Winkler sacks sampled a sufficient number of species to reliably predict total species richness. Although they collect less species, pitfall traps were more utilitarian, requiring no special equipment and are recommended to be used for ecological studies involving ants where species inventorying is not an objective.

Key words: Winkler extraction, pitfall traps, baiting, leaf litter ants, Formicidae, A.L.L protocol

2.1 Introduction

Each stratum of a tropical forest, from the canopy to the soil layer, is characterised by a set of biotic and abiotic factors (Parker 1995; Barrios 2003). This in turn determines the assemblages of animals that inhabit or forage within a particular stratum or range of strata (Longino & Nadkarni 1990; Simon *et al.* 2003). Complete biological inventorying ideally would use a variety of methods in all strata, but often collection time, available human resources and materials can place restrictions on the data collected. As a result, careful choices must be made when considering collection intensity and sampling method as they can influence the subset of fauna collected in a given area. While some ants are ubiquitous throughout the many strata in a rainforest ecosystem, most appear to be restricted to a particular level (Longino & Nadkarni 1990; Brühl *et al.* 1998; Primack & Corlett 2005). Furthermore, ants (individual foragers as well as colonies) are distributed non-randomly in space and time, thus requiring careful choice of methods which may vary according to the aim of the project (Bestelmeyer *et al.* 2000).

Currently, there is a variety of methods for collecting ants in tropical forest, but standardised techniques exist for only ground dwelling ants (Agosti *et al.* 2000).

Delabie *et al.* (2000) analysed these sampling methods and determined that a combination of two or more methods collected the largest number of species in a given site. The first recommended method is litter sampling using Winkler sacks (Bestelmeyer *et al.* 2000). This is a commonly utilised method for many litter dwelling arthropod groups, and it appears to work best in closed canopy forests where leaf litter is abundant and moist throughout the year (Parr & Chown 2001; Underwood & Fisher 2006).

The second suggested method is pitfall trapping, which is a passive sampling method that is cheaper and less labour intensive in the field than litter sampling. Pitfall traps come in a variety of sizes, hence the sampling of the ant fauna can be biased by the size of the trap (Abensperg-Traun & Steven 1995) and the relative activity of the ant fauna (Olson 1991). Another passive collection method is baiting, which is also inexpensive and easy to deploy. The use of multiple bait types (protein, sugars, fats) can attract a variety of ants, but their activity can be affected by time of day, season and presence of dominant species at the baits (Bestelmeyer *et al.* 2000). Direct sampling of the ant fauna can also be carried out by searching for nests in different habitats within the collection area. This method is often difficult to standardise, as differences between the skill and efficiency of each investigator will influence the samples collected (Bestelmeyer *et al.* 2000).

A standardised collecting procedure, called the ALL (Ants of the Leaf Litter) protocol was developed in order to allow comparisons of ant data collected from different regions of the world. Agosti and Alonso (2000) suggested using 20 Winkler extractions and 20 pitfall traps along a 200 m transect, with additional direct sampling if possible, to maximise the number of species caught. It has been utilised in a number of studies and has proven to be efficient at collecting the majority of ant species in an area (Fisher *et al.* 2000; King & Porter 2005).

Historical ant collections in Sri Lanka have been based on direct sampling in forest and agricultural areas; only recently have passive methods such as Winkler sacks and pitfall traps been used. This is one of the first Sri Lankan studies where high intensity sampling and a quantitative analysis of ant sampling techniques were carried out in the Sinharaja Forest Reserve. The collections made in this study utilised the two main collection methods recommended by the ALL protocol, Winkler extraction and pitfall trapping. At two of the three locations, baiting was also was used in conjunction with the two main methods to test whether further ant species could be collected. The efficacy of these methods for collecting ants in Sinharaja Forest Reserve is here analysed, with the main comparison being between Winkler extraction and pitfall trapping.

2.2 Methods

2.2.1 Sites

The study area was in the the Sinharaja Forest Reserve (SFR), a 11,000 ha reserve located in the Sabaragamuwa Province in Sri Lanka (6° 21-26' N, 80° 21-34 E). The reserve is mid elevation (300 – 1200 m), mixed dipterocarp (*Mesua-Shorea* type) rain forest, set upon a series of ridges runnning in an east-west direction in the south-western quarter of the country (Gunatilleke *et al.* 2004b).

The SFR receives monsoonal rains from May to July and from October to December, with average annual rainfall between 2000 mm and 4000 mm. Collections were carried out four times at each site, between March 2005 and November 2006, with two periods being just after each high rainfall and low rainfall season (See Figure 2.1 and 2.2).

Samples were taken within old logged forest (LF), adjacent unlogged forest (UF) and a long-term Forest Dynamics Plot (FDP) located along south-west facing ridges within western SFR (Figure 2.3). Five plots were established along three transects, each at a different elevation along the slopes. The slopes ranged between 300 m and 700 m. Each transect within each forest type was separated by at least 200 m. The old logged sites were located at least 1 km from the unlogged sites (though the logged forest abutted the unlogged forest), whereas the forest research plot was about 2 km away from both the logged and unlogged sites. Each plot measured 10 m by 10 m and were spaced 20 - 25 m away from each other. When possible, these plots were placed in a straight line but, due to the undulating topography of the area, some sites had to be accomodated adjacent to others.

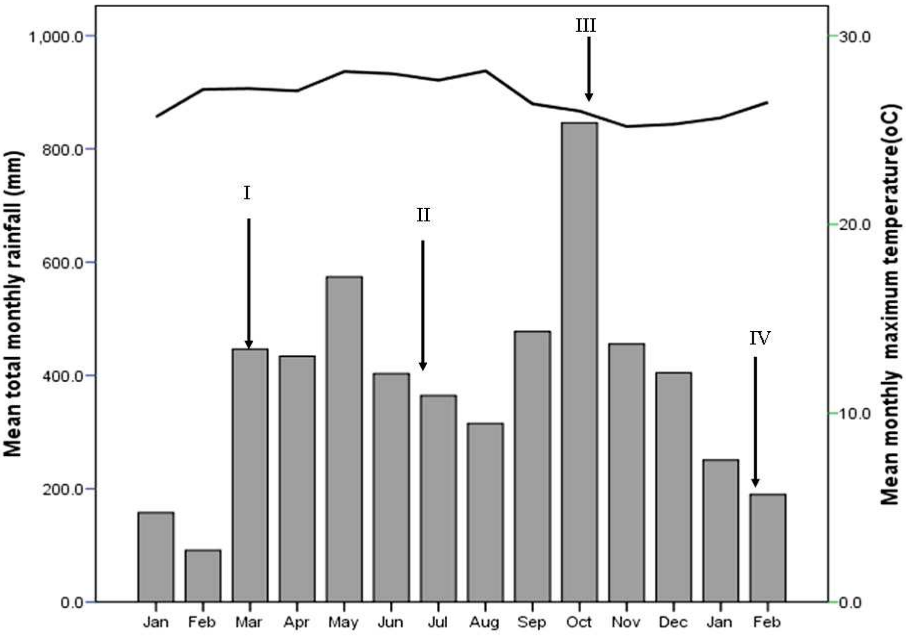

Figure 2.1. Total monthly rainfall and mean monthly maximum temperature during collection (2005) within the logged and unlogged forest. The arrows indicate the four periods when collection was carried out.

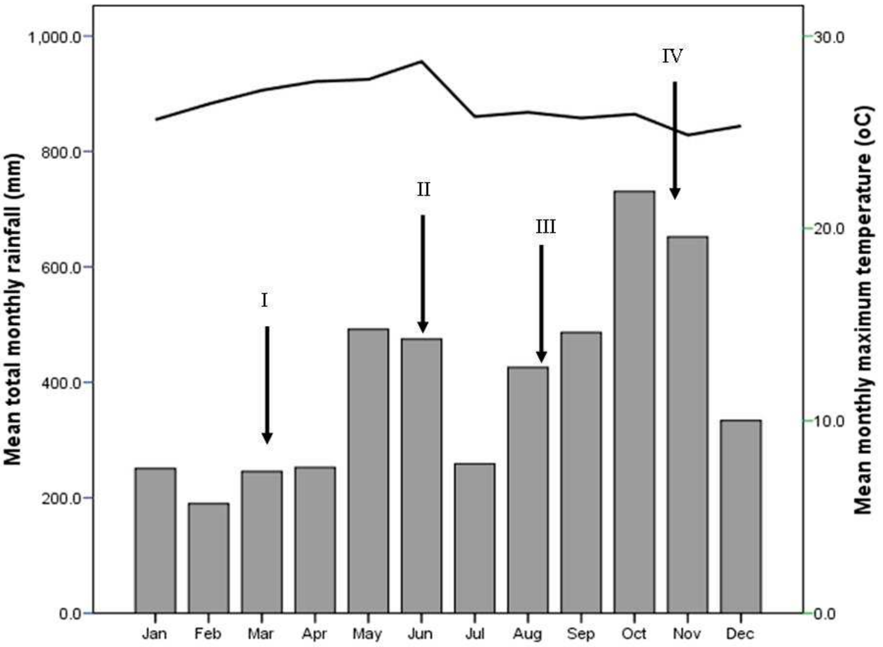

Figure 2.2. Total monthly rainfall and mean monthly maximum temperature during collection (2006) within the Forest Dynamics Plot. The arrows indicate the four periods when collection was carried out.

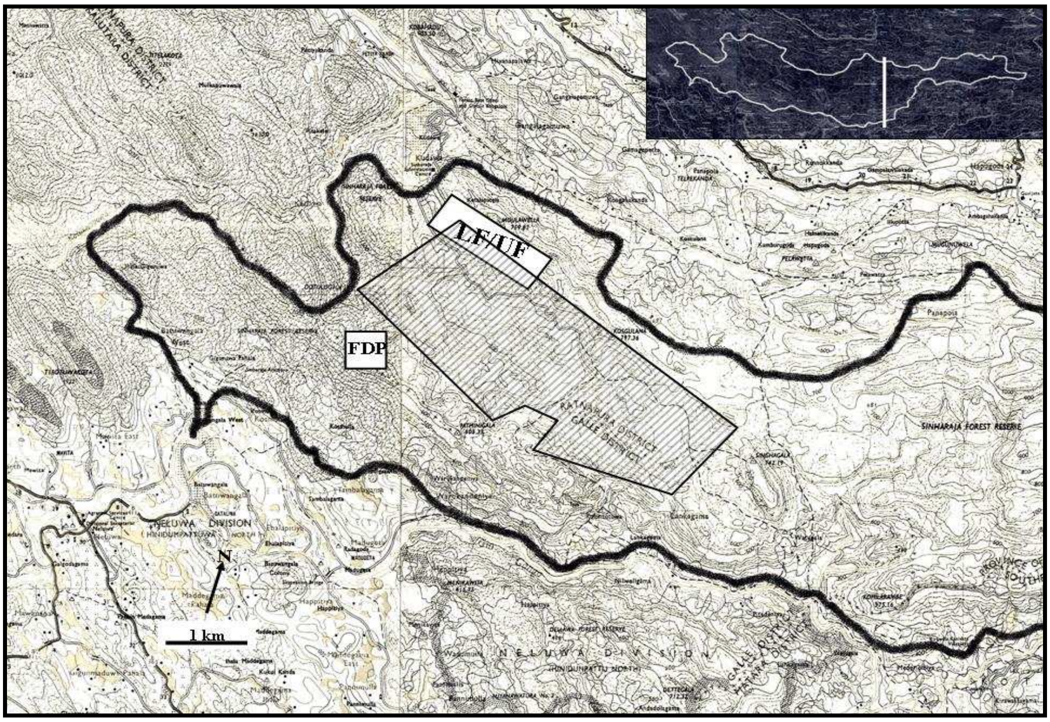

Figure 2.3. Sri Lanka Survey Department Map of Sinharaja Forest Reserve showing the collection sites in logged and unlogged forest are (L/UL) and the Forest Dynamics Plot (FDP). The stippled area shows the extent of the selective logging that occurred between 1972 and 1977.

2.2.2 Collection methods

In each plot, four leaf litter samples, four pitfall traps and two baits were set out to maximise the number of ground dwelling ants collected. Leaf litter was collected in a 1 m by 1 m quadrat and was sifted using a litter sifter (Bestelmeyer *et al.* 2000). The sifted material was then hung inside a mini-Winkler sack (Fisher 1999a) for 48 hours with the leaf litter being removed and shaken after the first 24 hours. All material collected from the Winkler sack was then removed and stored in ethanol. The material was then sorted in the laboratory, and invertebrates removed and preserved in 70% ethanol. The ants were separated from the sample, point-mounted and identified to morphospecies.

The pitfall trap consisted of a standard plastic drinking cup (mouth diameter 7 cm) which was inserted into the ground and left for 1 week (to reduce the ‘digging-in’ effect (Greenslade 1973)) before being filled with ~70 ml of methylated spirits. The pitfalls were then capped with another plastic cup with large triangles cut out of the sides to provide a lid to prevent rainfall from flooding the cup. After 72 hours the material in the cups was collected and the cups left in the ground filled with leaf litter for use in the next sampling period. The collected material was then washed with fresh methylated spirits and returned to the lab. All invertebrate material was removed from the samples and stored in 70% ethanol. The ants were then separated from the invertebrate material and point-mounted and identified to morphospecies.

In the logged and unlogged forest two types of baits were used at each site; protein bait (tinned mackerel) and sugar bait (fruit jam). At each site, one bait of each type was laid out 2 m apart and left for 2 hours. Baiting was carried out between 9 am and 3 pm during each sampling period. The baits were laid out on pieces of 5 cm by 5 cm white card which were picked up at the end of the collection period and placed in sturdy plastic bags. The samples were then sprayed with methylated spirits to kill the ants. The ants were then removed and stored in 70% ethanol and returned to the lab. These ants were also point-mounted for subsequent identification.

Once a reference collection of point-mounted specimens had been created, all excess ants were stored in 90% ethanol. Ants were identified to species where possible, with certain genera being sent to specialists for confirmation of species identification. For species where a taxonomist or taxonomic key were unavailable, a unique species number was assigned. Both wet and dry specimens are housed in Peradeniya University Entomology Museum, with a representative collection stored in the Curtin University of Technology Entomology Museum.

2.2.3 Data analysis

Ant abundances in all three forest types (LF, UF and FDP) were tabulated and converted to presence/absence data. This is a standard conversion for ant data analyses, as ants are social insects and tend to be clumped spatially which causes the data to appear aggregated when sampling occurs near colonies (Longino 2000). Within each forest type, the data from the five plots at each of the three elevations were combined; the data from each season were also combined to remove any potential seasonal variation. Each elevation (considered one site) in the LF and UF had 200 sample points (80 Winkler extractions, 80 pitfall traps and 40 baits) and the FDP had 160 sample points (80 Winkler extractions and 80 pitfall traps) at each site.

The number of individuals (abundance) and the number of species (occurrence) were analysed using independent-sample t-tests. First, species occurrence and abundances caught by the three methods in logged and unlogged forest were compared with each other. Then the two main methods (Winkler extraction and pitfall traps) were then compared across all nine sites using the same tests to determine significant differences in species occurrence and abundance. Multi-dimensional scaling (MDS) using Euclidean distances for a binary matrix with 100 iterations was utilised to graphically demonstrate differences in assemblages across the forest types and methods. All statistical analyses were carried out using SPSS 15.0.

Incidence-based estimations of species richness (using Chao and Bootstrap indices (Colwell & Coddington 1994)) were carried out for each method, and a mean species accumulation graph was produced to illustrate the standard deviation from random permutations of the data from each of the nine sites (Gotellli & Colwell 2001). These analyses were carried out using SPECPOOL and SPECACCUM functions in the Vegan package within R (R Development Core Team 2005).

2.3 Results

A total of 13,973 ants were collected, representing 146 species and morphospecies (hereafter included as species) in 11 subfamilies and 49 genera (Table 2.1).

Table 2.1. Genera collected using the three collection methods in the logged and unlogged forest.

Genus	No. of species	Genus	No. of species	Genus	No. of species
Pheidole	19	*Aenictus*	2	*Pseudolasius*	1
Tetramorium	17	*Dolichoderus*	2	*Acanthomyrmex*	1
Cerapachys	11	*Technomyrmex*	2	*Cardiocondyla*	1
Camponotus	6	*Gnamptogenys*	2	*Cataulacus*	1
Crematogaster	6	*Protanilla*	2	*Meranoplus*	1
Hypoponera	5	*Carebara*	2	*Myrmecina*	1
Leptogenys	5	*Myrmicaria*	2	*Pristomyrmex*	1
Anochetus	4	*Pheidologeton*	2	*Recurvidris*	1
Monomorium	4	*Solenopsis*	2	*Rhopalomastix*	1
Pachycondyla	4	*Tetraponera*	2	*Rhopalothrix*	1
Paratrechina	4	*Aneuretus*	1	*Rogeria*	1
Pyramica	4	*Amblyopone*	1	*Tyrannomyrmex*	1
Strumigenys	4	*Acropyga*	1	*Crytopone*	1
Polyrhachis	3	*Forelophilus*	1	*Discothyrea*	1
Tapinoma	3	*Lepisiota*	1	*Harpegnathos*	1
Vollenhovia	3	*Myrmoteras*	1	*Myopias*	1
				Ponera	1

Two myrmicine genera, *Pheidole* (19 species) and *Tetramorium* (17 species) were the most speciose, with *Cerapachys* (11 species) following close behind. In the

LF and UF, Winkler extraction (hereafter called Winklers) collected 101 species, while 81 species fell into the pitfall traps and 44 species were attracted to the baits.

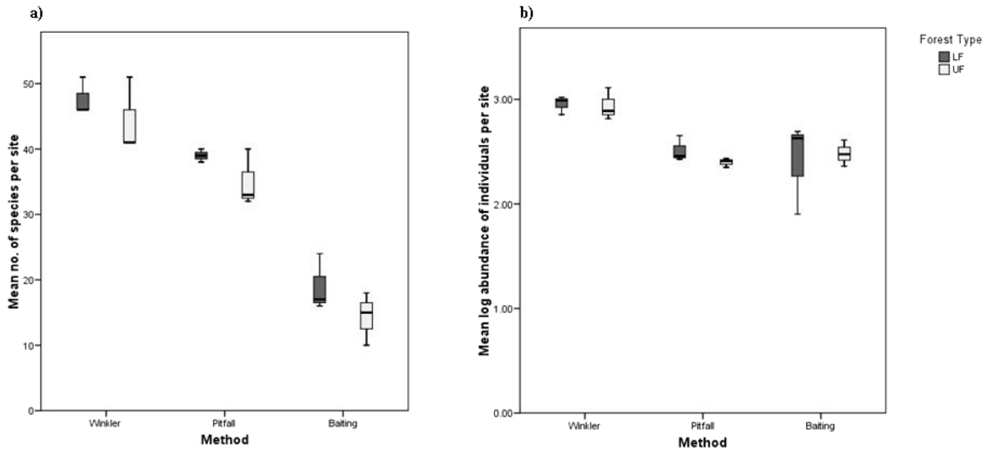

Figure 2.4. Graphs of a) mean number of species and b) individuals collected by the three methods, of the three methods utilised in logged forest (LF) and unlogged forest (UF), Winkler extraction collected the highest number of species and individuals per site. Pitfall traps yielded the second highest number of species but were comparable in abundance of individuals attracted to baits.

There were small significant differences between Winklers and pitfalls in terms of abundance (ln transformed) and occurrence of species (Figure 2.4), with baiting catching significantly fewer species than the two other methods (independent-sample t-test = 10.651, *P* = 0.00) (Table 2.2). The break-down of each method's collecting efficacy by subfamily is shown in Table 2.3.

Table 2.2. Pairwise comparisons (independent-sample t-tests) of species abundance and occurrence, showing significant differences between all three methods, with the exception of abundances of ants caught using Winklers and baiting.

Method	Data type	t-value	Sig. (2-tailed)
Winkler/Pitfall	Abundance (ln)	1.98	0.050
	Occurrence	2.45	0.015
Pitfall/ Baiting	Abundance (ln)	3.32	0.001
	Occurrence	4.52	0.000
Baiting/ Winkler	Abundance (ln)	-1.54	0.125
	Occurrence	7.25	0.000

Table 2.3. Number of species caught within each subfamily by each collection method in the logged and unlogged forest.

Subfamily	Winkler	Pitfall	Baits
Myrmicinae	54	49	33
Ponerinae	17	12	1
Formicinae	12	10	5
Cerapachyinae	9	2	0
Dolichoderinae	2	5	4
Aneuretinae	1	1	1
Aenictinae	1	1	0
Pseudomyrmicinae	1	1	0
Amblyoponinae	1	0	0
Ectatomminae	1	0	0
Leptanillinae	1	0	0
Total	101	81	44
% unique	24.6	11.6	2.1

Almost a quarter of all species were collected solely by Winkler extraction, a further 11% were collected only in pitfall traps and baiting attracted an additional 2% of the total. The two species caught solely by baiting in the LF and UF were collected by the other two methods in the FDP. The majority of the ants caught by baiting were *Pheidole* species, which were fast recruiters to the food sources, and other miscellaneous species which were ubiquitous throughout the forest. All of these species were caught using either or both of the first two methods, and so supported my decision to exclude baiting from further analysis.

Winkler and pitfall collections for the three forest types were combined and singletons (species represented by only one individual caught) were removed, 112 species were analysed for comparison. Species richness and abundances caught by Winklers were significantly different from pitfalls (t-tests; $P < 0.01$). As can be seen in the MDS plot, assemblages caught in Winkler sacks are clearly separated from assemblages caught in pitfall traps across all forest types (Figure 2.5).

Species accumulation curves (using all species collected including singletons, Figure 2.6) show both Winkler and pitfall trap collections approaching an asymptote, thus permitting a comparison of the species richness estimators. Winklers collected more species than pitfall traps (Table 2.4). The species accumulation curve for pitfall traps appears to flatten out more than the Winkler species accumulation curve, indicating that pitfall sampling effort was high enough to approach the maximum number of species collectable by this method. This is supported by the Chao and the

Boostrap estimates. Pitfall traps collected 97 species and it is estimated that there are potentially only 10 to 15 more species that could be collected using this method.

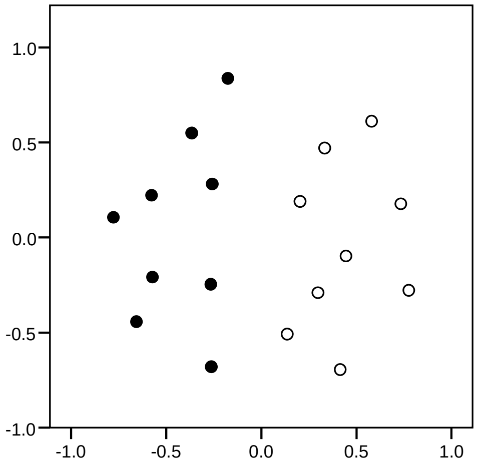

Figure 2.5. Multi-dimensional scale plot using ant assemblages collected by the two main collection methods, Winkler extraction (black circles) and pitfall traps (clear circles).

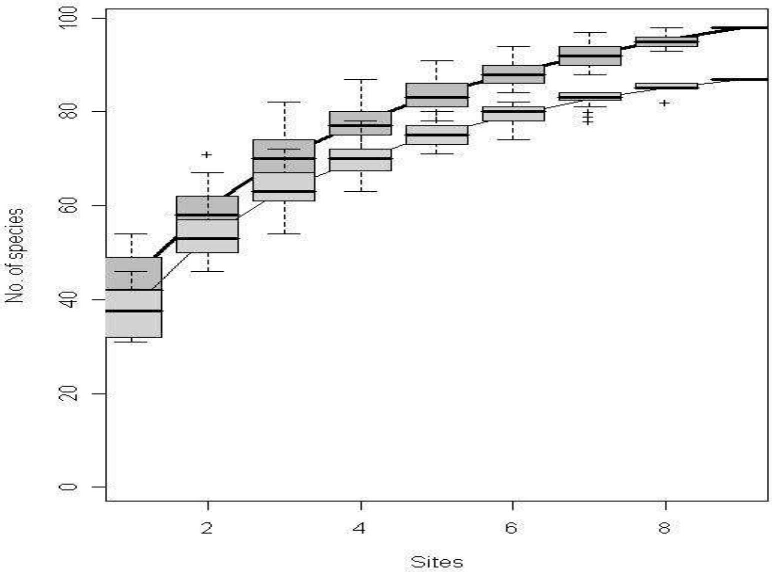

Figure 2.6. Species accumulation curves for Winkler extraction (upper line) and pitfall traps (lower line) using randomised selection of samples across the nine sites. Each site represents 80 sample points.

Table 2.4. Species richness estimators and their standard errors (SE) for the two main methods across the nine sites.

Method	Species	Chao	SE	Bootstrap	SE	n
Combined	146	182.5	15.4	164.8	6.4	18
Winklers	122	188.4	28.7	140.7	7.4	9
Pitfalls	97	112.7	8.4	109.3	5.9	9

By contrast, the results for Winklers estimate that between 20 and 40 more species could potentially be found by this method. However, the Chao species richness estimated from the Winkler collection alone was similar to that estimated by the number of species caught by both methods together.

2.4 Discussion

Based on historical collections by Bingham (1903) and smaller recent collections, Dias (2002a) lists 246 ants for the whole of Sri Lanka. This study lists 146 ground dwelling species in about 0.45 ha of lowland wet forest, some from genera that have not been previously recorded for the country. In tropical environments, it has been accepted that it would be impossible and impractical to completely capture all the species in a hyperdiverse taxon like ants, especially in complex environments like tropical forest (Longino & Colwell 1997; Fisher 1999b). Complete inventorying of a taxon is rarely the aim of ecological studies (Longino *et al.* 2002a), and time and cost greatly influence the choice of methods for collecting a given taxa.

The two methods utilised in this study were highly complementary and were both efficient at collecting a large proportion of the diversity in this forest type in Sri Lanka. In terms of species richness caught by each method, the difference was only slight and shows that both methods are comparable in their efficiency at collecting ground dwelling ants. However, looking at the Chao species richness estimator, the extrapolated species richness from Winkler samples is very close to that extrapolated from the combination of data from Winklers and pitfalls. Winkler extraction alone may be adequate enough to capture a large enough number of species to reliably predict the species diversity in other forest patches. In this forest type, where litter is readily available, Winklers have been advocated in a number of studies (Fisher 1999b; Delabie *et al.* 2000; Underwood & Fisher 2006). Brühl (2001) utilised Winkler extraction as his collection method for lowland dipterocarp forest in Sabah, but excluded ants larger than 15 mm in length and generally only included ants that were considered typical leaf litter inhabitants. In the SFR, where the litter dwelling assemblage is not yet fully known and generally few species were larger than 15 mm (N. Gunawardene pers. obs.), it would have been difficult to confidently exclude certain species from the analysis.

In terms of sampling effort, pitfall traps used the least amount of time for deployment, collection and processing. This makes them a good choice for small scale studies that lack extensive funding and time. Pitfall traps were also useful in their applicability during inclement weather. Sudden heavy downpours halted leaf litter collection and baiting. Their 24-hour operation also increased the chance of capturing species that are more active during different hours of the day. Leaf litter collection and baiting occurred during the day, which precluded the collection of night active or crepuscular species.

The impact on the litter environment is also reduced by pitfall trapping, as lower amounts of litter are removed than during litter extraction, and colonies are not damaged. This can have a substantial impact when considering the large scales of some ecological studies. The ecological impact of removing rare species is as yet unknown and untested. In ecological studies, where rare species are often not included in the data sets for comparison of sites, it would seem unnecessary to collect them at all. Even for more commonly occurring ants, the effect of removing entire colonies from the leaf litter may also be detrimental to community functioning. For the charismatic, IUCN Red-Listed ant, *Aneuretus simoni*, which is a small ant with small colonies (>100 workers (Jayasuriya & Traniello 1986)), I calculated that I removed the equivalent of roughly one to two nests per site during litter collection. Since ant data tends to be analysed as presence/absence data, obtaining high numbers of individuals is also unnecessary.

Pitfall traps are by far the most widely used method for invertebrate sampling. They are cost effective, time efficient and easily deployable, making them a popular method for field biologists. In a recent review of the use of ants in monitoring studies by Underwood and Fisher (2006), 75% of 58 ant studies used pitfall traps either solely or in conjunction with other methods. This study shows that in rainforest, pitfall traps can capture a large proportion of the high diversity of ground dwelling ants in the SFR. Gotelli and Colwell (2001) state that only when taxon accumulation curves approach a clear asymptote would species richness counts be reliable for comparing habitats. Therefore, in reaching close to an asymptotal value for predicted species richness, pitfall trap assemblages would be good to use for comparison across the different sites in the SFR.

However, if pitfall traps were used exclusively in the SFR, the extrapolated total species richness would have been a considerable underestimate. Other studies with single methods face this same issue. For example, Basu (1997), working in a similar lowland dipterocarp forest in the Western Ghats, collected much larger abundances of ants using only pitfall traps (over 32,000 ants) but only 31 species and 24 genera were identified. Studies have shown that vegetation complexity can affect the capture rate of pitfall traps (Majer 1997; Melbourne 1999). Pitfall traps appear to function better in drier, open systems like savanna (Parr & Chown 2001). The high complexity of rain forest vegetation perhaps provides ants with many alternative pathways to cross the ground when foraging, thus reducing their chances of being trapped.

Therefore, in terms of obtaining overall species richness for ground dwelling ants, both methods should be utilised in conjunction with each other. Further sampling using these two methods would be unlikely to collect many more species but would perhaps add individuals to the many species where only one individual was caught. Direct sampling of the leaf litter should be added as a method for capturing more species to improve the inventory. For ecological rather than inventory studies, pitfall traps are recommended where time, cost and manpower are limiting factors.

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3. Sampling ants over a small elevation gradient in a lowland forest reserve in south-west Sri Lanka

Abstract

The growing threat of forest loss and degradation in tropical areas has heightened the need to document species in these pockets of high diversity. However, the species within these habitats are not necessarily uniformly distributed. The study of species diversity patterns along environmental gradients can provide important information on the distribution of not only species numbers, but also the lines along which species organise themselves. With this information, protection and management of remaining forest reserves can be better formulated for the long-term preservation of biodiversity. This study looked at the differential influence of small elevation changes in south-west Sri Lankan forests on ground dwelling ant species diversity, where tropical forest remnants are distributed along small hill ranges. Ant species were collected from dipterocarp dominated forest across an elevation gradient of only 230 m vertical distance. Plots were located in two unlogged forest areas and one old-logged (>30 years previous) forest area. There appeared to be a monotonic decrease in species richness as elevation increased, though the differences were not significant between low and high elevation. Species assemblages on the other hand, were significantly different along the slope, but appeared to be more influenced by the surrounding forest type than elevation. Vegetation characteristics, such as foliage density at the shrub level, and leaf litter cover and depth, appeared to influence ant assemblages along the slope. It is more likely that the ant species are responding to environmental factors that are determined by tree species heterogeneity, which in turn is potentially controlled by physical factors such as soil and moisture availability.

Keywords: species richness, species diversity, altitude gradient, scale effects, tropical wet forest, Sinharaja, Formicidae

3.1 Introduction

Increasing our understanding of tropical ecosystems and the distribution of biodiversity is imperative in the face of the rapid loss and degradation of tropical forests worldwide. Identifying the distribution patterns of species within these systems can give us better frameworks for protecting the areas within which they live. Relatively new threats, such as global warming and cryptic degradation by activities such as over-hunting (Laurance *et al.* 2006), have placed additional pressure on already isolated forest reserves, further emphasizing our need to understand and protect them.

The majority of the Earth's species live within the tropics, especially within moist tropical forest (Pimm & Brown 2004; Primack & Corlett 2005). The high species diversity of these forests has sparked many theories regarding their patterns of co-existence (Givnish 1999). Within the tropics, there have been numerous studies documenting species distributions along various gradients, both natural and human-made (Ludwig & Cornelius 1987; Jose *et al.* 1996; Kaspari & Weiser 2000; Hassall *et al.* 2006; Engelbrecht *et al.* 2007; Hoffmann & James 2007). One of the better studied gradients is elevational or altitudinal change (Lomolino 2001). There is general agreement that species richness of any given group decreases with increasing elevation (Stevens 1992; Rahbeck 1995). Currently, two patterns of decrease have been observed, namely: 1) a monotonic decline; and 2) a hump shaped decline, with richness peaking at mid elevations rather than lower elevations (Sanders 2002). In a review of 204 datasets on the changes in species-richness patterns over altitudinal gradients, Rahbeck (2005) found that roughly half of the studies demonstrated a hump shaped trend in species richness with increasing elevation, with about one quarter showing a monotonic decline. There are a variety of theories as to why species diversity decreases with increasing elevations (Sanders 2002; Almeida-Neto *et al.* 2006), invoking factors such as lower primary productivity, harsher climatic factors and reductions in physical space at higher elevations.

The existence of at least two patterns of decrease can be attributed to a number of factors. Rahbeck's (2005) analysis of studies (standardised for sampling effort and area) showed that a hump shaped trend was observed in the majority of studies that looked at single transects along a slope, whereas this trend fell into the minority when regional data were analysed. The lack of replication of collection in both space and time can potentially influence the species trends up a slope (McCoy 1990). Rahbeck (2005) also drew attention to the issue of spatial scale on the type of analysis utilised by researchers. Macro-ecological studies, which span large biogeographic regions, can give insight into large-scale patterns of diversity, although care must be taken when considering the range sizes of the taxa under consideration (Rahbeck 2005; Dunn *et al.* 2007). Chust *et al.* (2003) found that finer grain definitions of habitat patches better explained species composition and endemic species richness of soil fauna in the Pyrenees, suggesting that landscape unit definition should be taken from the taxon’s perspective rather than a human perspective.

Tropical organisms tend to display relatively narrow tolerance ranges to physical conditions and thus have narrower ranges along altitudinal gradients (Stevens 1989; Olson 1994). Thus, the issue of scale becomes significant when considering smaller-ranging but highly diverse groups such as invertebrates. While many of the influential studies of species richness across elevation gradients have been conducted on largely vagile species of animal such as birds and mammals (Terbourgh 1977; Rahbeck 1997; see Heaney *et al.* 2001), or historically well distributed plant groups (Stevens 1992; Lieberman *et al.* 1996; Grytnes 2003), there have been fewer studies that have looked at ground dwelling invertebrates (Janzen *et al.* 1976; Collins 1980; Leakey & Proctor 1987). These studies have predominantly looked at species richness and abundance or biomass, rather than species distribution or assemblages (Olson 1994). More recent studies in the tropics have looked at community composition along elevational gradients of specific invertebrate groups, such as termites (Gathorne-Hardy *et al.* 2001), opilionids (Almeida-Neto *et al.* 2006) and orbatid mites (Hasegawa *et al.* 2006).

Ants have long been recognised as a significant group in ecosystem functioning in tropical regions. Studies on tropical ant species have found them to be ubiquitous from low to high elevations, with a limit at about 2700 m a.s.l (Ward 2000). Studies spanning greater than 1000 m in elevation gradient have shown that there is generally a hump shaped pattern rather than a monotonic decline in species richness up a slope (Samson *et al.* 1997; Fisher 2000; Ward 2000). There are still a number of theories attempting to explain this pattern in ants. Sanders *et al.* (2007) determined that temperature rather than productivity can better explain ant species diversity along slopes (regardless of spatial scale) in deciduous forest in south-western USA, whereas others such as Ribas *et al.* (2003), Richardson *et al*. (2005) and Ribas and Schoereder (2007) have concluded that habitat heterogeneity is a more important factor in determining ant species distribution.

The current study seeks observable patterns in ant species richness and ant species composition at a very fine spatial scale along a small elevation gradient in relation to physical and vegetation characteristics of lowland wet forest in Sri Lanka. Studies on tree species distribution in these forests have shown that, even across a small elevation gradient (≤500 m), there are observable increases in stem density and the number of large diameter trees (Gunatilleke *et al.* 2004b). Gunatilleke *et al.* (2005) also found distinct species assemblages traversing slopes from valleys to ridges (≤1000 m change in elevation) in these remnant forest patches of south-western Sri Lanka.

Only 5% of the original extent of lowland tropical wet forest remains as small patches and reserves in the highly-populous south-western Sri Lanka (Pethiyagoda 2005). These remnants have persisted due to their location on ridges and slopes too steep for agriculture, and in areas where they are recognised as valuable watershed protectors (Gunatilleke *et al.* 2005). The largest of these remnants, Sinharaja Forest Reserve (SFR), is a World Heritage Site that is renowned for its long history of protection and as a refuge for much of Sri Lanka's endemic flora and fauna. This study will contribute to a growing body of research on the distribution patterns of biota, other than vascular plants, in this biodiversity hotspot.

3.2 Methods

3.2.1 Study site

Sinharaja Forest Reserve (SFR) is a mixed dipterocarp (*Mesua-Shorea* type), lowland, wet forest in south-western Sri Lanka (6° 21-26' N, 80° 21-34' E). The 11,000 ha reserve runs along a series of east-west running ridges, with an elevation range of 300 m to 1200 m a.s.l. The forest is considered aseasonal, receiving between 4000 – 5000 mm of rain annually, with no period where the average monthly rainfall drops below 60 mm. There are two periods in the year when the forest receives monsoonal rain, the south-west monsoon from May to June and the north-east monsoon from September to November, resulting in higher rainfall in these two perionds.

The sites were located in the western quarter of the SFR along south-west facing hills ranging between 300 m and 800 m. This part of the SFR contains once-selectively logged forest (30 years ago), unlogged forest in a public access zone and unlogged forest in a long-term Forest Dynamics Plot (Gunatilleke *et al.* 2004b). Five 10 x 10 m plots were installed in three parallel transects in each of the three forest types. They traversed an elevation gradient extending from 430 m to 660 m. Each plot was assigned to the nearest 10 m elevation section, resulting in a total of 23 sections. These were then grouped into three categories, namely: low elevation plots which fell into sections 1-8 (430 m -510 m); middle elevation plots which fell into sections 9-16 (511 m – 590 m), and high elevation plots which fell into sections 17-23 (591 m – 660 m). Fifteen plots were located in each forest type: old-logged forest (LF); disturbed unlogged forest (UF); undisturbed unlogged forest (FDP). Four collections were made in each plot between March 2005 and November 2006, with at least 2 months between collection periods.

3.2.2 Ant collection

Ants were collected using two established collecting methods: pitfall traps and Winkler extraction (Bestelmeyer *et al.* 2000). In each plot, four pitfall traps were laid out 5 m apart and, in addition, 4 x 1 m^2 samples of litter were collected, sieved and placed in Winkler sacks. The pitfall traps were run for 72 hours and the Winkler extractions were run for 48 hours, with the litter being removed, shaken and returned after the first 24 hours. All ants were removed from the samples and sorted to morphospecies. Voucher specimens of each morphospecies were point-mounted and a reference collection created, all other specimens were stored in 70% ethanol. Ants were then identified to species where possible; where species could not be determined, a unique collection number was assigned. The mounted voucher specimens and wet collection are stored in the Peradeniya University Entomology Museum and a mounted voucher collection stored in the Curtin University Entomology Museum.

3.2.3 Environmental variables

At each plot, four readings of air temperature (1 m above ground level) and relative humidity (1 m above ground level and at ground level) were recorded using a Centre® 310 RS-232 humidity/temperature meter. Four readings of insolation at ground level were recorded using a TPS® MC-88 digital light meter. These four readings were averaged for each plot within each collection period. These variables were designated as physical variables.

Ground cover characteristics of each plot were quantified by estimating the percentage coverage by bare ground, leaf litter, large rocks, and plant stems in a 1 m^2

quadrat. Also, in the same quadrat, the number of dead branches and fallen tree trunks (>10 cm) were recorded and the depth of the leaf litter was measured using a ruler. Four quadrats were measured in each plot in each season and averaged. This group represented the litter structure variables.

Canopy cover was estimated during each collection period using a GRS® densitometer at 40 points within each plot. Understorey foliage density was also estimated using a Levy pole (Majer 1981), with readings taken at four points within each plot. The pole was divided into four intervals: 0 (ground) – 50 cm; 51 cm-100 cm; 101 cm -150 cm; and 151 cm – 200 cm. The number of points where the pole was touched by vegetation was counted, after which, the number of plant touches at each interval for each of the four recordings was summed and divided by the total number of recordings taken for the plot over the course of the collection period (16 points within a site). These variables represented the plant density variables.

3.2.4 Data analysis

All ant species were entered into a data matrix and the data from each collection period were combined. The number of species present at each plot was then totalled and treated as species richness for that plot. The species richness of all the plots within each elevation category was then summed and divided by the total number of plots for each category to ensure that there were no biases for categories with larger numbers of plots. The total number of individuals per species was also recorded and these abundances were analysed in the same way as species richness.

Species richness data, species abundance and the 15 environmental variables (results averaged for all collection periods) were analysed in relation to the three elevation categories and the three forest types using general linear modelling (GLM). Environmental data were normalised using appropriate transformations and Levene's test of equality was run before the GLM was carried out. Co-linear variables were identified using a Spearman rank correlation with a two-tailed test of significance. These co-linear variables were then removed from the matrix. All of the above analyses were carried out using SPSS 15.0.

Differences between ant species assemblages in each elevation category were tested using permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001; McArdle & Anderson 2001). This is a non-parametric partitioning of variance using similar within-group and between-group sum of squares calculations as used in traditional multivariate analysis of variance (MANOVA) (Anderson 2001, 2005). However, it utilises dissimilarity measures between points rather than Euclidean distances, thus freeing the data from the constraints of assuming normality and homogeneity of spread. It produces a probability value based on the comparison of the observed test-statistic (F observed) and a test-statistic (pseudo F) calculated by permutations of the data. A multi-factorial design was chosen using forest type (Logged; Unlogged; Forest Dynamics Plot) as a fixed factor, and randomly nested within were the three elevation categories (low, middle, high). The species assemblages present in each plot were first compared with the assemblages in every other plot using a Bray-Curtis dissimilarity measure (Kruskal 1964), which is commonly used for ecological data which tends to consist of large datasets with many zeros (Anderson & Robinson 2003). A total of 9999 permutations were run for an α-level of 0.005.

Principal coordinate analysis (PCO) was then carried out to visually present the dissimilarity between plots in multi-dimensional space. It utilises the same unconstrained ordination methods as non-metric multi-dimensional scaling but preserves the actual dissimilarities between variables rather than their rank orders (Anderson 2003b). It complements the results of the PERMANOVA, as they are both based on the actual dissimilarities rather than the rankings of dissimilarities.

Canonical analysis of principal coordinates (CAP) is a constrained ordination method that allows the usage of the same dissimilarity matrix (Bray-Curtis) as the previous analyses. A discriminant analysis is performed on *a priori* groupings (in this case elevation category) using permutations of a set number of principal coordinate axes that best encompasses the variation in the data matrix (Anderson 2003a; Anderson & Robinson 2003; Anderson & Willis 2003). The CAP was also utilised to assess the relationship between the environmental variables and the ant assemblages in each of the plots. This uses a canonical correlation analysis of the environmental variables in conjunction with the Bray-Curtis dissimilarity matrix of ant species (Anderson 2003a). Co-linear environmental variables ($r > 0.80$) were removed from the matrix and a $\ln(x+1)$ transformation was carried out on the remaining environmental variables to reduce any large variances before the CAP was performed.

All the above procedures (PERMANOVA, PCO and CAP) were carried out using the program Primer v.6.1.9 permanova+β18.

3.3 Results

3.3.1 Ant species analysis

A total of 146 species and morphospecies (hereafter included as species) in 52 genera, representing 11 subfamilies, were caught within western Sinharaja Forest Reserve. Of the species collected, *Technomyrmex bicolor* was the most ubiquitous and abundant ant, occurring in all 45 plots. It was closely followed by *Paratrechina* sp. SL001 and *Aneuretus simoni* in terms of frequency of occurrence in plots (present in >40 plots in the study area) and abundance and, in terms of frequency of occurrence but not abundance, by *Carebara* sp. SL012, *Strumigenys* sp. sl-01, *Strumigenys* sp. sl-02, *Technomyrmex albipes* and *Tetramorium* sp. SL002. Forty one species occurred in only one plot and, for 35 of those species, only one individual was caught. Table 3.1 displays the entire species list together, showing the presence of each species in each elevation category, starting from those that occurred across all three elevation categories through to those that occurred within only one category.

Those that were recorded in both the low and high elevation categories but not in the middle elevation category were assumed to also occur in the middle elevation range. This is shown as percentages of total species in each elevation category in Figure 3.1. The middle elevation had fewer generalist species (species that occurred across all three elevation categories) than the upper and lower plots. The two most speciose genera, *Pheidole* and *Tetramorium*, had the majority of their species occurring in all three elevation categories, although there were some species (within these two genera) that had restricted ranges. For the third most speciose genus, *Cerapachys*, equal numbers of species exhibited broad as well as restricted ranges.

Table 3.1. List of all species collected in western Sinharaja Forest Reserve. Part (a) shows the species that occurred in all three elevation categories (EC): L (low); M (middle); H (high); part (b) lists species that were restricted to one EC only; and part (c) shows species that were either found in the lower sites (L+M) or the upper sites (M+H).

a) All EC

Subfamily	Genus	Species	L	M	H
Aneuretinae	*Aneuretus*	*simoni*	*	*	*
Cerapachyinae	*Cerapachys*	sp. SL101	*	*	*
	Cerapachys	sp. SL106	*	*	*
Dolichoderinae	*Technomyrmex*	*albipes*	*	*	*
	Technomyrmex	*bicolor*	*	*	*
Formicinae	*Acropyga*	sp. SL093	*	*	*
	Camponotus	sp.nr *angusticollis*	*	*	*
	Camponotus	sp. SL083	*		*
	Myrmoteras	*binghami*	*	*	*
	Paratrechina	sp. SL001	*	*	*
	Paratrechina	sp. SL036	*	*	*
	Paratrechina	*minutula* gp.	*	*	*
	Polyrhachis	*bugnioni*	*	*	*
Myrmicinae	*Carebara*	sp. SL012	*	*	*
	Crematogaster	sp. SL119	*		*
	Monomorium	*floricola* gp.	*	*	*
	Monomorium	*hildebrandii* gp.	*	*	*
	Monomorium	*destructor* gp.	*	*	*
	Myrmicaria	*brunnea*	*	*	*
	Pheidole	sp. SL0ZA	*	*	*
	Pheidole	sp. SL0ZB	*	*	*
	Pheidole	sp. SL0ZC	*	*	*
	Pheidole	sp. SL006	*	*	*
	Pheidole	sp. SL019	*	*	*
	Pheidole	sp. SL027	*	*	*
	Pheidole	sp. SL028	*	*	*
	Pheidole	sp. SL030	*	*	*
	Pheidole	sp. SL049	*	*	*
	Pheidole	sp. SL063	*	*	*
	Pheidole	sp. SL067	*	*	*
	Pheidole	sp. SL070	*	*	*
	Pheidole	sp. SL077	*	*	*
	Pheidole	sp. SL091	*	*	*
	Pheidole	sp. SL141	*	*	*
	Pheidologeton	sp. SL013	*	*	*
	Pristomyrmex	sp. nr *profundus*	*	*	*
	Solenopsis	sp. SL038	*	*	*
	Strumigenys	sp. sl-01	*	*	*
	Strumigenys	sp. sl-02	*	*	*
	Strumigenys	sp. SL098	*	*	*
	Tetramorium	sp. SL002	*	*	*
	Tetramorium	sp. SL05A	*	*	*
	Tetramorium	sp. SL05B	*	*	*
	Tetramorium	sp. SL054	*	*	*
	Tetramorium	sp. SL055	*	*	*
	Tetramorium	sp. SL058	*	*	*

Part (a) cont'd

Subfamily	Genus	Species	L	M	H
Myrmicinae	*Tetramorium*	sp. SL082	*	*	*
cont'd	*Tetramorium*	sp. SL117	*	*	*
	Tetramorium	sp. SL123	*	*	*
	Tetramorium	sp. SL127	*		*
	Vollenhovia	sp. SL033	*	*	*
Ponerinae	*Anochetus*	sp.nr *nietneri*	*	*	*
	Cryptopone	*testacea*	*	*	*
	Harpegnathos	*saltator*	*		*
	Hypoponera	sp. SL016	*	*	*
	Hypoponera	sp. SL114	*	*	*
	Leptogenys	sp. SL065	*	*	*
	Leptogenys	sp. SL072	*	*	*
	Leptogenys	sp. SL125	*	*	*
	Pachycondyla	*rufipes*	*	*	*
	Pachycondyla	*melanaria*	*	*	*
	Pachycondyla	*truncata*	*	*	*
	Ponera	sp. SL048	*	*	*

b) One EC

Subfamily	Genus	Species	L	M	H
Cerapachyinae	*Cerapachys*	sp. SL130			*
	Cerapachys	sp. SL144			*
Formicinae	*Camponotus*	sp. SL138			*
	Lepisiota	sp. nr *capensis*			*
	Polyrhachis	*hippomanes*			*
Leptanillinae	*Protanilla*	sp. SL108			*
Myrmicinae	*Myrmecina*	curtisi			*
	Pheidole	sp. SL107			*
	Strumigenys	sp. SL109			*
	Tetramorium	sp. SL059			*
Ponerinae	*Anochetus*	sp. nr *longifossatus*			*
	Hypoponera	SL052			*
Aenictinae	*Aenictus*	*binghami*		*	
Amblyoponinae	*Amblyopone*	sp. SL128		*	
Cerpachyinae	*Cerapachys*	sp. SL011		*	
	Cerapachys	sp. SL104		*	
	Cerapachys	sp. SL111		*	
Dolichoderinae	*Dolichoderus*	sp. SL075		*	
	Dolichoderus	sp. SL089		*	
	Tapinoma	sp. SL056		*	
	Tapinoma	sp. SL131		*	
Ectatomminae	*Gnamptogenys*	*laevior* gp.		*	
Formicinae	*Forelophilus*	sp. SL092		*	
	Paratrechina	*bourbonica*		*	
	Polyrhachis	*illaudata*		*	
Myrmicinae	*Carebara*	sp. SL112		*	
	Cataulacus	*latus*		*	
	Crematogaster	sp. SL136		*	
	Crematogaster	sp. SL146		*	
	Crematogaster	sp. SL148		*	
	Meranoplus	*loebli*		*	
	Pheidole	sp. SL064		*	
	Pyramica	sp. SL143		*	
	Pyramica	sp. SL163		*	
	Rhopalomastix	*rothneyi*		*	

Part (b) cont'd

Subfamily	**Genus**	**Species**	**L**	**M**	**H**
Myrmicinae cont'd	*Rogeria*	sp. SL057		*	
	Solenopsis	sp. SL113		*	
	Tetramorium	sp. SL135		*	
	Tetramorium	sp. SL162		*	
Ponerinae	*Hypoponera*	sp. SL051		*	
	Leptogenys	sp. SL175		*	
	Leptogenys	sp. SL176		*	
	Myopias	*amblyops*		*	
Pseudomyrmecinae	*Tetraponera*	*difficilis*		*	
Cerapachyinae	*Cerapachys*	sp. SL165	*		
	Cerapachys	sp. SL173	*		
Ectatomminae	*Gnamptogenys*	*coxalis* gp	*		
Formicinae	*Camponotus*	sp. SL169	*		
	Camponotus	sp. SL172	*		
Myrmicinae	*Monomorium*	*floricola*	*		
	Pyramica	sp. SL159	*		
	Pyramica	sp. SL164	*		
	Tetramorium	sp. SL118	*		
	Tyrannomyrmex	sp. nv.	*		
	Vollenhovia	sp. SL149	*		
Ponerinae	*Anochetus*	sp. nr *nietneri*	*		
	Pachycondyla	*sulcata*	*		

c) Two EC

Subfamily	**Genus**	**Species**	**L**	**M**	**H**
Aenictinae	*Aenictus*	sp. nr *punensis*		*	*
Cerapachyinae	*Cerapachys*	sp. SL074		*	*
Formicinae	*Camponotus*	sp. nr *infuscus*		*	*
	Pseudolasius	sp. SL140		*	*
Myrmicinae	*Acanthomyrmex*	*luciolae*		*	*
	Cardiocondyla	sp. SL122		*	*
	Pheidole	sp. SL029		*	*
	Tetramorium	sp. SL015		*	*
	Tetramorium	sp. SL020		*	*
	Vollenhovia	sp. SL115		*	*
Ponerinae	*Anochetus*	sp. nr *longifossatus*		*	*
	Discothyrea	sp. SL050		*	*
	Leptogenys	sp. SL041		*	*
Cerapachyinae	*Cerapachys*	sp. SL026	*	*	
Dolichoderinae	*Tapinoma*	sp. SL147	*	*	
Leptanillinae	*Protanilla*	sp. SL129	*	*	
Myrmicinae	*Crematogaster*	sp. SL022	*	*	
	Crematogaster	sp. SL062	*	*	
	Myrmicaria	sp.A	*	*	
	Pheidole	sp. SL142	*	*	
	Recurvidris	*pickburni* sp. nv.	*	*	
	Rhopalothrix	sp. SL102	*	*	
	Tetramorium	sp. SL134	*	*	
Ponerinae	*Hypoponera*	sp. SL066	*	*	
Pseudomyrmicinae	*Tetraponera*	*attenuata*	*	*	

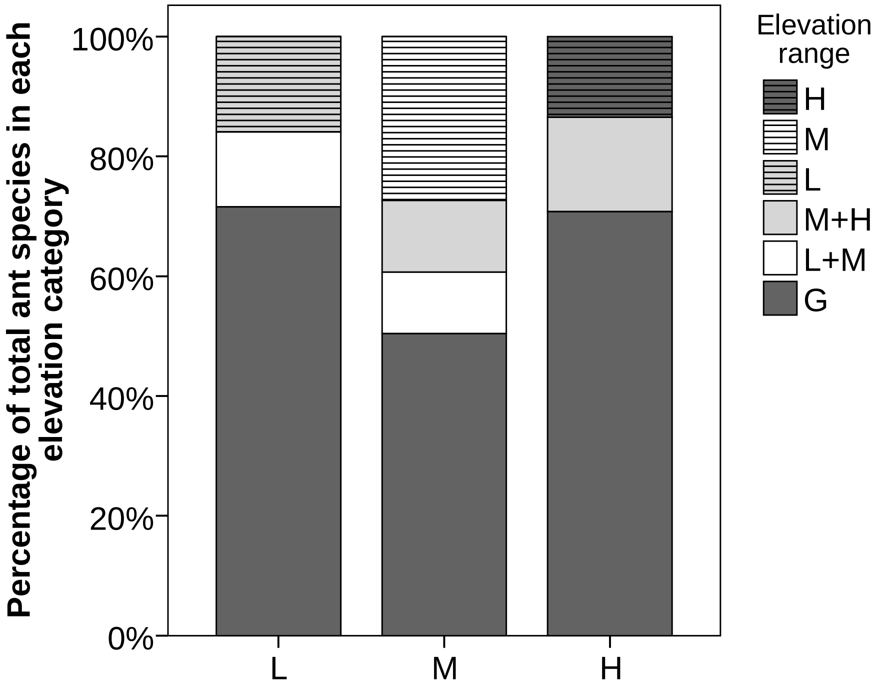


Figure 3.1. The elevation ranges of all ant species found in each elevation category (Low, Middle and High). There were greater numbers of generalist species (G) in the low and high categories compared to the middle elevation plots. The middle plots also had higher numbers of species that were found only in the middle range (M) when compared to the number of species restricted to the low (L) and high (H) elevation plots.

3.3.2 Relationship with elevation and forest type

After the designation of each plot with an elevation range group number, 10 plots were located in the lower elevation range, 22 in the mid elevation range, and 13 plots fell in the higher elevation range (Figure 3.2). The low elevation category is henceforth referred to as LEC, the middle as MEC and the high as HEC. As there were uneven numbers of plots in each range, species richness and abundance was averaged for each elevation category. This showed that there was a monotonic decrease in mean abundance and the mean number of species as elevation increased (Figure 3.3), whereas total species richness for each elevation category showed the MEC as having the highest number of species. The forest dynamics plot (FDP) had the highest abundance and species richness, while the unlogged forest (UF) had the lowest abundance and species richness (Figure 3.3).

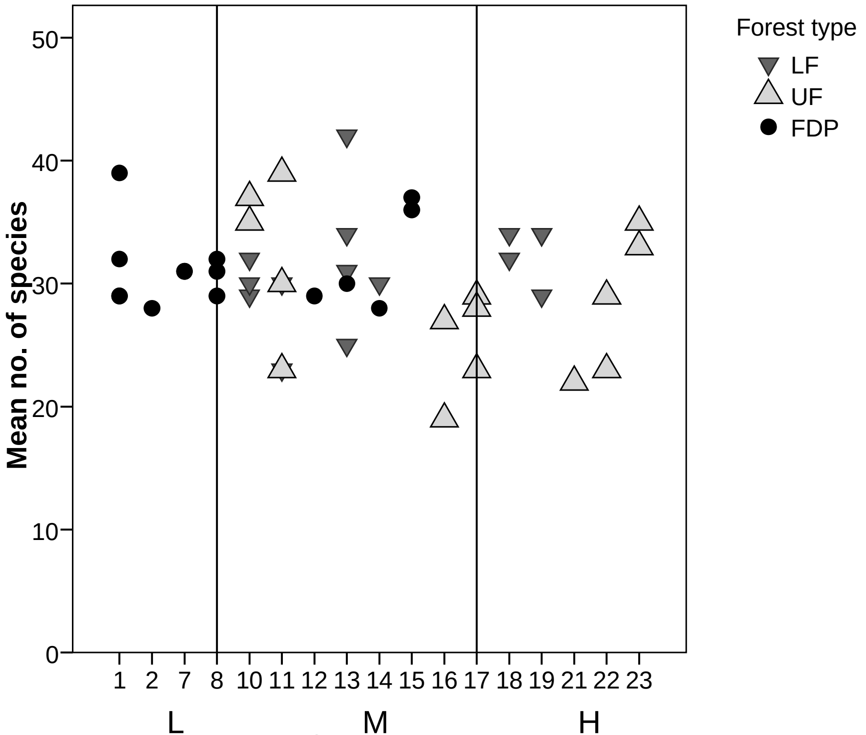
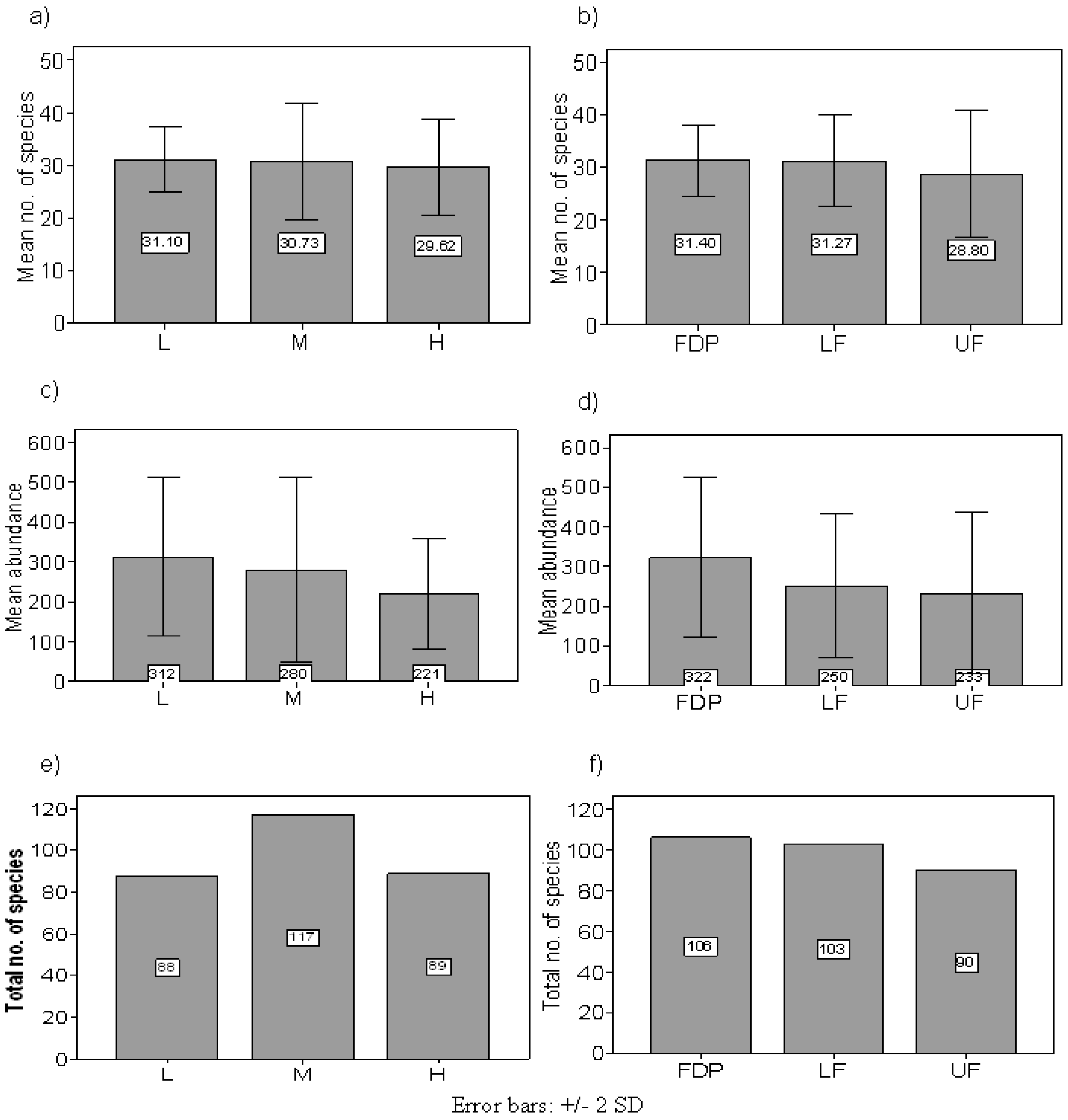


Figure 3.2. Mean number of species in each plot numbered according to its elevation group (1-23) within the three different forest types: Forest Dynamics Plot (FDP); logged forest (LF); and unlogged forest (UF). The lines represent the cut-off points for the three elevation categories: low (L); middle (M); and high (H).

General linear modelling results (Table 3.2) showed no significant linear relationship between ant species richness (and abundance), elevation category (EC) and forest type (FT). Five variables were significantly associated with EC, namely: air temperature; % litter cover; litter depth; canopy cover; and foliage density 0-50 m. These same five variables were also significantly associated with FT, along with % plant cover and % stone cover.

Air temperature decreased as elevation increased, as did relative humidity and insolation. Litter cover, plant cover, number of branches and litter depth increased as well, whereas stone cover decreased. For plant density, both canopy cover and foliage density (0-50 m) exhibited no monotonic trend with elevation. Canopy cover was lowest in the middle elevation with significant differences between the lower and middle elevations. Foliage density (0-50 m) showed the same trend, with the middle elevation having the lowest values but the significant differences lay between the middle and higher elevations.



Error bars: +/- 2 SD

Figure 3.3. Comparison of elevation categories (low (L); middle (M); and high (H)) and forest type (Forest Dynamics Plot (FDP), logged forest (LF) and unlogged forest (UF)) by: average number of species (graphs (a) and (b)); mean abundance of ants (graphs (c) and (d)); and total number of species (graphs (e) and (f)). This demonstrates the effect of the increased amount of area sampled in the middle elevation category is to increase the number of species collected but, when species richness is averaged for the number of plots, there is a monotonic decline as elevation increases. There were equal numbers of plots in each forest type; there is a direct relationship between total number of species and abundance.

Table 3.2. Results of general linear modelling (GLM) with ant species richness and transformed environmental variables in relation to elevation category and forest type. For both site factors, air temperature, litter cover and depth, canopy cover and foliage structure (0-50 cm) were significantly associated.

Factor	Dependent Variable	Type III	df	F	*P*
Elevation category:	Ant species richness	.873	2	.018	.982
Low	**Temperature air**	**5.38**	**2**	**11.4**	**.000****
Middle	Rh air	.002	2	.971	.388
High	Insolation	.837	2	8.05	.001
	% Litter cover	**.132**	**2**	**4.42**	**.019***
	% Plant cover	.226	2	.249	.781
	% Stone cover	2.02	2	2.31	.112
	No. of branches	.209	2	2.28	.116
	Litter depth	**5.53**	**2**	**18.5**	**.000****
	% Canopy cover	**.026**	**2**	**4.06**	**.025***
	Foliage structure 0-50 cm	**6.84**	**2**	**10.5**	**.000****
	Foliage structure 50-100 cm	.038	2	.045	.956
	Foliage structure 100-150 cm	1.34	2	.949	.396
	Foliage structure 150-200 cm	.282	2	.365	.697
Forest type:	Ant species richness	64.7	2	1.37	.267
Logged forest	**Temperature air**	**3.85**	**2**	**8.17**	**.001****
Unlogged forest	Rh air	.015	2	5.99	.005
Forest Dynamics	Insolation	.597	2	5.74	.007
Plot	**% Litter cover**	**.102**	**2**	**3.42**	**.043***
	% Plant cover	**3.47**	**2**	**3.82**	**.030***
	% Stone cover	**3.29**	**2**	**3.76**	**.032***
	No. of branches	.125	2	1.36	.268
	Litter depth	**1.02**	**2**	**3.42**	**.043***
	% Canopy cover	**.090**	**2**	**14.0**	**.000****
	Foliage structure 0-50 cm	**12.5**	**2**	**19.2**	**.000****
	Foliage structure 50-100 cm	1.84	2	2.19	.126
	Foliage structure 100-150 cm	1.26	2	.895	.417
	Foliage structure 150-200 cm	.647	2	.836	.441
Elevation category	Ant species richness	38.1	1	1.61	.212
and	Temperature air	.024	1	.102	.751
forest type	Rh air	0.02	1	.018	.893
	Insolation	.094	1	1.81	.186
	% Litter cover	**.078**	**1**	**5.23**	**.028***
	% Plant cover	.612	1	1.35	.253
	% Stone cover	.957	1	2.19	.147
	No. of branches	.010	1	.229	.635
	Litter depth	.535	1	3.58	.066
	% Canopy cover	**.016**	**1**	**5.02**	**.031***
	Foliage structure 0-50 cm	**1.46**	**1**	**4.48**	**.041***
	Foliage structure 50-100 cm	1.36	1	3.24	.080
	Foliage structure 100-150 cm	.349	1	.495	.486
	Foliage structure 150-200 cm	1.11	1	2.88	.098

* $P < 0.05$; ** $P < 0.01$

Many of the environmental variables did not show uniform trends in relation to forest type; temperature and insolation were highest in the logged forest (LF), whereas relative humidity and canopy cover were the lowest here. Plant cover, stone cover, litter depth and ground foliage density were higher in the unlogged forest.

3.3.3 Ant species composition

Results of the PERMANOVA showed that both EC (Pseudo F = 2.01, *P* (perm) = 0.014) and FT (Pseudo F = 1.48, *P* (perm) = 0.007) affected ant assemblage distribution, with FT showing a greater Pseudo-F ratio (Table 3.3).

Table 3.3. Results of a two-way crossed PERMANOVA with elevation category nested within forest type (FT). Both factors are significant at the *P* = 0.01 level. The final column shows the high number of unique permutations (U perms) run out of 9999 permutations.

Source	SS	df	Pseudo-F	*P* (perm)	U perms
Forest type	6233.6	2	2.01	0.007**	9893
Elevation category (FT)	4657.6	3	1.48	0.014**	9845
Residual	40794	39			
Total	51774	44			

Pair-wise tests of forest types and elevation group showed significant differences only between the low and middle elevation groups within the FDP (t = 1.36, *P* (perm) = 0.014), and also between the UF and FDP (t = 1.585, *P* (perm) = 0.011). The PCO plot of the data grouped the low elevation plots below the ‘cloud’ of middle and higher elevation plots (Figure 3.4). Up to 32.7% of the variation was explained by the first three PCO axes. Ten PCO axes were necessary to account for 78 % of the variation. These 10 axes (*m* = 10) were used to generate the CAP ordination (Figure 3.5), with elevation category set as the grouping factor. While misclassification error was high (47% or 24 out 45 plots), the ordination shows clumping of the low elevation plots, and hence most of the FDP plots, below the middle and high elevation plots. There is little separation of the middle and upper plots, although the logged forest plots are concentrated more to the left of the cloud of plots.

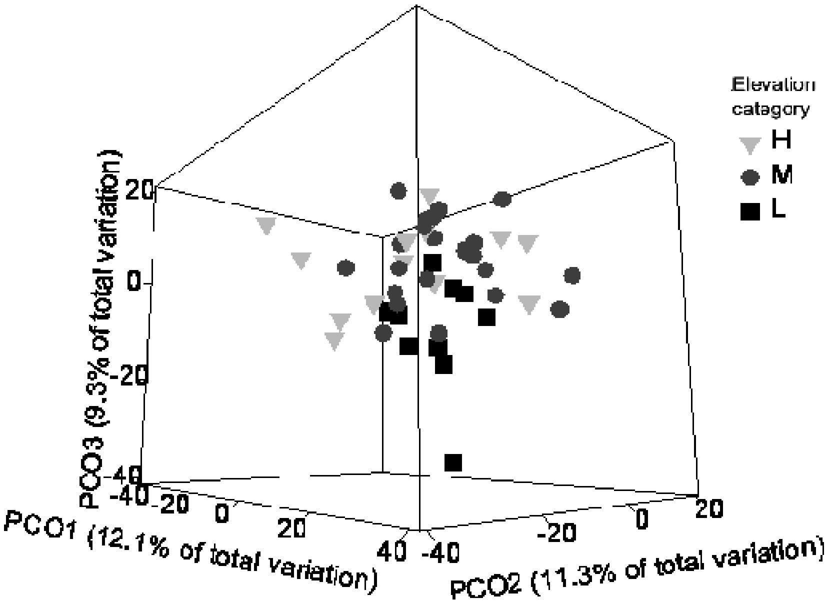


Figure 3.4. Principal coordinates plot drawn in three dimensions, it explains 32% of the variation and shows the low (L) elevation plots falling slightly below the middle (M) and high (H) elevation plots.

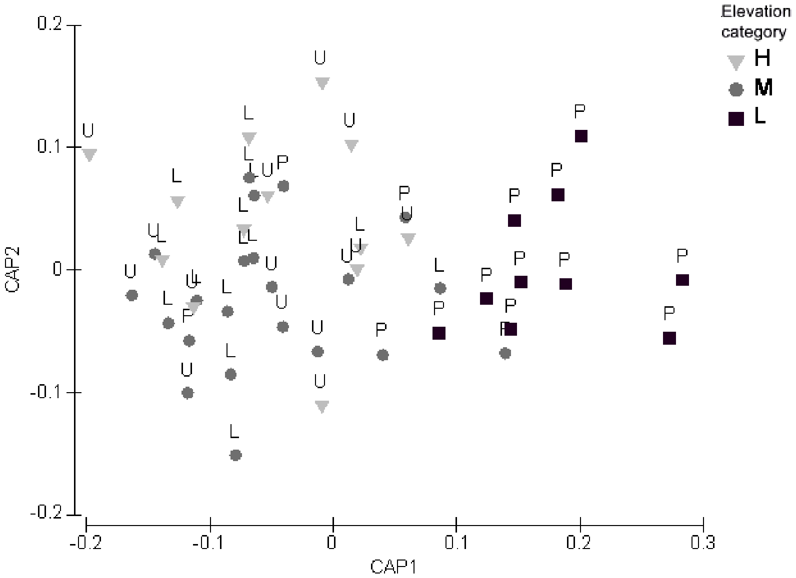


Figure 3.5. Canonical analysis of principal coordinates (CAP) of ant species assemblages in the three elevation categories (low (L); middle (M); high (H)) in relation to the three forest types (logged (L); unlogged (U); Forest Dynamics Plot (P)). The first ten principal coordinate axes were used in the analysis (m = 10) which accounted for 78% of the variation in ant assemblages. Mis-classification error was at 46.7 %, meaning only 24 out of the 45 sites are placed accurately.

Environmental variables related to ant species assemblages were revealed in the CAP analysis (Figure 3.6). Foliage density in the 0–50 cm category was associated with the middle and higher elevations, whereas relative air humidity was associated more with the lower elevations. Other variables of influence were plant cover and litter cover.

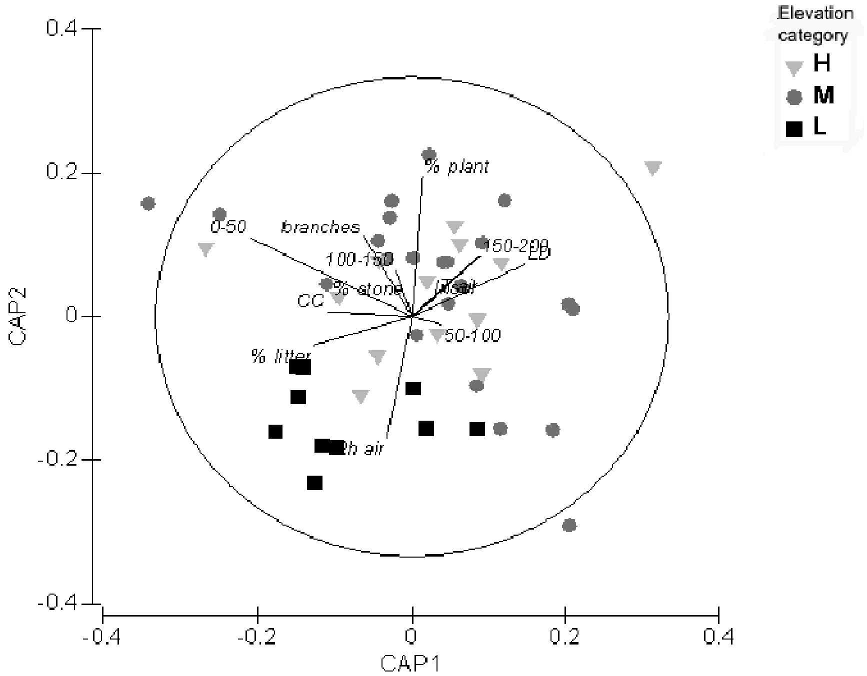


Figure 3.6. Canonical analysis of principal coordinates (CAP) of ln (x+1) transformed environmental variables in relation to ant species assemblage in the three elevation categories (Low, Middle, High). Environmental variables shown are: temperature air (Tair); relative humidity air (Rhair); insolation (Insol); % cover litter (% litter); % cover plant (% plant); % cover stone (% stone); no. of branches (branches); litter depth (LD); canopy cover (CC); plant structure 0-50 cm (0-50); plant structure 51-100 cm (50-100); plant structure 101-150 cm (100-150); plant structure 151-200 cm (150-200).

3.4 Discussion

3.4.1 The ants

This study represents one of the first comprehensive collections of ant species in the SFR and demonstrates the high species richness in this forest remnant. Although the study was restricted to looking at ground dwelling ant fauna, it demonstrates that the diversity of ants in this forest is more comparable to values in

South East Asian dipterocarp forest rather than to the mixed forests of the Western Ghats in neighbouring India (Gadagkar *et al.* 1993; Basu 1997; Gadagkar *et al.* 2000). Current collections in Sri Lanka list 12 subfamilies for the island (Dias 2006) and all, except Dorylinae, were collected in this study.

While the myrmicine genera *Pheidole* and *Tetramorium* were the most speciose, they were not the most abundant ants in the forest. *Technomyrmex bicolor*, *Paratrechina* sp. SL001 and, unexpectedly, *Aneuretus simoni* were highly abundant and widely distributed. Their numerical dominance could be more pronounced as a result of the chosen collection methods. *Technomyrmex bicolor* was predominantly found in shallow nests in the leaf litter and therefore could have been more frequently picked up during litter collection. The latter two abundant species are relatively small and perhaps slower moving; they may therefore be unable to escape quickly during litter collection unlike faster moving *Pheidole* species. These three abundant species did not demonstrate a common trend in abundances across elevation categories. Both *T. bicolor* and *Paratrechina* sp. SL001 had their peak abundances in the lower elevation, whereas *A. simoni* peaked at mid elevation, perhaps indicating a lowered competitiveness within the more speciose ant assemblages at low elevations.

Although sampling intensity was relatively high, almost one third of species occurred at only one plot, with most of these having just one specimen representing them. Possible explanations may be that these species are canopy dwellers that only occasionally visit the leaf litter (e.g., *Polyrhachis*), are cryptic soil dwellers that tend to have low densitiy populations (e.g., *Pyramica*), or are disturbed area inhabitants (e.g., *Meranoplus bicolor*). There is the potential that some of these singletons are disturbed area inhabitants, since they were found mostly in the middle elevation plots. These plots were located adjacent to either access roads (in the case of the LF and UF) or secondary forest (FDP) which may have allowed the encroachment of these species at the edges. However, there were also many singletons found in the lower and upper elevation plots, suggesting that the singletons were comprised of species that were not from disturbed areas. The rarity of certain species poses the question as to whether some species are just simply found in low numbers in the forest. Using the example of *Tyrannomyrmex* sp. nv, only two other species have been recorded for this genus (*Tyrannomyrmex rex* and *T. dux*), each of them also described from only one woker specimen. Further investigation on these rare species would further our understanding of the ecological functions of rare species.

As there is a paucity of data on ant species diversity, distribution, endemicity and behaviour in the Indian subcontinent, it is difficult to make assumptions regarding the species assemblages found in the SFR and the elevational ranges of the species collected. Future studies should include methods that allow sampling of the upper vegetation and the canopy to determine which ants are truly ground dwellers and which are visitors. The current collection does add to the growing knowledge-base of global species distribution and provides a better idea of the species richness in Sri Lankan rain forest.

3.4.2 Elevation

There was a slight monotonic decrease in overall average abundance of ants, despite the relatively small elevation range (230 m) of this study. Based on elevational studies of ants elsewhere in the tropics (Leakey & Proctor 1987; Olson 1994; Samson *et al.* 1997; Fisher 1998, 1999a), ant species richness and abundance is known to increase up to about 500 m to 1000 m, after which it starts to decline. Previous studies on ant species richness have used elevation spans greater than 1000 m across a variety of forest types, with differences between elevation categories being more than 200 m. Those studies that show a monotonic decline did not appear to sample below 500 m (Brühl *et al.* 1999; Araújo & Fernandes 2003) and therefore potentially still could demonstrate a humpshaped decline in species richness.

Rahbeck (2005) observed that studies conducted on smaller gradient lengths (≤1000 m) tended to exhibit a monotonic decline in species richness. Studies on the relationship between productivity and species richness have also shown that hump-shaped trends are more prevalent amongst studies that crossed community types (Mittelbach *et al.* 2001). The hills in western SFR do not extend higher than 800 m or lower than 300 m, so a natural limitation on range is placed on the fauna. Sampling sites were restricted to dipterocarp dominated forested areas; elevations above 700 m had a lower canopy height and increased canopy openess, while elevations below 300 m were on the edges of the reserve, thus increasing the potential for confounding the data with edge effects. It is thus possible that since vastly different community boundaries and large elevation gradients were were not crossed in this study, a hump-shape trend in species richness was not observed.

From the previous studies mentioned, one would still expect an increase in species richness towards the upper elevations, rather than a decrease. The upper limit in this study was only 630 m, which is well within the high species richness bands of other studies, so it is of interest that a decline in species richness was observed across the small elevation gradient. A possible reason why we did not see a general increase in ant species towards the upper plots in this study could be attributed to the *Massenerhebung,* or mountain mass, effect.

The *Massenerhebung* effect is the observed differences in the elevation at which biota change along mountain slopes of varying heights. Small isolated peaks and ridges tend to have the transition zone between lowland tropical forest and montane forest at lower altitudes than are normally found on larger moutains (Richards 1996). Grubb and Whitmore (1966) suggest that fog or mist cover, rather than temperature change due to altitude, determines the limits of vegetation types along mountain slopes. Increasing the frequency of fog collection decreases radiation and therefore ground temperature, as well as increasing soil moisture which slows down the mineralization of organic matter (Grubb & Whitmore 1966; Grubb 1971). The smaller the mountain, the lower the altitude at which fog/mist collects (Grubb 1977) and this creates montane characteristics at lower elevations; this could then lower the elevation at which the peak in species richness occurs. Leakey and Proctor (1987) observed this effect in oligochaete biomass when comparing two mountains in Sabah, Malaysia and McCain (2005), testing 56 datasets for nonvolant small mammals from around the world, found this effect to occur as well.

The small elevation range in this study was associated with significant decreases in temperature and insolation. Although not quantified, the occurrence of mist in the upper plots in this collection was noticeably higher than at the lower elevations. Decreasing temperature and radiation (due to mist) can reduce the foraging time available to ants (Brühl *et al.* 1999) and therefore may have affected the number of ant species caught in higher elevation plots. Lower air humidity and closely correlated soil humidity would also have influenced species richness. Studies elsewhere have found significant decreases in ant activity along moisture gradients from ravine bottoms to ridgetops, suggesting that even small changes in moisture availability can affect foraging activity (Levings 1983; Kaspari & Weiser 2000).

Litter structure variables mostly appeared to increase up the slope, which should potentially increase ant species richness by increasing habitat complexity, litter prey availability and nest site availability (Kaspari 1996; Andersen 2000; Perfecto & Vandermeer 2002). The fact that species richness was lower at the higher elevations shows that the physical characteristics, like temperature and light availability, of the upper elevations potentially have a greater influence on the number of ant species.

It has been difficult to tease apart the influences of forest type on the ant assemblages along this elevation gradient. While species richness values were not significantly different across the three forest types or the three elevation gradients, species assemblages and environmental variables were. When setting out plots for this study, care was taken to avoid the highest and lowest elevations along the slope, as there was a noticeable change in the forest stature and structure at these ends. Along the upper ridge of the slope, the vegetation reduced markedly in stature, while the valley bottom was traversed by a stream which flooded after rains, causing a break in the tree line and a dominance of shrubs that could persist in waterlogged soils. While the plots were located away from the open forest, the degree to which the effects of the edge penetrates into the forest is unknown. The potential variability of environmental factors at these 'edges' could mean that more generalist species will dominate (Didham 1997). This could explain why there were greater numbers of wide-ranging species (species that were found in all three elevation categories) in the lower and upper plots than in the middle plots. Almeida-Neto *et al.* (2006) suggest the term 'ends are bad' for hypothesizing why species richness is lowered at the extreme ends of an elevation range. While overall species richness did not follow this pattern, the variability of environmental factors at these 'ends' may have increased the richness of generalist species.

3.4.3 Forest type

The fact that the majority of the FDP plots represented the low elevation plots makes separate assesment of the two factors (elevation and forest type) difficult. The FDP plots were separated from the other plots by 3 km of secondary forest, which may have had an influence on discriminating this assemblage of ants from the others.

Tree density, tree species richness and structural heterogeneity have all been shown to be positively associated with ant species richness and composition (Ribas *et al.* 2003; Ribas & Schoereder 2007) and forest hetereogenerity has been found to affect the community of litter invertebrates more at lower elevations (Richardson *et al.* 2005). Vasconcelos *et al.* (2003) also found topography to be significant in determining the abundance and diversity of ants in Amazonian forest. Long-term ecological studies of vegetation in the FDP have revealed increased stem density and numbers of trees in large diameter classes along slopes from 300 m to 500 m in elevation (Gunatilleke *et al.* 2004b). These studies have also found that gap formation may be more frequent in the valleys, since the trees have shallower root systems due to periodic waterlogging. This high stem density and topographical heterogeneity may have contributed to increasing species richness in the FDP, possibly resulting in distinguishing the ant assemblage from those in the other forest types. It would be of interest to look specifically at the change in species assemblages within the FDP to see if there are any patterns of ant species composition in relation to topography, tree species composition and structural heterogeneity.

Many of the middle elevation sites were in the logged forest, which had significantly different physical attributes to the other forest types. The logged forest had less canopy cover, the highest temperatures and insolation, and the lowest humidity. The disturbance that logging caused, albeit 30 years previous, may have contributed to the logged forest having higher species richness than the unlogged forest, even though these two forests were adjacent to each other. There have been a number of studies demonstrating that remnant effects of logging can persist for decades after the logging event (Bengtesson *et al.* 1997; Negrete-Yankelevich *et al.* 2007). In terms of the principle coordinate space (Figure 3.5), the logged forest plots are placed further away from the FDP than the unlogged plots. This suggests that while logged forest ant assemblages resemble those that are characteristic of adjacent unlogged forest, there are still some compositional differences that can persist for decades after the disturbance.

The unlogged forest had the lowest ant species richness, which can be linked to the fact that many of the higher elevation sites were in this forest type. Hong-Wa and Dong (2006) found that species richness of trees decreased along this same slope within the unlogged forest, and suggest that potential intolerance to water stress could be a driving factor in tree species composition at higher elevations. This is supported by Engelbrecht *et al.* (2007), who suggest that soil water availability drives tree species distributions in tropical forests. It would be hard to say whether the ants are responding to the direct effect of physical changes due to elevation (e.g., soil moisture) or indirectly due to lower structural heterogeneity afforded by lower tree species richness. Richardson *et al.* (2005) suggest that litter invertebrates adapt to a resource rather than to climatic factors, since the tree species would determine the quality and quantity of the leaf litter within which the animals dwell. Since ant species composition, rather than species richness, was significantly different in this study, further research should be undertaken to see if there are any particular associations between ant species and tree species in the unlogged forest.

There is a high degree of endemicity in tree species in the SFR, often with few individuals per species. In a survey of three different areas of the SFR, Gunatilleke and Gunatilleke (1985) found that 40% of trees had less than 10 individuals per species in a 25 ha area, and 43% were restricted to one or two of 60 sites sampled. Montane areas are renowned for their relictual endemism and species persistence (Jetz *et al.* 2004); it is thus possible that the ground dwelling ant species assemblages are responding more to this patchy tree diversity that has resulted from the undulating topography of the reserve. Since forest type had greater significance than elevation as a factor determining ant species composition, the other forest fragments remaining in south-west Sri Lanka could harbour further distinguishable sets of ants. Since these fragments are fast disappearing or degrading, it is vital that we expedite the identification of flora and fauna in these relictual refuges as soon as possible.

In this study, species richness alone does not adequately demonstrate the intricate differences that are present between similar forest types and along small gradients of change. With the increasing availability of software for analysis, it is imperative that species composition be looked at when formulating conservation plans, since species richness alone may not provide adequate information on how unique an area can be.

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4. Ant species assemblages in old-logged forest and unlogged forest in western Sinharaja, Sri Lanka: investigating remnant effects of selective logging

Abstract

The residual effects of logging on forest fauna and flora have been well studied in other regions of the world, with many studies finding that recovery of species richness and abundance can occur within one or two decades after the logging event. In this study, we use ant species to compare logged (>30 years) and unlogged forest in the Sinharaja Forest Reserve, a World Heritage Site in Sri Lanka. Species richness and abundance were higher in the logged forest than in the unlogged forest, but not significantly so. Species assemblages, on the other hand, were significantly different and were associated with different environmental variables in the logged forest and unlogged forest. The findings from this study corroborate other studies that have shown that species composition in logged forest does not appear return to unlogged forest composition, even after three to six decades have passed. Since this study was not a before-and-after comparison, it is difficult to confirm whether the differences arise from the residual effects of logging or from the general patchiness of species distribution in tropical forest. However, the cumulative results do suggest that there is a residual effect of logging on ant species composition in this forest, even after more than 30 years of regeneration.

Key words: Logging, residual effects, ground dwelling ants, Formicidae, ant species richness, ant species abundance, regeneration

4.1 Introduction

Sri Lanka’s lowland rainforest has been reduced to small patches within the south-western provinces of the country (Ashton & Gunatilleke 1987). Many of these patches have been subjected to human-related disturbance as a result of the long history of habitation and increasing population density in the area (IUCN 1993). The forests have long been used by the villagers in the area for firewood extraction and non-timber forest products and have always been recognised for their resource value (McDermott 1986). During the 1970’s, many of these forests were gazetted for logging concessions and were selectively logged until a government moratorium on logging was issued in 1978 (Gunatilleke & Gunatilleke 1980; IUCN 1993).

One of the largest and most contiguous patches within this zone is Sinharaja Forest Reserve (SFR), an UNESCO World Heritage Site (IUCN 1993; Ashton *et al.* 1997). Between 1972 and 1977, 1400 ha of the western portion of the SFR was selectively logged for plywood (Gunatilleke & Gunatilleke 1980) and up to 60% of the canopy was opened by the logging activity; a network of skid trails was also left behind (de Zoysa *et al.* 1991). The vegetation on most of these skid trails have since regenerated, the exceptions being those maintained by the Forest Department for tourist access and educational use. To date, there has been little research into the effects of this logging event on the flora and fauna of the SFR (de Zoysa *et al.* 1991) and few published studies have been performed on the long-term residual effects of selective logging in this region of the world.

Selective logging is still one of the main management regimes in south east Asian tropical forests, as many tropical tree species are very important to the timber industry (Fimbel *et al.* 2001b). Selective logging occurs at different intensities (no. of trees removed per hectare) and with different felling regimes, according to the objectives of the forest managers (Johns 1985). Once an area is logged, natural regeneration is allowed to take place, often with the intention of re-harvesting the area at 20-40 year intervals (Fimbel *et al.* 2001a). The recovery rate of forest diversity and structure varies according to the intensity at which the logging occurs and to the ecosystem dynamics of the forest itself (Putz *et al.* 2001). Although only a small percentage of timber is generally extracted (< 5%), up to 50% of the surrounding vegetation is often destroyed or damaged (Johns 1986). Thus, selective logging has been found to increase the density of understorey vegetation, decrease the average basal diameter of the trees and increase the width and number of canopy gaps (Johns 1985; Chapman & Chapman 1997; Vasconcelos *et al.* 2000; Fimbel *et al.* 2001b; Widodo *et al.* 2004). In the long term, this can affect leaf litter composition and the soil chemistry (Negrete-Yankelevich *et al.* 2007).

These physical changes can affect the faunal diversity of the litter stratum, which is dominated by invertebrates. Invertebrates can comprise up to 93% of the tropical forest animal biomass (Wilson 1987) and they contribute to almost all forest processes. Comparisons of butterfly, beetle, termite and soil microfauna species richness and composition in logged and unlogged forests have produced a variety of results, which are often related to differences in spatial and temporal scales of the studies (Ghazoul & Hill 2001). However, many studies have adequately demonstrated that the effects of logging on flora and fauna can persist for decades after the logging event (Bengtesson *et al.* 1997; Hamer *et al.* 2003; Padmawathe *et al.* 2004; Clarke *et al.* 2005; Kariuki *et al.* 2006; Negrete-Yankelevich *et al.* 2007).

Ants form a large part of the forest litter fauna and their applicability for indicating the status or health of an ecosystem has been well demonstrated (Majer *et al.* 2007). Ants, together with termites, form a substantial proportion of invertebrate fauna in tropical forests, however ants are more diverse in their ecological impact as they fill a whole spectrum of biological niches (Primack & Corlett 2005). Despite this, there have been few studies that have specifically looked at responses of ants to selective logging in the Asian tropics.

In this study, we carried out an analysis of ant assemblages in the logged and adjacent unlogged forest to investigate whether there any residual effects of selective logging 30 years after the disturbance. An additional aim of this research also is to provide a comprehensive assessment of the ant species richness of a well known biodiversity hotspot and to contribute to a greater understanding ant species distribution in the Asia-Pacific tropical region.

4.2 Methods

4.2.1 Study site

The study was carried out in the the Sinharaja Forest Reserve (SFR), a 11,000 ha reserve located in the Sabaragamuwa Province in Sri Lanka (6° 21-26’ N, 80° 21-34’ E). It is the largest remaining contiguous stand of mixed dipterocarp (*Mesua-Shorea* type) forest in the area. The reserve is mid-elevation rain forest (300 – 1200 m a.s.l.), set upon a series of ridges runnning in an east-west direction in the south-western quarter of the country.

Collections were carried out four times over one year, every three months starting from March 2005 and ending in February 2006. This was to allow for potential seasonal effects, since Hamer *et al.* (2005) found that the degree of difference in butterfly diversity in logged forest and unlogged forest was affected by monsoonal variation in rainfall. They suggested that misleading results can be obtained in short-term studies, even in relatively aseasonal regions. Though the SFR is considered aseasonal wet forest, the south-west of Sri Lanka is visited by two monsoons, the south-west monsoon from May to June and the north-east monsoon from September to November, resulting in higher rainfall in these two periods. March 2005 (first collection) was unusual in that there were a few days of heavy rain, which resulted in slightly higher rainfall recorded than for July 2005 (second collection). October 2005 (third collection) experienced the highest rainfall for the year and February 2006 (fourth collection) was a predictably dry month.

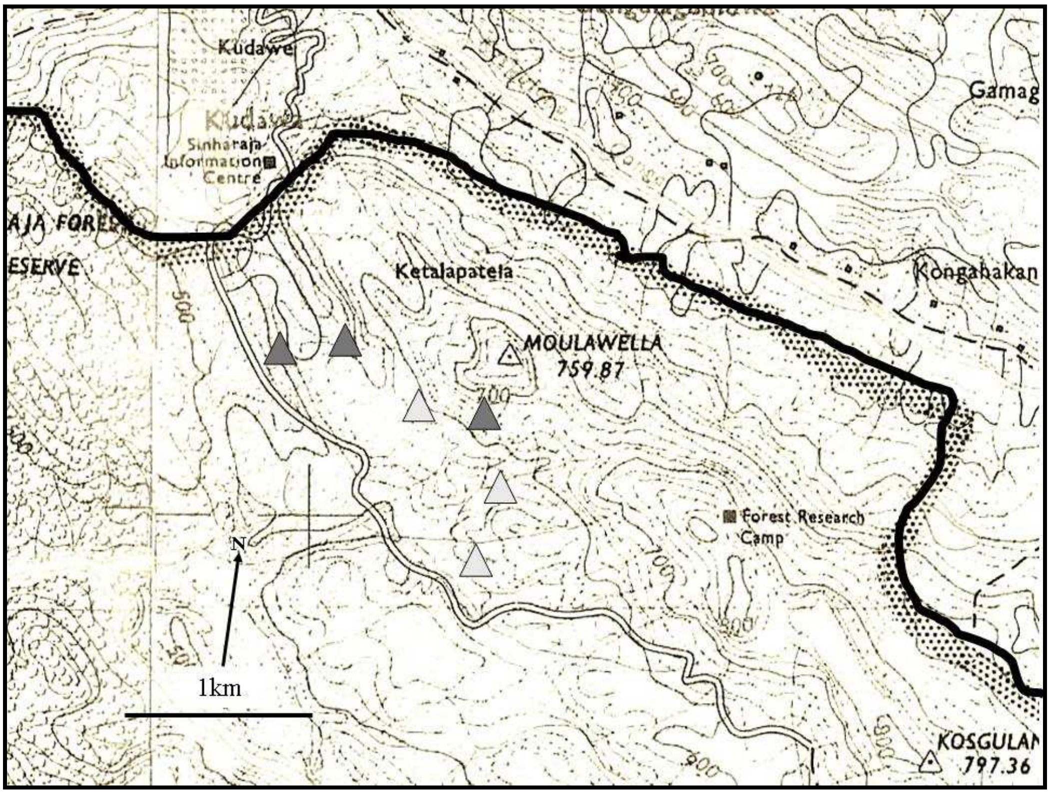

Figure 4.1. Sri Lanka Survey Department map of western Sinharaja Forest Reserve showing the location of the collection sites. The dark shaded triangles are the unlogged forest sites and the light shaded triangles are the logged forest sites.

Samples were taken within the old-logged forest (LF) and adjacent unlogged forest (UF) at three elevations along south-west facing ridges within western SFR (Figure 4.1). These areas are accessible through the old logging skid trails and are currently used by the Forest Department for tourism and education purposes. Five plots were established at ~500 m (low elevation), ~550 m (mid elevation), and ~600 m (high elevation) in each forest type. The five plots for each elevation (considered one site) within each forest type were at least 0.5 km horizontal distance from the next elevation. The logged sites were located at least 1 km from the unlogged sites, although the logged forest abutted the unlogged forest. Each plot measured 10 m by 10 m and all were spaced 20 - 25 m away from each other. When possible, these plots were located adjacent to each other but, due to the undulating topography of the area, some plots had to be accomodated further up the slope (Figure 4.2).

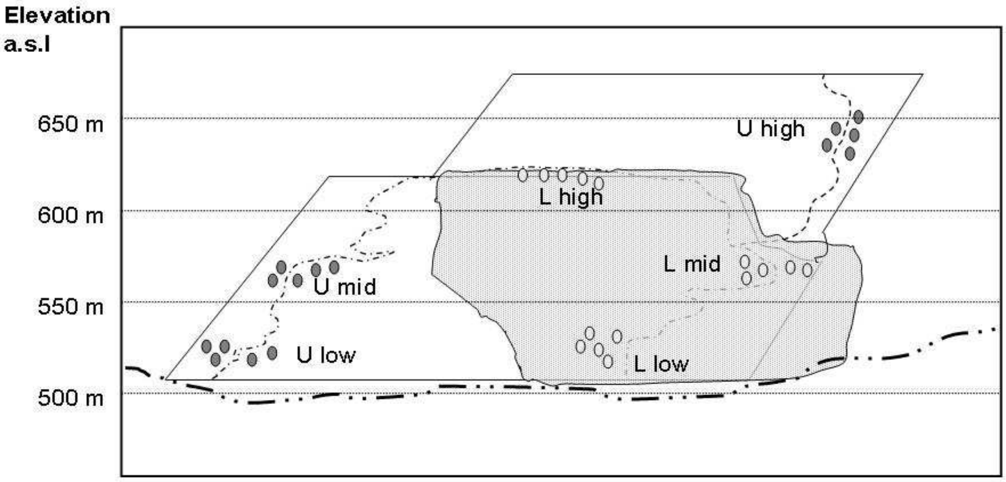

Figure 4.2. Location of the five plots within each site in the logged forest (L) and unlogged (U) along the visitor trails (light dotted lines) and the main access road (dark dotted line). There was a slight plateau at about 600 m where the L high plots were. Elevation range of the collection sites is also shown. The stippled area represents the extent of the logged forest within this area. The figure is not to scale.

4.2.2 Ant collection

Ants were collected using three established collecting methods: baiting, pitfall traps and Winkler extraction (Bestelmeyer *et al.* 2000). In each plot two baits were laid, four pitfall traps were placed 5 m apart, and 4 x 1 m^2 samples of litter were collected and sifted. At each plot, a protein bait (tinned mackerel) and a sugar bait (fruit jam) were laid out 2 m apart and left for 2 hours. Baiting was carried out between 9 am and 3 pm during each sampling period. The baits were laid out on pieces of 5 x 5 cm white card which were picked up at the end of the collection period and placed in sealed plastic bags. The samples were then sprayed with methylated spirits to kill the ants. The ants were then removed and stored in 70% ethanol and returned to the lab.

The pitfall traps (7 cm diameter plastic coffee cups filled with ~70 ml methylated spirits) were run for 72 hours. Ants were extracted from the litter using Winkler sacks. These were hung for 48 hours, with the litter being removed, shaken and returned after the first 24 hours. All ants were removed from the samples and sorted to morphospecies. Voucher specimens of each morphospecies were point-mounted and a reference collection created; all other specimens were stored in 70% ethanol. Ants were then identified to species where possible; where species could not be determined, a unique collection number was assigned. The mounted voucher specimens and wet collection are stored in the Peradeniya University Entomology Museum, with a representative mounted collection stored in the Curtin University of Technology Entomology Museum.

4.2.3 Environmental variables

Rainfall was measured daily throughout the year by a standard measuring gauge at the SFR Forest Research Camp (see Figure 4.1), located about 2 km from the study sites. The daily measurements were then averaged for the months during which the ant collections took place.

At each plot, four readings of the air temperature (1 m above ground level) and relative humidity (1 m above ground level and at ground level) were recorded using a Centre® 310 RS-232 humidity/temperature meter. Four readings of insolation at ground level were recorded using a TPS® MC-88 digital light meter. These four readings were averaged for each plot within each collection period. These variables were grouped as physical variables.

Ground cover characteristics of each plot were quantified by estimating the percentage coverage by bare ground, leaf litter, large rocks, and plant stems in a 1 m^2 quadrat. Also, in the same quadrat, the number of dead branches and tree trunks (>10 cm) were recorded and the depth of the leaf litter was measured using a ruler. Four of these quadrats were carried out in each plot in each collection period and averaged. This group represented the litter structure variables.

Canopy cover was estimated using a GRS® densitometer at 40 points within each plot in each collection period. Understorey foliage density was also estimated using a Levy pole (Majer 1981), with readings taken at four points within each plot.

The pole was divided into four intervals: 0 (ground)–50 cm; 51-100 cm; 101-150 cm; and 151–200 cm. The number of points where the pole was touched by vegetation was counted. At each interval, the number of plant touches for each of the four recordings was summed and divided by the total number of recordings taken for the plot over the course of the collection period (16 points within a plot). These variables were grouped as plant density variables.

4.2.5 Data analysis

All ant species occurrences and abundances were entered into separate matrices for each collection period for each forest type. For each plot, the data from the four pitfall traps, the four leaf litter samples and the two baits were combined. The data from the five plots were then further combined and total species richness and total ant abundance per site were calculated and log transformed to normalise variance. Each collection period, collection method, and forest type were compared using one-way analysis of variance (ANOVA) using Levene's test to check for homogeneity of variance. Data from the three methods and the four collection periods were then combined and tested again for significant differences between forest types using one-way ANOVAs.

The data was then converted into a presence/absence matrix for each forest type. Ants are social insects and tend to be aggregated in space and time (Longino 2000). This would affect abundance data analyses since some methods, particularly litter sampling methods, would most likely have captured entire colonies; hence, presence/absence data is more preferable for analysis. Species accumulation curves were run using the observed species richness as well as with values estimated by two commonly used species richness estimators, first-order Jack-Knife and Bootstrap (Colwell & Coddington 1994). These were then plotted against sampling effort to obtain an indication of whether there was adequate sampling to capture the majority of species that could be collected using the three methods. ANOVAs were carried out using SPSS 15.0, while species richness estimates were calculated using EstimateS (Colwell 2000).

Comparison of ant assemblages in the two forest types (logged/unlogged) was performed using a Bray-Curtis dissimilarity measure (Kruskal 1964), which allows the comparison of the ant assemblage at each site with every other site (Clarke &

Warwick 2001). Analysis of similarity (ANOSIM) was then run to find any significant differences between the two forest types. This Bray-Curtis matrix was then used to generate an ordination of plots using non-metric multi-dimensional scaling (MDS) of all the sites using 999 permutations of the data. The ANOSIM and the MDS was then run for each forest type using the three elevation groupings as a factor. These two tests were carried out using the program Primer v.6.1.9 permanova+β18.

The environmental variable measurements from each collection period were averaged for each plot and ln (x+1) transformed for homogeneity of variance (tested using Levene's Test) and the two forest types compared using multiple one-way ANOVAs (analysis of variance) using SPSS 15.0. In order to relate environment variables to the ant assemblage data, the BIO-ENV procedure in the above Primer package was utilised (Clarke & Warwick 2001). First, highly correlated (Spearman rank correlation $P < 0.05$) environmental variables were removed from the dataset so as not to cloud the matrix. Then the variables were ln (x+1) transformed to reduce the variance in the data, since all of them were skewed in their normal distribution curves. The BIO-ENV procedure then took the Bray-Curtis dissimilarity matrix of the ant assemblages and performed a rank correlation with a Euclidean distance matrix of the environmental variables. It then selected the best subset of environmental variables that was most closely related to the patterns of distribution in ant assemblages (Clarke & Gorley 2006). The data (biotic and abiotic) from logged and unlogged forest were analysed separately.

4.3 Results

4.3.1 Overview

A total of 125 species and morphospecies (hereafter included as species) were collected, with 101 species occurring in logged forest (LF) and 92 species occurring in unlogged forest (UF) (Appendix 4.1). The most speciose genera, *Pheidole, Tetramorium* and *Cerapachys,* were more or less evenly distributed across the two forest types, but the genera with only one species represented tended to be restricted to one forest type or the other. There were 16 species that were collected only in LF whereas only 9 were restricted to UF (Table 4.1).

Table 4.1. The number of species and morphospecies caught per genus in logged forest (L) and unlogged forest (U). Eleven subfamilies were represented by 47 genera from a total of 125 species and morphospecies.

Subfamily	Genus	L	U
Aneuretinae	*Aneuretus*	1	1
Amblyoponinae	*Amblyopone*	1	0
Aenictinae	*Aenictus*	1	2
Cerapachyinae	*Cerapachys*	7	7
Dolichoderinae	*Dolichoderus*	2	0
	Tapinoma	2	1
	Technomyrmex	2	2
Ectatomminae	*Gnamptogenys*	0	1
Formicinae	*Acropyga*	1	0
	Camponotus	4	4
	Forelophilus	1	0
	Lepisiota	0	1
	Myrmoteras	0	1
	Paratrechina	4	2
	Polyrhachis	2	2
	Pseudolasius	0	1
Leptanillinae	*Protanilla*	1	1
Myrmicinae	*Acanthomyrmex*	1	0
	Cardiocondyla	1	0
	Carebara	2	1
	Cataulacus	1	1
	Crematogaster	3	3
	Meranoplus	1	0
	Monomorium	2	2
Myrmicinae cont'd	*Myrmecina*	0	1
	Myrmicaria	1	2
	Pheidole	18	16
	Pheidologeton	1	2
	Pristomyrmex	1	1
	Pyramica	1	0
	Recurvidris	1	1
	Rhopalomastix	1	0
	Rogeria	1	0
	Solenopsis	1	2
	Strumigenys	4	3
	Tetramorium	15	12
	Vollenhovia	2	2
Ponerinae	*Anochetus*	3	2
	Cryptopone	1	1
	Discothyrea	0	1
	Harpegnathos	0	1
	Hypoponera	3	4
	Leptogenys	1	4
	Myopias	1	0
	Pachycondyla	3	3
	Ponera	1	1
Pseudomyrmicinae	*Tetraponera*	1	0
Total 11	**47**	**101**	**92**

The species accumulation curves for each forest type in terms of observed species and estimated species shows that the ant fauna of unlogged forest seems to be closer to reaching an asymptote than that of the unlogged forest (Figure 4.3). The Jack-Knife and Bootstrap estimate a further 33 and 14 species respectively can be found in LF, whereas only a 23 and 10 species can be found additionally in UF.

Although there was an indication that logged forest supported a higher species richness and abundance per plot (Figure 4.4), there were no significant differences between forest types for ant species richness and abundance when data from the three methods and four collection periods were combined (species richness, $F_{1,28} = 1.783$, $P = 0.192$; abundance, $F_{1,28} = 1.276$, $P = 0.268$). When methods were analysed individually, Winkler sack data displayed significant differences between collection period for both species richness ($F_{1,23} = 4.676$, $P = 0.012$) and abundance ($F_{1,23} = 3.633$, $P = 0.031$). Pitfall traps showed a significant difference between seasons in terms of species richness only ($F_{1,23} = 4.659$, $P = 0.013$), baiting data did not detect any significant differences between season. However, none of the datasets from the three methods demonstrated any significant differences between the two forest types in terms of species richness and abundance. Figure 4.5 shows the species richness values for each collection period plotted against the rainfall recorded for that month. While the differences were not significant when methods were combined, the LF exhibited a tendency for lower species richness to be recorded during the wetter collection periods, whereas the UF did not demonstrate any observable trends.

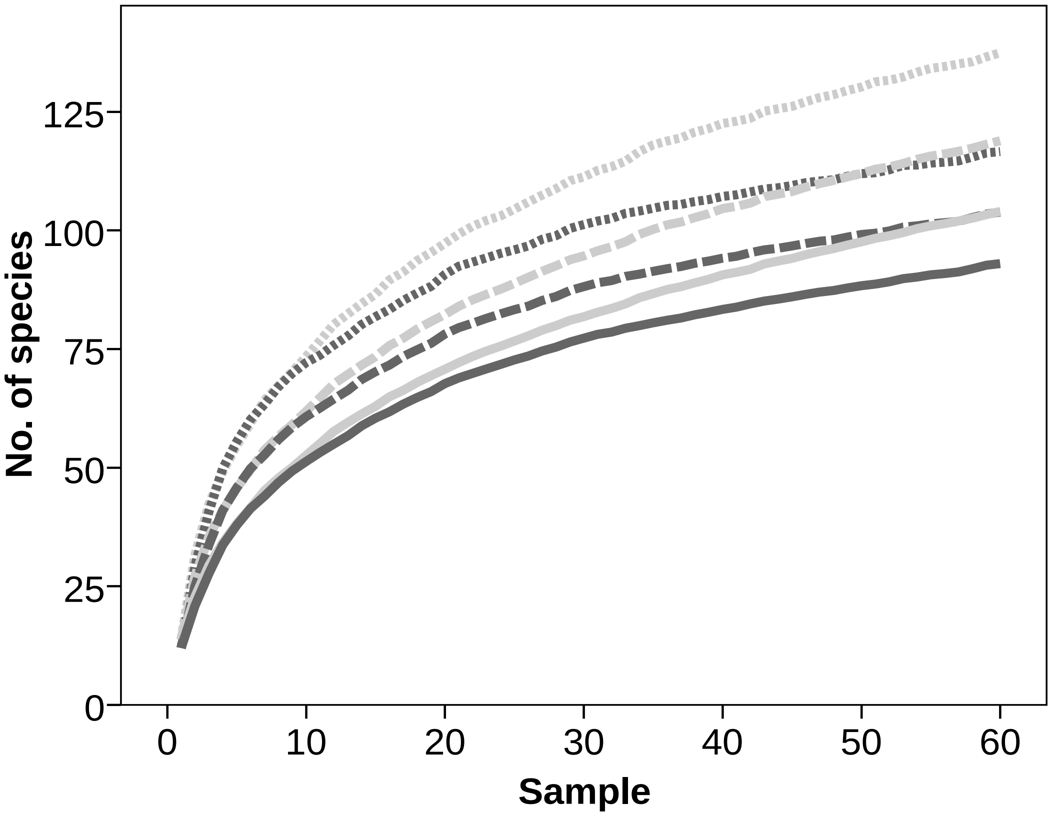

Figure 4.3. Observed species richness (solid lines) and species richness estimators Bootstrap (dashed lines) and Jack-Knife (dotted lines) for logged forest (light coloured lines) and unlogged forest (dark coloured lines). Logged forest had a steeper slope for all three species richness estimates.

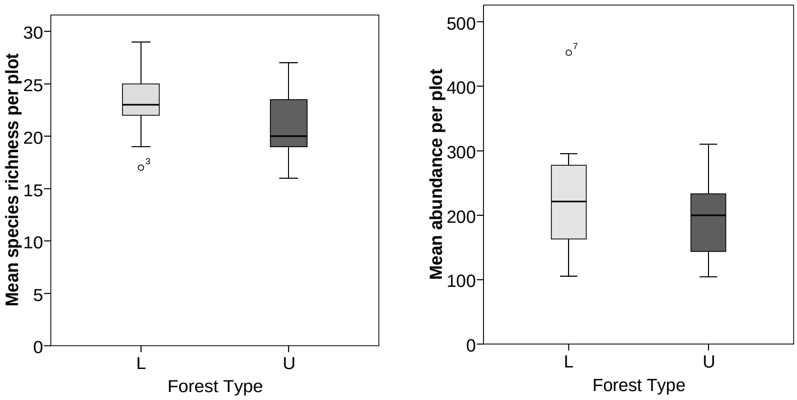

Figure 4.4. Average species richness and abundance in logged forest (L) and unlogged forest (U). Overall, logged forest supported a greater number of species and individuals than unlogged forest.

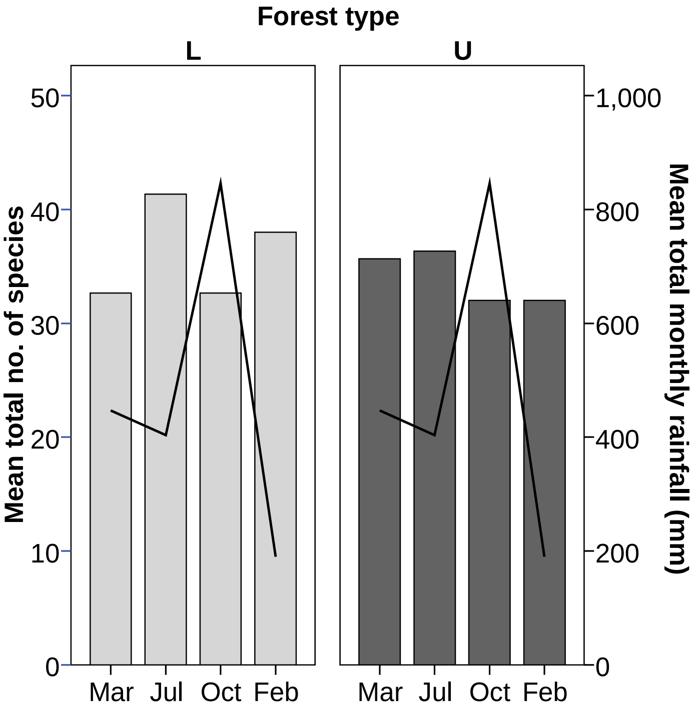

Figure 4.5. Total number of species in logged (L) and unlogged forest (U) plotted against total rainfall during the collection month. Trends in the logged forest suggest that higher rainfall may decrease the number of species collected whereas in unlogged forest this variable does not appear to respond to rainfall. Total abundances of ant species collected in the two forest types (not shown) exhibited similar trends.

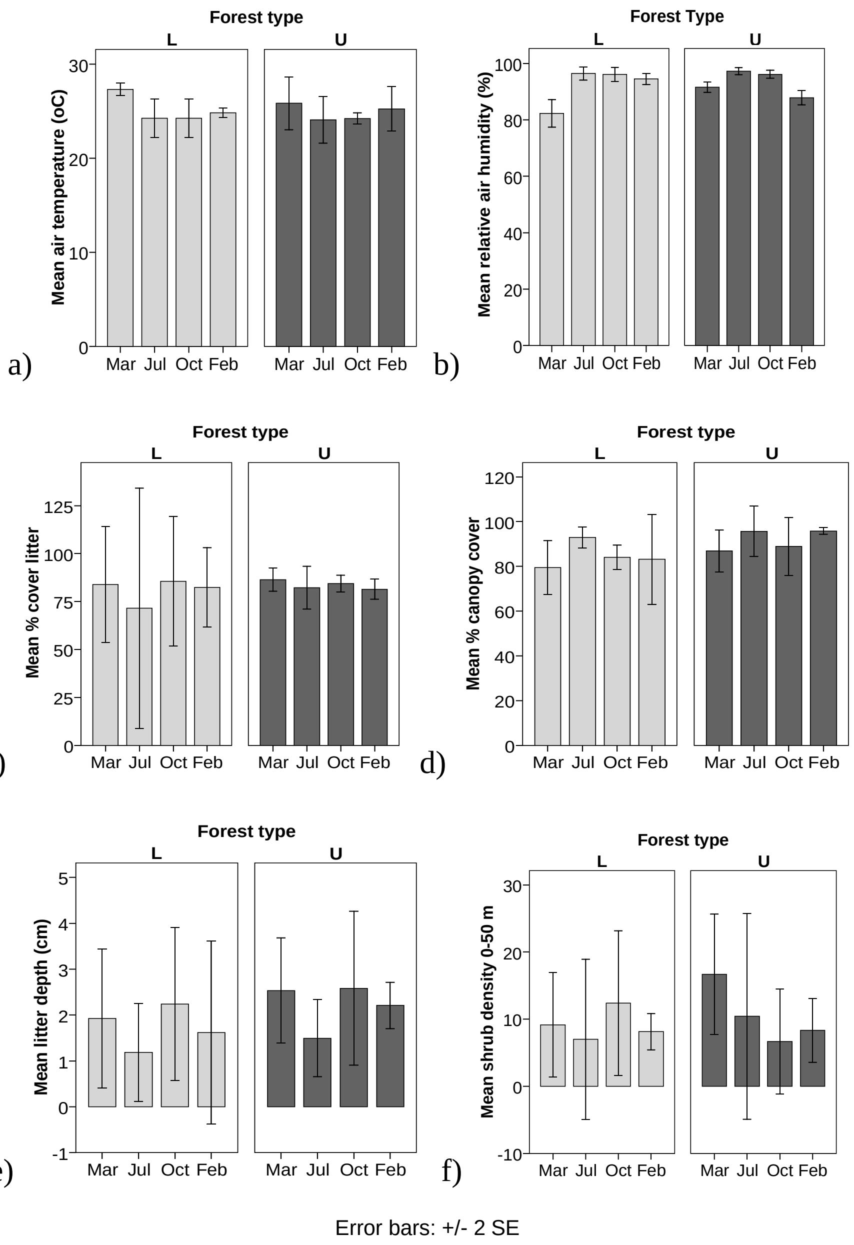

Figure 4.6. Mean results for six of the 15 environmental variables measured during the four sampling periods. The physical variables such as mean air temperature (a) and relative air humidity (b), displayed similar trends across collection period in logged forest (L) and unlogged forest (U). Percentage litter cover (c) appeared to be more variable within logged forest than within unlogged forest. Logged forest also showed less canopy cover (d) and litter depth (e) than unlogged forest. Mean foliage density (f) at the ground level was higher in the wetter months of March (Mar) and October (Oct) than in the drier months of July (Jul) and February (Feb) in the logged forest, but there were no discernible trends in unlogged forest.

4.3.2 Changes in the environment

Figure 4.6 shows six representative environmental variables and the trends suggest that the influence of rainfall on the environmental variables was also not very apparent in either forest type. Mean understorey air temperature showed similar trends in both LF and UF, with the warmer temperatures occurring in March and February. Opposite trends were shown with relative humidity (both air and soil), with the lowest humidity occurring in March and February.

The litter structure variables also exhibited a variety of trends, the most noticeable of which was the percentage cover of leaf litter. Logged forest showed much greater variability in its litter cover across sites within a collection period in comparison with UF, which appeared to be more uniform in its litter cover across collection periods. Mean litter depth, on the other hand, was variable across sites for both forest types but showed a general increase during the wetter months. Mean foliage density at 0-50 m, on the other hand, showed this trend only in logged forest, whereas unlogged forest appeared to have higher densities in the hotter months of March and February. Canopy cover (ANOVA; $F_{1,29} = 14.5$, $P = 0.001$) and litter depth (ANOVA; $F_{1,29} = 4.4$, $P = 0.045$) were the only environmental variables that were significantly different between the two forest types.

4.3.3 Changes in ant assemblages

There was a significant difference between the LF and UF in terms of ant assemblage (ANOSIM; Global R = 0.19, $P = 0.001$), which is clearly seen in the MDS diagram (Figure 4.7). There appears to be a greater spread of sites within the UF when compared to the LF. This is further demonstrated by looking at the differences between sites in each forest type. While there was a significant difference between LF sites (ANOSIM; Global R = 0.159, $P = 0.05$), they were much less significant when compared to the difference between UF sites (ANOSIM; Global R = 0.379, $P < 0.004$). Figure 4.8 shows the ordination of the plots in each site within each forest type. The difference between sites in the LF only appears to be between the lower and higher elevation plots, whereas the greatest difference in the UF is between the higher plots and all other plots (Table 4.2).

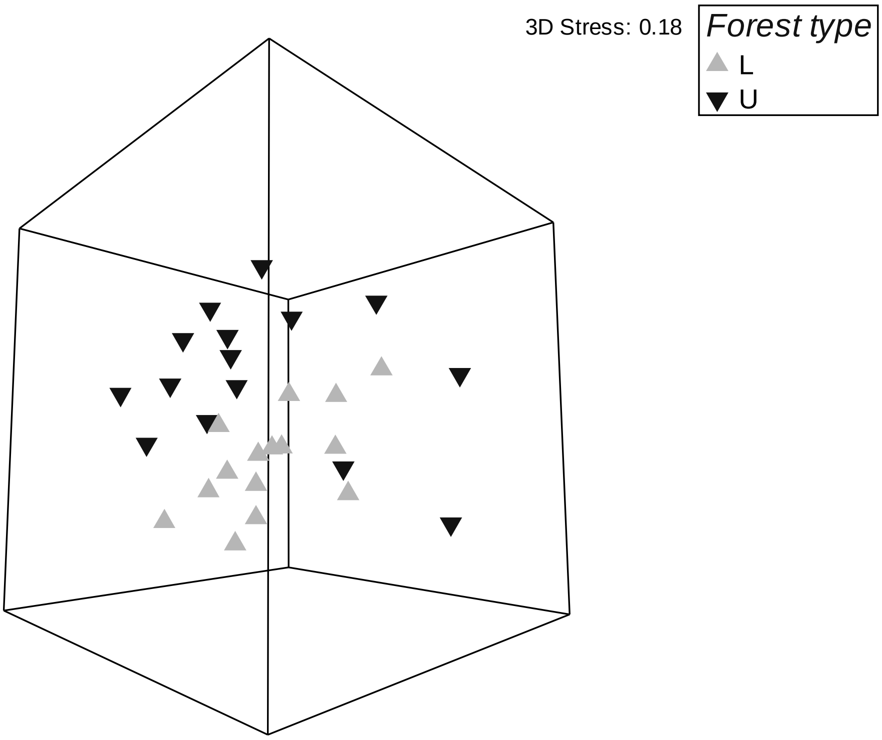

Figure 4.7. Multi-dimensional scaling (MDS) of sites in logged (L) and unlogged forest (U) using a Bray-Curtis similarity measure based on presence/absence data of all ant species. Logged forest appears to be more clumped in multi-dimensional space in comparison to unlogged forest, which has a greater spread around the logged forest assemblages.

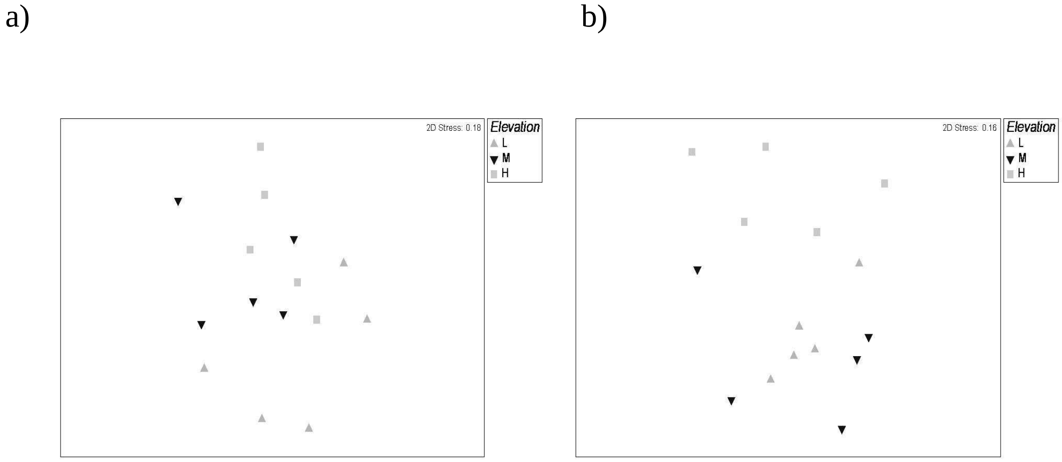

Figure 4.8. Ordination of all plots in two dimensional space within logged forest (a) and unlogged forest (b) showing the three elevation groupings: low (L); middle (M); and high (H).

Table 4.2. Analysis of variance (ANOVA) results for testing differences between elevation group in logged forest (a) and unlogged forest (b). Significance level (column 3) shows the degree of significance for each pairwise test carried out for each elevation group: low (L); middle (M); and high (H).

a)

Groups	R statistic	Significance	Possible	Actual	Number
L, M	0.074	0.286	126	126	36
L, H	0.270	0.048	126	126	6
M, H	0.136	0.183	126	126	23

b)

Groups	R statistic	Significance	Possible	Actual	Number
L, M	0.044	0.357	126	126	45
L, H	0.620	0.008	126	126	1
M, H	0.588	0.008	126	126	1

4.3.4 Relationship between ants and environmental variables

The BIO-ENV analysis for logged forest showed that a combination of the following five variables was associated with the ant species distribution at the highest correlation coefficient (Spearmans Rho = 0.316): relative air humidity, insolation, no. of branches, % canopy cover, and foliage density at 51-100 cm. Four important variables gave the highest correlation coefficient with ant species distribution in unlogged forest (Spearmans Rho = 0.207); these were air temperature, relative air humidity, litter depth, and foliage density at 101-150 cm.

4.4 Discussion

4.4.1 The forest after 30 years

The majority of visitors to Sinharaja forest do not realise that most of the forest they walk through has been logged and many are hard-pressed to tell the difference visually. In terms of the environmental variables measured, only canopy cover was significantly different; it could be indicative of an ongoing process that is preventing the canopy from fully reforming after logging. A potential hindrance to the recovery of the canopy is the rapid colonising ability of lianas in gaps left behind by logging. Burghouts *et al.* (1994) found that lianas contributed to a large percentage of the leaf fall in logged forest compared to unlogged forest. Increased litter fall from lianas and young trees in logging gaps would create a mosaic of leaf litter cover which could explain why the logged forest in this study had such variable leaf litter cover across the sites. Although not quantified, the liana and vine growth in the logged forest appeared to be denser than in the unlogged forest. It is possible that, as a result of the canopy openness in logged forest, greater numbers of lianas and vines can reach the canopy and topple small trees, thus maintaining the openness of the canopy. This structural change appears to be long-lasting as the differences still persist between logged and unlogged forest in some sites that were logged up to 60 years ago (Plumptre 1996; Kariuki *et al.* 2006).

A thorough study of plant species composition in the logged and unlogged forest would be necessary to see if there are any compositional differences between these two areas of western SFR. *Shorea megistophylla* was one of the tree species that was selectively logged in the SFR and, as a result of their reduced population densities, Murawski *et al.* (1994) found a greater amount of inbreeding in these trees in logged than in unlogged forest. This could potentially be affecting the regeneration potential of the logged forest to return to pristine forest tree species composition. The logged forest also contains some exotic species of tropical hardwood tree (e.g., mahogany) which were planted in an attempt to promote the future potential of the forest for logging concessions. The competitive success of these exotic trees may also be contributing to maintaining structural and compositional differences between the forest types (de Zoysa *et al.* 1991). Chapman and Chapman (1997) found that after 26 years, heavily logged forest in Kibale, Uganda, still had many gaps that had not been re-colonised by new tree growth. They suggested that one of the reasons for this lack of recovery was colonisation of these gaps by an aggressive herb or shrub layer, which prevented recruitment by forest trees. While mahogany would most likely contribute to closing canopy gaps, its interaction with native species of the SFR would need to be studied further in order to assess its affects on the forest.

4.4.2 Ant species richness post logging

Although ant species richness was not significantly different between the two forest types, the logged forest had a far greater number of species that were only found in that forest type. Although the biology of many of these species is still unknown, based on collections made outside of the forest there are at least four species that could be considered disturbed area inhabitants. Absent in unlogged forest, *Tapinoma* SL131, *Paratrechina* SL088, *Polyrhachis* SL085 and *Tetraponera* SL121 were common in plantations or roadsides outside of the forest (N. Gunawardene, unpublished data). The logged forest is most likely open enough or heterogeneous enough to allow for these ants to co-exist with forest dwelling ants.

The logged forest also supported more ant species overall, which is not unusual for disturbed habitats. The intermediate disturbance hypothesis (IDH) states that secondary or successional forest can maintain higher species diversities than climax forest, as long as low levels of disturbance prevent the forest from proceeding towards later stages of succession where diversity starts to decline (Connell 1978). It has generally been found that ant species will increase with increased habitat heterogeneity (Ribas & Schoereder 2007) and logging increases habitat heterogeneity by opening up of the canopy to provide large pockets of regenerating forest tree species together with gap specialists (Grieser Johns 1997). In naturally created canopy gaps (tree falls, landslides), increased intensity and availability of light promote new and rapid vegetation growth (Denslow 1987), which in turn increases herbivore abundances and their subsequent predators (Richards & Windsor 2007), of which ants form a large percentage (Richards & Coley 2007). Increased ant presence in gaps may also be a result of highly productive gap specialist plants being able to attract ants (using extra floral nectaries and food bodies) as a metabolically cheap form of defence against herbivory (Schupp & Feener 1991). Armbrecht *et al.* (2004) found that increasing the diversity of a resource (twigs), rather than simply the abundance of one resource type, augmented the diversity of twig-dwelling ants by 80% in a coffee agroecosystem in Colombia.

The fact that sampled ant species were reduced during periods of high rainfall in the logged forest, but not in the unlogged forest suggests that ants inhabiting logged forest are potentially more exposed to changes in the environment; their colonies may be locally extinguished or their activity may simply be reduced during such unfavourable periods. Kaspari and Weiser (2000) found that ants in Costa Rican rain forest were sensitive to desiccation, and activity was reduced during dry periods. Slightly higher average temperatures and lower average relative humidity in logged forest suggest a more exposed understorey environment. Ant species that would normally inhabit gap or edge type habitats would likely be able to cope with this sort of variable environment within the logged forest. This would contribute to elevating species numbers in the logged forest, as undisturbed forest specialists, gap specialists and forest edge generalists would tend to co-exist.

Previous studies involving invertebrates in the leaf litter have often used abundance and richness to compare assemblages in logged forest and unlogged forest

(Burghouts *et al.* 1992; Belshaw & Bolton 1993; Eggleton *et al.* 1995; Vasconcelos *et al.* 2000; Hassall *et al.* 2006) and in disturbed forests in general (Holloway *et al.* 1992; Watt *et al.* 2002; Dunn 2004). These studies have shown that while there is a difference in numbers, it is rarely significant, irrespective of the different logging intensities and different ages since logging was terminated. This study has shown the same trend by revealing tendencies, although it has not demonstrated a significant difference in ant species richness and abundances between the logged and unlogged forest.

Based on this alone, one could say that selective logging has minimal impact on the species richness of a given forest, regardless of the logging intensity. Given sufficient time, a forest can recover its species numbers. Other groups of animals have demonstrated such responses. Bats have shown recovery in numbers after logging (Clarke *et al.* 2005), as have amphibians (Pearman 1997), birds (Mason & Thiollay 2001) and non-volant small mammals (Wells *et al.* 2007). Grieser Johns (1997) concludes that, generally, vertebrates do not appear to exhibit local elimination or reduction in species richness in logged forest, as long as suitably large areas are studied. This is most likely due to their mobility and adaptability to changes in their environment. Dunn (2004) suggests that smaller, less vagile organisms would be more sensitive to habitat changes, but data are lacking in these groups.

4.4.3 Ant species assemblage post logging

Research to date has shown that both floral and faunal species composition of many groups do appear to shift as a result of the structural changes brought about by logging. Differences in ant species composition were quite significant in this study; up to a third (35 species out of 101) of the species in logged forest was collected in only logged forest and about one quarter (25 out of 92) of species collected in unlogged forest were unique to this forest type. The logged forest also appeared to be more uniform in assemblage make-up along the slope than the unlogged forest. In the unlogged forest, the ant assemblage of the higher elevation site was quite different from that at its two lower elevation sites. This could potentially be due to the fact that it was furthest away from all the other sites and also that it was situated at a slightly higher altitude (about 10-20 m higher than the high elevation logged plots). It has been demonstrated that even small changes in elevation can significantly affect the species composition along a slope (see Chapter 3). Changes in invertebrate species distribution at forest edges is also well documented in tropical forests, and is generally related to the changes in microclimate that occur as a result of the change in forest structure (Didham 1997). The low elevation sites (both logged and unlogged) were located closer to the main access road (50-100 m) and the low and middle elevation unlogged sites were located in forest that was contiguous with the logged area. These factors together would have contributed to differentiating the high unlogged site from the other unlogged sites and perhaps may have contributed to creating the greatest compositional variation between the two forest types.

Ant species assemblages in both forest types appeared to respond to environmental variables in all three categories, physical, litter structure and plant density. Relative humidity appeared to be an important factor in both forest types, which is understandable since ants are sensitive to desiccation. Kaspari and Weiser (2000) found ant activity to increase 200 % along a moisture gradient from ridge top to ravine bottom. Since both logged forest and unlogged foest sites were located along a slope, the small differences in humidity (lowest at the high elevation sites) may have influenced ant species distribution. Foliage density also seemed to be associated with the ants (albeit at different heights from the ground in the two forest types). This understorey structure would have provided secondary protection from rain and also food resources for ants. No discernible trend was found in the foliage densities in logged and unlogged forest although, contrary to expectations, unlogged forest had an average foliage density three times greater than logged forest. Research in other parts of the forest (unlogged) have demonstrated that stem density is higher on ridges in upper elevations (Gunatilleke *et al.* 2006); closer analysis of site topography would potentially allow further understanding of ant distribution. Perhaps in the future, analysis of canopy and shrub dwelling-ants may also give a clearer picture of the relationship with foliage density.

The logged forest ant assemblages were more closely correlated to the subset of environmental variables, which could be indicative of a greater influence of the environment on ants than in unlogged forest. One could argue that if the logged forest offers a more heterogeneous or variable environment, then the ants would respond more closely to these factors and distribute themselves according to their habitat preferences.

One would assume that the proximity of the logged sites to the unlogged sites and the contiguity of the forest in general would have contributed to the recovery of the logged forest plant diversity and thus, presumably, to faunal diversity as well. But despite this, there is still a distinct difference in ant species assemblages. Since there were no studies of ant species distribution before the logging occurred, it is difficult to conclusively say whether logging has truly changed the species assemblage or if these differences existed prior to logging. It would be beneficial to study the ant species assemblage in other parts of the SFR to see if there are marked differences between unlogged forest sites, ensuring such factors as elevation and aspect are kept the same. Even in this relatively small section of the SFR, a difference in ant species composition was detected between sites within an area of about 200 ha, which demonstrates the extraordinary diversity that can occur in a tropical forest. Future studies would benefit from looking at tree species composition in relation to ant species diversity in different parts of the forest to see whether there is discernible a relationship.

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4.6 Appendix

Table 4.3. Complete list of species collected from the Sinharaja Forest Reserve showing their presence in logged forest sites (L) and unlogged forest sites (U).

Subfamily	Genus	Species	L	U
Aneuretinae	*Aneuretus*	*simoni*	*	*
Amblyoponinae	*Amblyopone*	sp. SL128	*	
Aenictinae	*Aenictus*	*binghami*	*	*
Cerapachyinae	*Aenictus*	nr *punensis*		*
	Cerapachys	sp. SL011	*	
	Cerapachys	sp. SL026	*	*
	Cerapachys	sp. SL074	*	*
	Cerapachys	sp. SL104	*	
	Cerapachys	sp. SL106	*	*
	Cerapachys	sp. SL111		*
	Cerapachys	sp. SL130	*	
	Cerapachys	sp. SL144		*
Dolichoderinae	*Dolichoderus*	sp. SL075	*	
	Dolichoderus	sp. SL089	*	
	Tapinoma	sp. SL056	*	*
	Tapinoma	sp. SL131	*	
	Technomyrmex	*albipes*	*	*
	Technomyrmex	*bicolor*	*	*
Ectatomminae	*Gnamptogenys*	*laevior* gp.		*
Formicinae	*Acropyga*	sp. SL093	*	
	Camponotus	sp. nr *infuscus*	*	*
	Camponotus	sp. nr *angusticollis*	*	*
	Camponotus	sp. SL083	*	*
	Camponotus	sp. SL138	*	*
	Forelophilus	sp. SL092	*	
	Lepisiota	sp. nr *capensis*		*
	Myrmoteras	*binghami*		*
	Paratrechina	sp. SL001	*	*
	Paratrechina	sp. SL036	*	*
	Paratrechina	*bourbonica*	*	
	Paratrechina	*minutula* gp	*	
	Polyrhachis	*hippomanes*		*
	Polyrhachis	*bugnioni*	*	*
	Polyrhachis	*illaudata*	*	
	Pseudolasius	sp. SL140		*
Leptanillinae	*Protanilla*	sp. SL108	*	
	Protanilla	sp. SL129		*
Myrmicinae	*Acanthomyrmex*	*luciolae*	*	
	Cardiocondyla	*wroughtoni*	*	*
	Carebara	sp. SL012	*	*
	Carebara	sp. SL112	*	
	Cataulacus	*latus*	*	*
	Crematogaster	sp. SL022	*	
	Crematogaster	sp. SL062	*	*
	Crematogaster	sp. SL119		*

Table 4.3 cont’d

Subfamily	Genus	Species	L	U
Myrmicinae	*Crematogaster*	sp. SL136	*	
(cont’d)	*Meranoplus*	*loebli*	*	
	Monomorium	*floricola* gp	*	*
	Monomorium	*hildebrandti* gp	*	*
	Monomorium	*destructor* gp	*	
	Myrmecina	*curtisi*		*
	Myrmicaria	*brunnea*	*	*
	Myrmicaria	sp. A		*
	Pheidole	sp. SL006	*	*
	Pheidole	sp. SL019	*	*
	Pheidole	sp. SL027	*	*
	Pheidole	sp. SL028	*	*
	Pheidole	sp. SL029	*	*
	Pheidole	sp. SL030	*	*
	Pheidole	sp. SL049		*
	Pheidole	sp. SL063	*	*
	Pheidole	sp. SL064		*
	Pheidole	sp. SL067	*	*
	Pheidole	sp. SL070	*	*
	Pheidole	sp. SL077	*	*
	Pheidole	sp. SL091	*	*
	Pheidole	sp. SL0Za	*	*
	Pheidole	sp. SL0Zb	*	*
	Pheidole	sp. SL0Zc	*	*
	Pheidole	sp. SL107	*	
	Pheidole	sp. SL142	*	
	Pheidologeton	sp. SL013	*	*
	Pheidologeton	sp. SL141		*
	Pristomyrmex	sp. nr *profundus*	*	*
	Pyramica	sp. SL143	*	
	Recurvidris	*pickburni* sp. nv.	*	*
	Rhopalomastix	*rothneyi*	*	
	Rhopalothrix	sp. SL102	*	
	Rogeria	sp. SL057	*	
	Solenopsis	sp. SL038	*	*
	Solenopsis	sp. SL113		*
	Strumigenys	sp. sl-01	*	*
	Strumigenys	sp. sl-02	*	*
	Strumigenys	sp. SL098	*	*
	Strumigenys	sp. SL109	*	
	Tetramorium	sp. SL002	*	*
	Tetramorium	sp. SL015	*	*
	Tetramorium	sp. SL020	*	*
	Tetramorium	sp. SL054	*	*
	Tetramorium	sp. SL055	*	*
	Tetramorium	sp. SL058	*	*
	Tetramorium	sp. SL059	*	
	Tetramorium	sp. SL05A	*	*
	Tetramorium	sp. SL05B	*	*
	Tetramorium	sp. SL082	*	*
	Tetramorium	sp. SL117	*	*

Table 4.3 cont'd

Subfamily	Genus	Species	L	U
Myrmicinae (cont'd)	*Tetramorium*	sp. SL118		*
	Tetramorium	sp. SL123	*	*
	Tetramorium	sp. SL127	*	
	Tetramorium	sp. SL134	*	
	Tetramorium	sp. SL135	*	
	Vollenhovia	sp. SL033	*	*
	Vollenhovia	sp. SL115	*	*
Ponerinae	*Anochetus*	sp. nr *longifossatus*	*	
	Anochetus	sp. nr *nietneri*	*	*
	Anochetus	sp. nr *longifossatus*	*	*
	Cryptopone	*testacea*	*	*
	Discothyrea	sp. SL050		*
	Harpegnathos	*saltator*		*
	Hypoponera	sp. SL016	*	*
	Hypoponera	sp. SL051		*
	Hypoponera	sp. SL052		*
	Hypoponera	sp. SL066	*	
	Hypoponera	sp. SL114	*	*
	Leptogenys	sp. SL041		*
	Leptogenys	sp. SL065	*	*
	Leptogenys	sp. SL072		*
	Leptogenys	sp. SL125		*
	Myopias	*amblyops*	*	
	Pachycondyla	*rufipes*	*	*
	Pachycondyla	*melanaria*	*	*
	Pachycondyla	*sulcata*	*	*
	Pachycondyla	*truncata*	*	*
	Ponera	sp. SL048	*	*
Pseudomyrmicinae	*Tetraponera*	*difficilis*	*	

5. Ant species assemblages in relation to tree species distribution and habitat type in a Forest Dynamics Plot in Sinharaja Forest Reserve, Sri Lanka

Abstract

Species distribution across a landscape can be attributed to a variety of spatial and temporal factors. In this study, ant species distribution in lowland dipterocarp dominated forest in Sri Lanka was analysed in relation to habitat heterogeneity and tree species composition. Four collections over a 1 year period revealed a high diversity of ground dwelling ant species. A total of 102 ants in 5 ha were collected, with significant differences in composition (P = 0.006) from valley bottom to ridge top. Ants were found to respond more to structural heterogeneity of vegetation rather than tree species richness, although ant species and tree species distribution were highly correlated (P = 0.003). The present study contributes to further understanding the distribution of the rich species diversity found in the Sinharaja Forest Reserve and highlights the need to protect entire slopes in a topographically heterogeneous forested landscape.

Keywords: habitat heterogeneity, species richness, species composition, tropical forest, Formicidae

5.1 Introduction

The vast diversity found in tropical ecosystems has spawned many theories regarding the co-existence of so many species (Rosenzweig 1995; Richards 1996; Pimm & Brown 2004). Examining the distribution of individuals across a landscape can give insight into the ecological interactions of a particular group (Condit *et al.* 2000; Theunis *et al.* 2005). Understanding how species distribute themselves and utilise resources is key to better assessments of biodiversity, hence improving the formulation of conservation and management plans for areas within which they live (Kremen *et al.* 1993; Leponce *et al.* 2004).

Many studies have found that ‘habitat heterogeneity’ or ‘habitat diversity’ can determine animal species diversity. Tews *et al.* (2004) reviewed 85 publications and found that 85% of the studies found positive relationships between animal species diversity and the vegetation structural variables measured. They introduce the term ‘keystone structure,’ a distinct spatial structure that is specific to the spatial scale of the taxon under study and which provides resources for that particular taxon. In most ecosystems, plant species composition and distribution will influence habitat structural heterogeneity (Tews *et al.* 2004) but the patchiness of distribution and low densities of tree species in tropical forests is still not well understood (Richards 1996). Tree species can directly influence animal diversity by providing food resources, affecting light availability and microclimate, providing substrate resources, and changing soil resource qualities (Palik & Engstrom 1999). In terms of ground dwelling arthropods, tree species determine litter quality and density (by periodicity and synchronicity of leaf fall (Burghouts *et al.* 1994)) and provide food resources, such as seeds (Levey & Byrne 1993) and nectar (Dejean 1991).

Ants are ubiquitous in almost all regions of the world and in many levels of ecosystem functioning (Holldobler & Wilson 1990). They can easily constitute up to 15% of arthropod biomass in a given ecosystem (Fittkau & Klinge 1973; Sudd & Franks 1987), and sometimes up to 50% in a particular stratum (Yanoviak & Kaspari 2000). Ant species tend to be patchily distributed, especially in tropical ecosystems (Levings & Franks 1982; Kaspari 1996). The possible drivers for this patchy distribution, specifically in ground dwelling ants, are continually being studied. Ribas and Schoereder (2007) found that tree density and structural heterogeneity affected ant species composition and increased structural heterogeneity, leading to increased ant species richness. Others have found ant species distributions to be related to leaf litter quantity and litter weight (Theunis *et al.* 2005) and local topography (Catterall *et al.* 2001; Vasconcelos *et al.* 2003). Experiments conducted by Armbrecht *et al.* (2004) showed that increased litter twig heterogeneity increased ant species diversity, although twig (tree) species composition did not appear to be the determining factor.

In the Asian tropics, the forests are dominated by the Dipterocarpaceae family of trees, known for their towering heights, large, wind-dispersed fruit and their irregular but synchronous mast-fruiting (Corlett 2007). They are insect-pollinated and obligately ectotropic mycorrhizal (Ashton 1988). But the relationship between the distribution of these trees and the distribution of arthropod fauna has been little studied.

Due to the need for long-term research on tropical trees in general, a number of forest dynamics research plots were set up by the Centre for Tropical Forest

Science under the auspices of the Smithsonian Tropical Research Institute. The Sinharaja Forest Dynamics Plot (FDP) was set up in 1993 in the Sinharaja Forest Reserve (SFR), a UNESCO World Heritage Site in south-west Sri Lanka (Gunatilleke *et al.* 2004b). A plot measuring 500 x 500 m was laid out in undisturbed forest in the western portion of the reserve and every tree greater than 1 cm in diameter at breast height was tagged, identified and measured (see Manorkan *et al.* (1990) and Condit (1995) for further details). Previous research on this and other plots within the forest has allowed researchers to look at tree species distribution in great detail and the continuous monitoring of tree phenology within the FDP has given many insights into the community organisation of the forest (Gunatilleke & Gunatilleke 1985; de Zoysa *et al.* 1991; Gunatilleke *et al.* 2004a). Gunatilleke *et al.* (2006) have summarised many of the findings to date on SFR and on the FDP and have investigated the relationships between tree species and habitat.

The existence of this body of work in the FDP by C.V.S. and I.A.U.N. Gunatilleke provided an opportunity to explore in detail the underlying relationship between tree species and an important arthropod group. The objective of this study is to utilise the tree species distribution and habitat data from the FDP to perform an analysis of ant species distribution in relation to structural and compositional heterogeneity in a tropical, lowland, wet forest in Sri Lanka. Ecological data on arthropod biota in Sri Lanka is limited and this will be the first study looking at ants in relation to tree species distribution in this forest. The results from this study will contribute to a growing body of data regarding the unique biodiversity of the SFR and Sri Lanka, as well as to the further understanding of ant species distributions in tropical rain forests.

5.2 Methods

5.2.1 Study Site

The 11,000 ha Sinharaja Forest Reserve (SFR) is a mixed dipterocarp (*Mesua-Shorea* type), lowland, wet forest in south-western Sri Lanka (6° 21-26’ N, 80° 21-34’ E). It has an elevation range of 300 m to 1200 m a.s.l. and receives between 4000 – 5000 mm of rain annually, with no period where the average monthly rainfall drops below 60 mm (IUCN 1993). The forest receives monsoonal rain from May to June (south-west monsoon) and from September to November (north-east monsoon), resulting in higher rainfall in these two perionds.

The 25 ha FDP is located in western SFR (6° 24’ N, 80° 24’) E, in an undisturbed area between the reserve border and an old-logged forest section (> 30 years old) (Figure 5.1). The collections were carried out in the northern quarter of the FDP, along its south-west facing slope (Figure 5.2). The topography of the FDP is highly variable, with a central valley containing a small stream and an elevation range of 424 – 575 m; the largest range in elevation is found on the south-west facing slope (Gunatilleke *et al.* 2004b). The FDP is divided into 625 quadrats 20 x 20 m in size. In each of these quadrats all trees greater than 1 cm diameter at breast height (d.b.h.) have been measured, tagged and identified and the habitat is categorised according to elevation, slope and convexity (Gunatilleke *et al.* 2006). Figure 5.3 shows the habitat categorisations of each of the quadrats in the FDP.

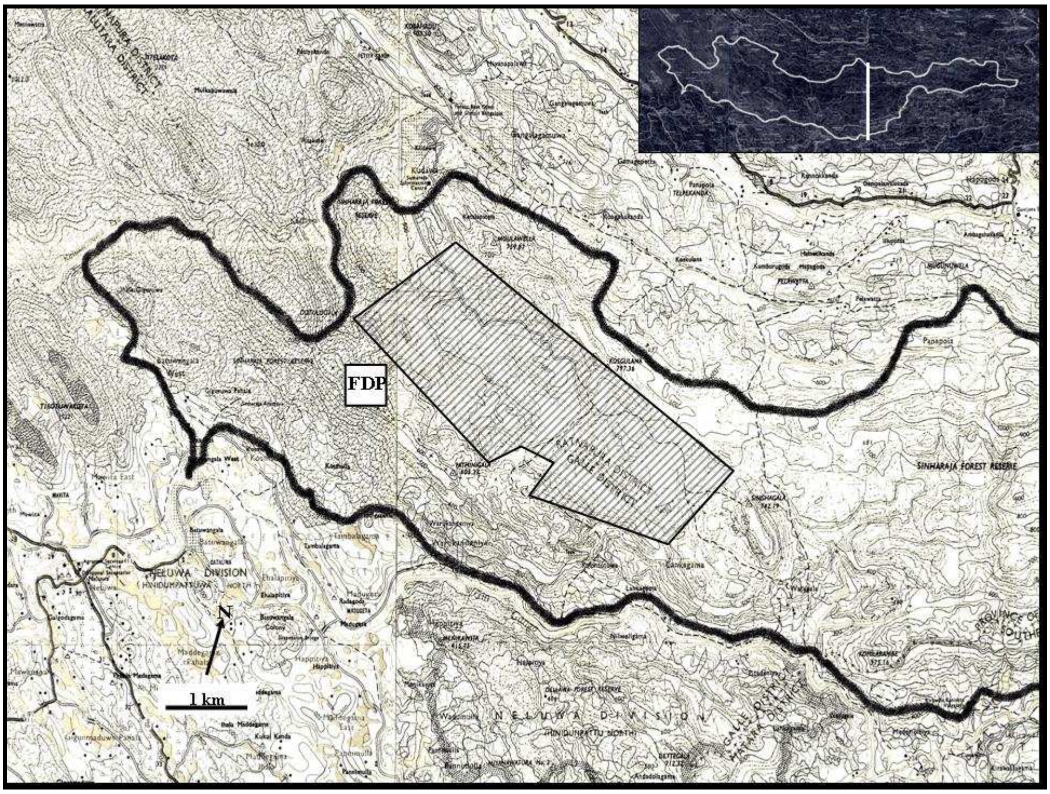

Figure 5.1. Sri Lanka Survey Department map showing the location of the 25 ha Forest Dynamics Plot (FDP) in the western portion of Sinharaja Forest Reserve (see inset for outline of entire reserve). The stippled area indicates where selective logging occurred in the reserve between 1972 and 1977.

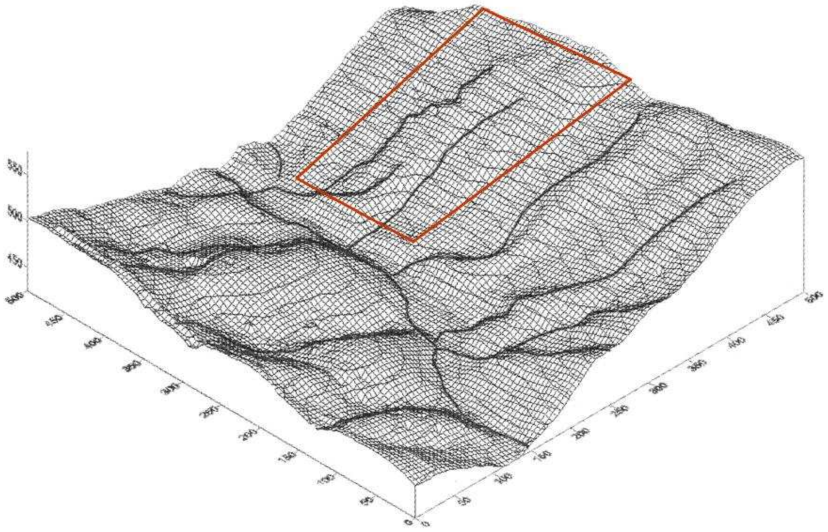

Figure 5.2. Topographical map of the 25 ha Forest Dynamics Plot (FDP) showing the elevation range of the site. The black lines along the slopes represent small drainage lines, while the line traversing the valley bottom is a permanent stream. The boxed area in red indicates the study area. Image is taken from Gunatilleke *et al*. 2004b.

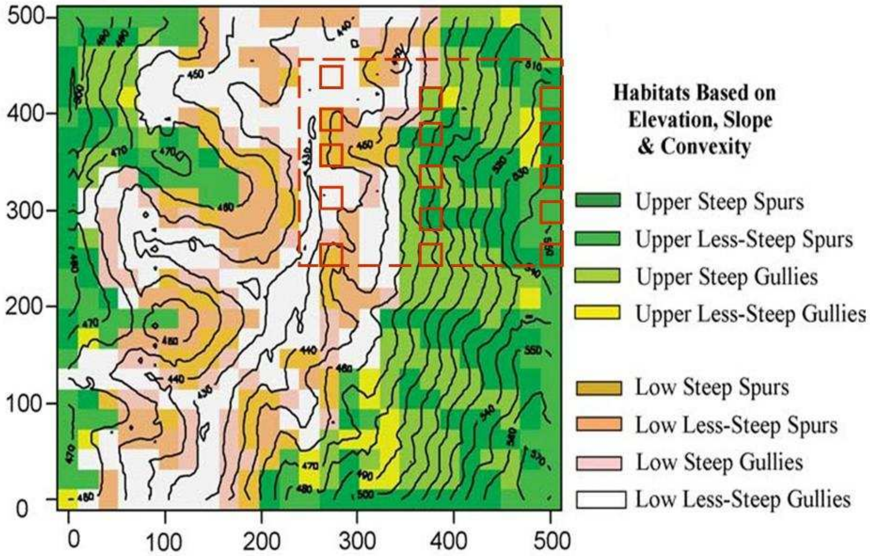

Figure 5.3. Contour map of the 25 ha Forest Dynamics Plot (FDP), indicating the 15 collection plots (red squares) and the habitat types defined by Gunatilleke *et al*. (2006) (map modified from Gunatilleke *et al*. 2006). Plots were laid out along the south-west facing slope from valley bottom (420 - 430 m) to ridge top (520 - 550 m).

Ants were collected in five 10 x 10 m plots, centred within the larger 20 x 20 m FDP quadrat. These plots were located along three parallel transects spaced 100 m apart on the south-west facing slope (Figure 5.3). Transects were labelled 1 to 3 from the top of the slope to the bottom. All fieldwork was carried out during four collection periods in 2006 (late March, early June, late August, late November). This high intensity sampling was done so as to eliminate potential effects of variable rainfall, as moisture availability has been shown to affect ant species activity, even in tropical wet forests (Kaspari & Weiser 2000).

5.2.2 Ant sampling

Ants were sampled using two established methods for invertebrate collection, Winkler extraction and pitfall trapping (Bestelmeyer *et al.* 2000). In each plot, four leaf litter collections and four pitfall traps were set out to maximise the number of leaf litter ants collected. Leaf litter was collected in a 1 x 1 m quadrat and was sifted using a Winkler litter sifter. The sifted material was then hung inside a Winkler sack for 48 hours, with the leaf litter being removed and shaken after the first 24 hours. All material collected in the Winkler sack was then removed and placed in 70% ethanol.

The pitfall trap consisted of a standard plastic drinking cup (mouth diameter 8 cm) which was inserted into the ground and left for 1 week before being filled with ~70 ml of methylated spirits. The pitfalls were then capped with another plastic cup with large triangles cut out of the sides to provide a lid to prevent rainfall from flooding the cup. After 72 hours, the material in the cups was collected and the cups left in the ground filled with leaf litter for use in the next sampling period. The material was washed with fresh methylated spirits and returned to the lab.

All invertebrate material was removed from the Winkler and pitfall samples and stored in 70% ethanol. The ants were subsequently separated from the invertebrate material and point mounted and identified to morphospecies. Once a reference collection of point mounted specimens was created, all excess ants were stored in 80% ethanol. Ants were identified to species where possible with certain genera being sent to specialists for confirmation of species. The wet and dry specimens are housed in Peradeniya University Entomology Museum and a mounted voucher collection is stored in the Curtin University Entomology Museum.

5.2.3 *Habitat structure and vegetation diversity*

Ground cover characteristics of each plot were quantified by estimating the percentage coverage by bare ground, leaf litter, large rocks, and plant stems in a 1 m^2 quadrat. Also, in the same quadrat, the number of dead branches and tree trunks (>10 cm) were recorded and the depth of the leaf litter was measured using a ruler. Four quadrats were measured in each plot in each collection period and the resulting data averaged. This group represented the litter structure variables.

Canopy cover was estimated using a GRS® densitometer at 40 points within each plot in each collection period. Understorey foliage density was also estimated using a Levy pole (Majer 1981), with readings taken at four points within each plot. The pole was divided into four intervals: 0 (ground)–50 cm; 51-100 cm; 101-150 cm; and 151–200 cm. The number of points where the pole was touched by vegetation was counted. At each interval, the number of plant touches for each of the four recordings was summed and divided by the total number of recordings taken for the plot over the course of the collection period (16 points within a plot). These variables were grouped as plant density variables.

The habitat categories used by Gunatilleke *et al.* (2006) were utilised for characterising the topography of the FDP quadrats within which ants were collected. They defined eight categories based on three habitat characteristics: above or below average elevation of the plot (460 m); above or below average slope degree (25°); and above or below average convexity. Each quadrat was thus either high elevation or low elevation, steep or less steep, and either a 'spur' or a 'gully.'

Tree species data were taken from the 2002 census data made available by C.V.S. Gunatilleke and I.U.A.N. Gunatilleke. Tree species diversity was measured as the total number of species present in each FDP quadrat within which ants were collected. Vegetation density was measured as the total number of stems per FDP quadrat. Tree species stem densities per quadrat were entered into a site matrix and designated as the tree species composition matrix.

5.2.4 Data analysis

For each plot, the ant data from the four pitfall traps and the four leaf litter samples were combined. The data from each collection period was then combined for each of the 15 plots. Species richness and abundance were calculated for each plot. Ant species for which only one individual was collected were also eliminated from the matrix, since it is possible that these ants were not litter or surface dwelling ants, i.e. they were possibly ‘tourists’ from the canopy. The data were then converted into a presence/absence matrix. Ants are social insects and tend to be aggregated in space and time (Longino 2000), this would affect abundance data analyses since some methods, particularly litter sampling methods, would most likely have captured entire colonies. For this reason, presence/absence data is more preferable for analysis.

Univariate comparisons of each of the three habitat characteristics (elevation, convexity and slope) were carried out using independent-sample Mann-Whitney U tests of ant species richness per plot, total ant abundance per plot, tree species richness and stem density per FDP quadrat. Non-parametric tests were carried out using SPSS 15.0. Differences in ant species composition per plot and tree species composition per FDP quadrat in terms of the habitat characteristics were analysed using a Bray-Curtis dissimilarity measure (Kruskal 1964). These differences were tested for significance using analysis of similarity (ANOSIM). Ant species and tree species that contributed the most to significantly differentiating any of the three habitat variables were identified by a decomposition of the Bray-Curtis dissimilarity matrix. This was carried out using the SIMPER function in Primer v.6.1.9 permanova+β18. Ant species distribution patterns across the 15 sites were then compared with tree species distribution patterns (square root transformed total stem density) using the RELATE procedure in Primer v.6.1.9 permanova+β18. This procedure is a non-parametric form of the Mantel test comparing the Bray-Curtis similarity matrices and measuring the agreement between two independent patterns (ants and trees) by performing a rank correlation (Clarke & Gorley 2006).

The ant species Bray-Curtis dissimilarity matrix was then analysed with five of the 11 structural variables (correlated variables removed ($r > 0.80$)), tree species richness and stem density per plot using a multivariate regression procedure DISTLM (distance based linear models, Anderson (2004)). These seven variables were ln (x+1) transformed to reduced variance. The 'Best' fit selection procedure was utilised (using AIC model selection criterion) to determine which variables best explained the variation in species assemblage clouds. The model with the best predictors was fitted against a distance based redundancy analysis (dbRDA, Legendre and Andersen (1999); McArdle and Anderson (2001)), which performs a constrained ordination of sample sites using the same Bray-Curtis dissimilarity matrix of the ant data. DISTLM and dbRDA procedures were run using Primer v.6.1.9 permanova+β18.

5.3 Results

5.3.1 Ant and tree species diversity

A total of 102 ground dwelling ant species were collected in 5 ha of forest within the FDP of Sinharaja (Table 5.1). The most abundant ants were *Paratrechina* sp. SL001, *Technomyrmex bicolor* and *Aneuretus simoni*, which were also among the most commonly occurring ants as well (Table 5.2). There were 27 ant species that were represented by one specimen (singletons) and 35 that were unique to one plot.

Table 5.1. Ant species and abundances caught by the two collection methods in each season. Daily rainfall was measured at the Sinharaja Forest Reserve field station and totalled for the month during which the collection occurred.

Method	Collection period	Total no. of species	Abundance	Total monthly rainfall (mm)	No. of dry days/ month
Winkler	March	43	1805	245.6	14
	June	59	1280	474.7	12
	August	31	242	425.8	8
	November	45	818	651.9	10
Pitfall	March	36	198	245.6	14
	June	37	207	474.7	12
	August	45	268	425.8	8
	November	35	172	651.9	10
	Total	**102**	**4990**	**1798.0**	**44**

Table 5.2. Species list showing the frequency of occurrence (Freq) and abundance (Ab) of each species collected in the three transects.

Genus	Species	Freq	Ab	1	1	1	1	1	2	2	2	2	2	3	3	3	3	3
Strumigenys	sp. sl-01	15	133	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Strumigenys	sp. sl-02	15	127	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Technomyrm	*bicolor*	15	682	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Tetramorium	sp. SL054	15	76	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Aneuretus	*simoni*	14	620	*	*	*	*	*	*	*	*	*	*	*	*	*		*
Paratrechina	sp. SL001	14	723	*	*	*	*	*	*	*	*	*	*	*		*	*	*
Tetramorium	sp. SL002	14	230	*	*	*	*	*	*	*		*	*	*	*	*	*	*
Carebara	sp. SL012	13	109		*	*	*	*	*	*	*	*	*	*	*	*		*
Pristomyrme	sp. nr	13	75	*	*	*	*	*		*	*	*	*	*	*	*		*
Technomyrm	*albipes*	13	217	*		*	*	*	*	*	*	*	*		*	*	*	*
Tetramorium	sp. SL117	12	34	*		*	*			*	*	*	*	*	*	*	*	*
Monomoriu	*floricola* gp.	11	71	*	*	*	*		*	*	*		*		*	*		*
Pheidole	sp. SL027	11	39		*	*			*	*	*	*	*	*	*	*		*
Vollenhovia	sp. SL033	11	38	*	*	*	*	*	*	*		*	*	*				*
Anochetus	sp. nr *nietneri*	10	16	*	*		*	*			*	*		*		*	*	*
Hypoponera	sp. SL016	10	101			*			*		*	*	*	*	*	*	*	*
Paratrechina	sp. SL036	10	220		*		*	*	*	*			*	*	*		*	*
Pheidole	sp. SL028	10	62		*	*	*	*		*				*	*	*	*	*
Pheidole	sp. SL142	9	53	*	*		*	*	*				*	*	*			*
Tetramorium	sp. SL05B	9	19	*	*	*		*	*	*		*	*		*			
Leptogenys	sp. SL065	8	49	*	*		*	*	*	*					*	*		
Pheidole	sp. SL030	8	216			*	*	*			*	*	*	*				*
Pheidole	sp. SL070	8	31	*		*	*	*			*	*		*				*
Pheidole	sp. SL091	8	26	*	*		*	*				*		*	*	*		
Tetramorium	sp. SL134	8	21	*	*						*	*		*	*		*	*
Monomoriu	*destructor* gp.	7	51	*	*				*	*	*		*					*
Pheidole	sp. SL077	7	49				*		*	*	*		*	*		*		
Tetramorium	sp. SL058	7	22	*				*		*		*	*	*				*
Tetramorium	sp. SL05A	7	11	*					*			*		*		*	*	*
Myrmicaria	*brunnea*	6	33	*	*	*	*	*				*						
Tetramorium	sp. SL082	6	65	*	*		*	*		*	*							
Monomoriu	*hildebrandi*	5	101				*	*						*		*	*	
Pachycondyl	*melanaria*	5	6				*	*				*		*			*	
Pheidole	sp. SL006	5	99					*			*	*		*		*		
Tetramorium	sp. SL055	5	16						*	*	*						*	*
Pachycondyl	*sulcata*	4	23							*	*						*	*
Pachycondyl	*rufipes*	4	6		*			*			*		*					
Pachycondyl	*truncata*	4	5			*		*	*	*								
Pheidole	sp. SL0ZB	4	32		*		*		*						*			
Pheidole	sp. SL063	4	7		*			*						*	*			
Pheidole	sp. SL019	4	5			*			*				*	*				
Pheidole	sp. SL067	4	4					*	*	*								*
Strumigenys	sp. SL098	4	6						*				*			*	*	
Camponotus	sp. SL083	3	4						*							*		*
Cerapachys	sp. SL106	3	6							*		*					*	
Crematogast	sp. SL062	3	13		*	*						*						
Myrmoteras	*binghami*	3	6													*	*	*
Paratrechina	*minutula* gp.	3	4						*		*			*				
Pheidole	sp. SL049	3	28		*								*					*
Pheidole	sp. SL0ZC	3	9			*	*								*			
Pheidole	sp. SL0ZA	3	4			*					*		*					

Table 5.2 cont'd

Genus	Species	Freq	Ab	1	1	1	1	1	2	2	2	2	2	3	3	3	3	3
Pheidologeton	sp. SL013	3	44				*								*	*		
Recurvidris	*pickburni* sp. nv.	3	11						*	*							*	
Tetraponera	*attenuata*	3	3					*	*	*								
Camponotus	sp. nr *angusticollis*	2	2					*				*						
Cerapachys	sp. SL026	2	9	*													*	
Cryptopone	*testacea*	2	5											*			*	
Hypoponera	sp. SL114	2	5										*	*				
Leptogenys	sp. SL125	2	31					*				*						
Leptogenys	sp. SL072	2	6					*		*								
Pheidologeton	sp. SL141	2	13	*					*									
Ponera	sp. SL048	2	2											*	*			
Protanilla	sp. SL129	2	14								*			*				
Tapinoma	sp. SL147	2	2		*							*						
Tetramorium	sp. SL123	2	10					*							*			
Tetramorium	sp. SL162	2	5		*		*											
Tetramorium	sp. SL118	2	2												*		*	
Acropyga	sp. SL093	1	1													*		
Aenictus	*binghami*	1	1			*												
Aenictus	sp. nr *punensis*	1	1					*										
Anochetus	sp. nr *longifossatus*	1	2	*														
Anochetus	sp. nr *nietneri*	1	1							*								
Camponotus	sp. SL169	1	1								*							
Camponotus	sp. SL172	1	1									*						
Cerapachys	sp. SL101	1	5												*			
Cerapachys	sp. SL104	1	1	*														
Cerapachys	sp. SL165	1	1														*	
Cerapachys	*typhlus*	1	1														*	
Crematogaster	sp. SL022	1	1														*	
Crematogaster	sp. SL119	1	1								*							
Crematogaster	sp. SL148	1	1				*											
Discothyrea	sp. SL050	1	2					*										
Dolichoderus	sp. SL089	1	1			*												
Gnamptogenys	*coxalis* gp	1	1										*					
Harpegnathos	*saltator*	1	1												*			
Hypoponera	sp. SL066	1	1											*				
Leptogenys	sp. SL175	1	1			*												
Leptogenys	sp. SL176	1	1	*														
Monomorium	*floricola*	1	1									*						
Myrmicaria	sp. A	1	1														*	
Polyrhachis	*bugnioni*	1	2										*					
Pseudolasius	sp. SL140	1	14				*											
Pyramica	sp. SL159	1	2											*				
Pyramica	sp. SL163	1	1				*											
Pyramica	sp. SL164	1	1											*				
Rhopalomastix	*rothneyi*	1	1				*											
Rhopalothrix	sp. SL102	1	2											*				
Solenopsis	sp. SL038	1	1											*				
Tetramorium	sp. SL127	1	1															*
Tyrannomyrmex	sp. nv.	1	1													*		
Vollenhovia	sp. SL149	1	3										*					
Vollenhovia	sp. SL115	1	1				*											

Figure 5.4 shows the species richness and abundance per plot, and demonstrates a slight decrease in ants from the top of the slope (transect no. 1) to the bottom (transect no. 3). The only anomalous plot is in plot no. 1, transect no.3 at the bottom of the slope, which shows that a greater number of species in high abundances were caught in this plot. In terms of overall trends in relation to habitat characteristics, there were generally slightly more species and greater numbers of ants in less steep slopes in both spurs and gullies (Figure 5.5). However, only ant species richness showed a significant relationship with slope steepness (Z = -2.361, P = 0.018).

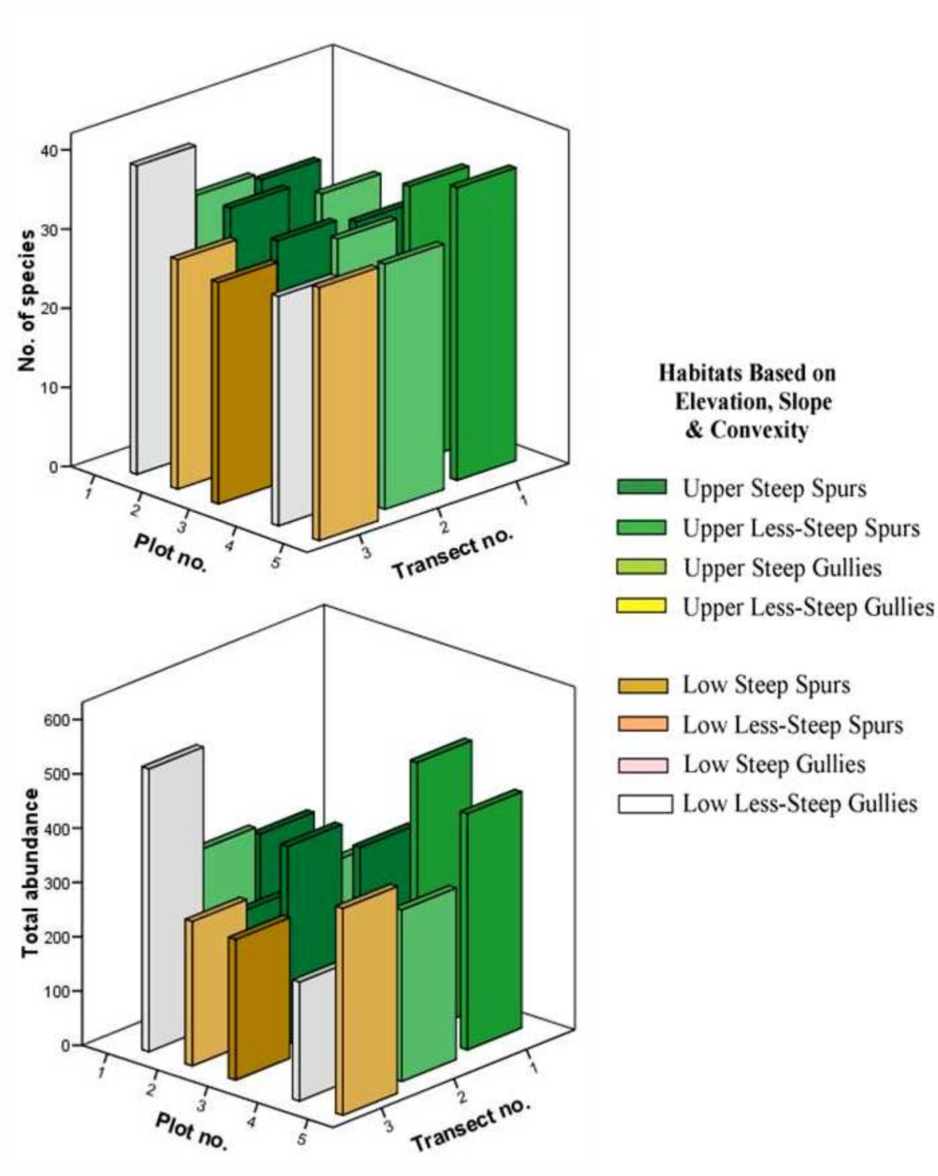

Figure 5.4. Ant species richness and abundance across all 15 plots, showing the habitat categories used by Gunatilleke *et al.* (2006).

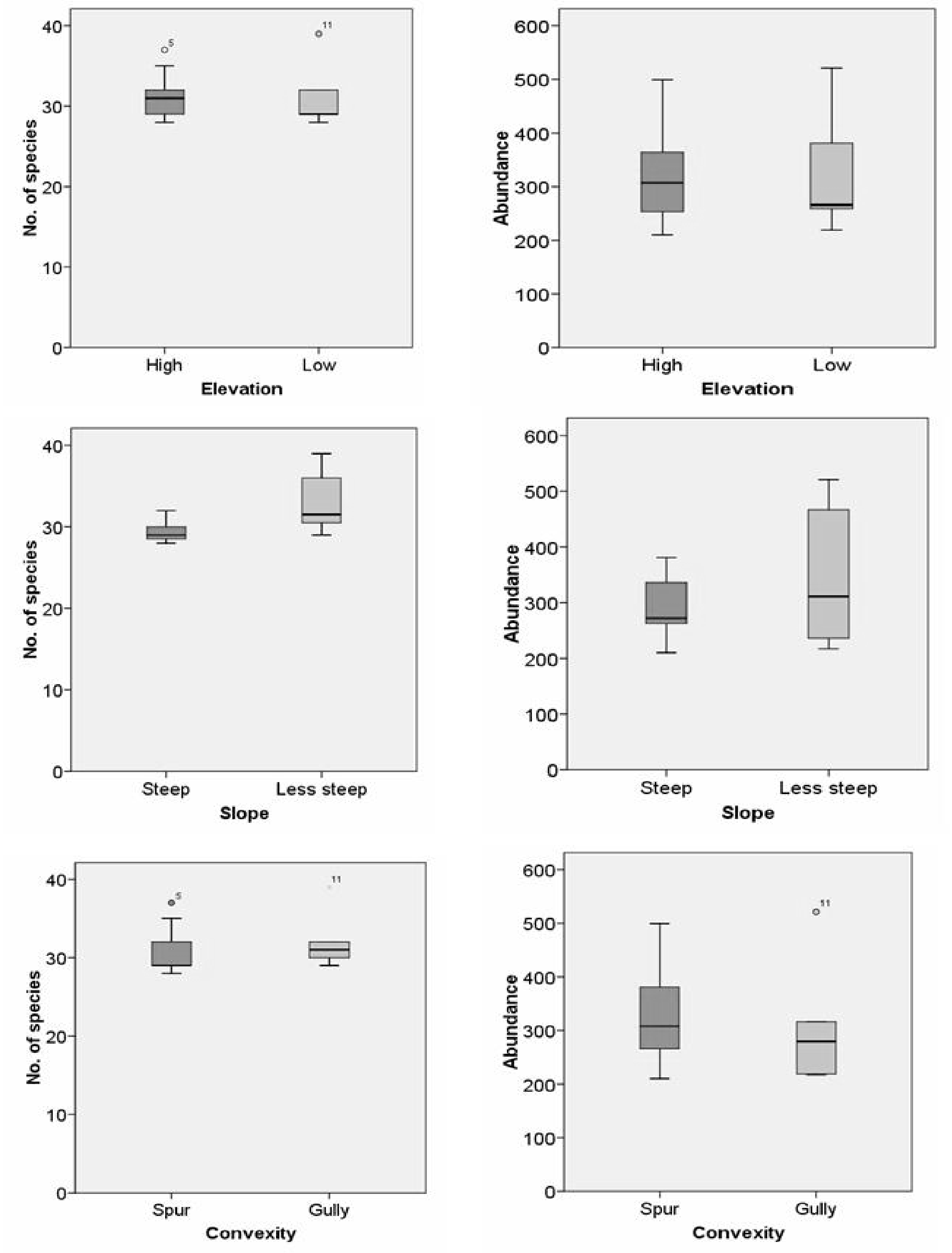

Figure 5.5. Average number of species and average abundances found in plots defined by three of the habitat variables, elevation, slope and convexity. The 15 plots were split into 10 plots with high elevation (hence, 5 with a low elevation), 10 with a steep slope, and 9 classed as spurs.

A total of 143 tree species (out of 205 tree species and 10 liana species, (Gunatilleke *et al.* 2006)) were present in the 15 quadrats analysed in the study. The most widespread tree species (found in all 15 quadrats) were *Myristica dactyloides* (a canopy tree) and *Garcinia hermonii* (an endemic, understorey tree). However, *Humboldtia laurifolia* (a myrmecophytic, understorey tree) and *Mesua nagassarium* (a canopy tree) had the highest stem densities, mostly in the upper two transects. Tree species richness and stem density in these quadrats did not appear to differentiate between convexities or slopes but there was a significant effect of elevation on tree species (Z = -3.073, $P = 0.002$).

5.3.2 Ant and tree species composition

Ant species and tree species assemblages both displayed similar trends in that significant differences were observed in terms of elevation only (Table 5.3). Ant species that contributed most (> 5%) to the ANOSIM for elevation were *A. simoni*, *Paratrechina* sp. SL001, *Strumigenys* sp. sl-01, *Strumigenys* sp. sl-02, *T. bicolor* and *Tetramorium* sp. SL054. The four common tree species (*M. dactyloides, G. hermonii, H. laurifolia* and *M nagassarium*) were also responsible for differentiating the two elevation groups (>5%), along with *Palaquium petiolare*, *Palaquium thwaitesii*, *Shorea affinis, Shorea cordifolia*, and *Shorea worthingtonii*. Ant species and tree species composition patterns across sites were very closely correlated (RELATE; Spearmans Rho = 0.333, $P = 0.003$).

Table 5.3. ANOSIM results relating ant species and tree species composition to the three habitat variables.

Habitat characteristic	Elevation	Slope	Convexity
Ant species assemblage	Global R = 0.276 *P* = 0.006	N.S.	N.S.
Tree species assemblage	Global R = 0.972 *P* = 0.004	N.S.	N.S.

5.3.3 Ant and vegetation structure

Two variables were chosen by the DISTLM model criterion: % plant cover (Pseudo F = 1.8144, $P = 0.05$); and foliage density 0–50 cm (Pseudo F = 2.7998, $P = 0.002$). However, when a model using up to four variables was looked at tree species richness and stem density were also chosen. The first two axes of the dbRDA (Figure 5.6) explained 77.5% of the model fitted with the four variables and 33% of the total variation of the data cloud. The dbRDA plot shows, to some extent, a separation of upper elevation plots and lower elevation plots. It also shows the influence of percent plant cover and plant density towards the lower elevation sites.

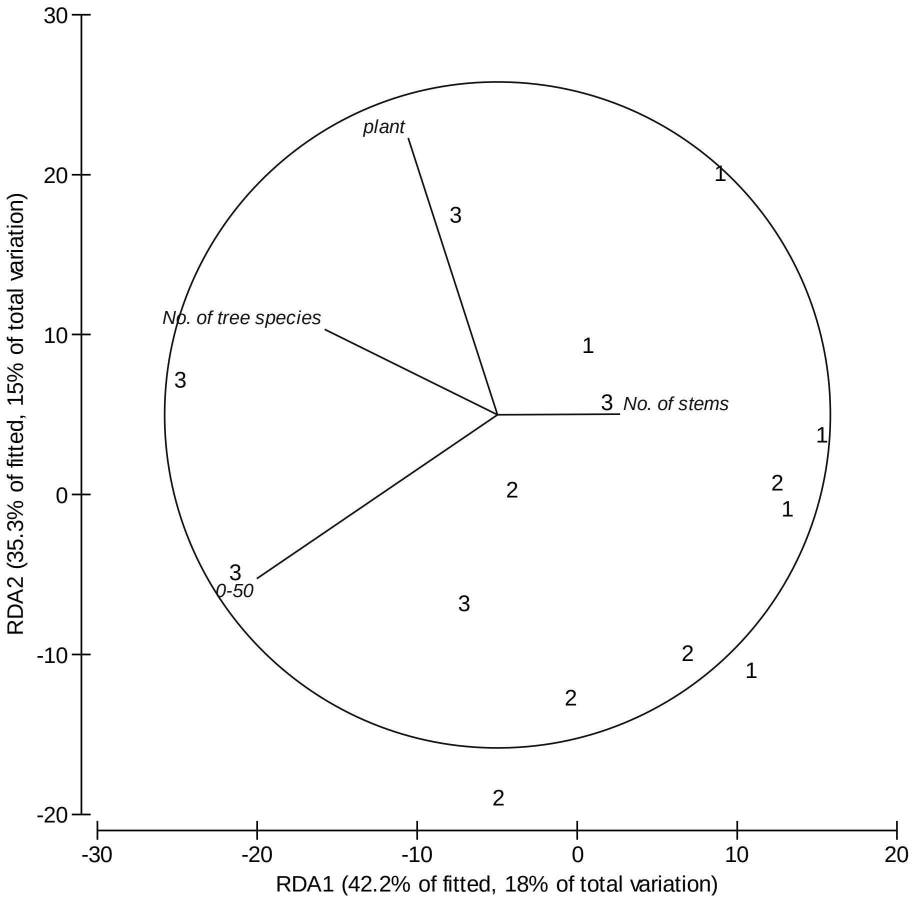

Figure 5.6. Constrained ordination of plots based on a Bray-Curtis dissimilarity matrix of ant species presence/absence. The ordination was fitted with four variables selected by a distance based linear model using a multivariate regression of seven environmental variables and the ant species dissimilarity matrix. The four variables were % plant cover, foliage density (0-50 cm), no. of tree stems per plot and no. of tree species per plot.

5.4 Discussion

The results from this study demonstrate the significant effect of small scale topographical and structural differences on ant species assemblages. Although significant differences in ant species richness were only detected between slope types, there were generally higher species numbers in less steep gullies at higher elevations. These differences in species richness could be attributed to soil moisture availability. In the FDP, ridge tops and spurs have thinner soils, which are prone to drying out as they are more exposed to wind (Gunatilleke *et al.* 2006). Less steep gullies are more likely to be moister and have more stable soil surfaces. Vasconcelos *et al.* (2003) also found higher ant species richness in valleys compared to plateaus in Amazonian forest, where ants are potentially tracking moisture gradients (Kaspari & Weiser 2000). Catterall *et al.* (2001) found greater abundances and more characteristic species assemblages in a variety of taxa, including ants, in riparian sites compared to sites 15 - 35 m higher up along a slope in sub-tropical eucalypt forest. They suggest that riparian habitats would be characterised by higher moisture availability, hence affecting the vegetation and litter dynamics.

However, in this study, there were generally fewer ant species and individuals in the low elevation plots. The lower elevation plots were adjacent to a permanent stream that traversed the valley bottom in the FDP (Figure 5.2). Two of the main drainage lines flowed through the collection area, emptying into the stream. During rainfall, much of the water falling on the top of the ridge would have passed through the lower plots. During the collection period, there was a noticeable increase in water flow in the drainage lines and an increase in soil inundation in the plots (N. Gunawardene, pers. obs.). Soil inundation has been shown to affect ant nesting and reduce species diversity and abundance (Majer & Delabie 1994; Ballinger *et al.* 2007; Deblauwe & Dekoninck 2007).

Persistently moist litter may also have affected the extraction of ants from the leaf litter. During collection in the SFR, the leaf litter sieve quickly became soaked by the moisture from the leaf litter, especially after rains. This had the potential of allowing contamination of the litter samples, as ants occasionally stuck to the wet material. Comparatively lower abundances and species numbers were caught using Winkler extraction during the collection period with the lowest number of dry days (Table 5.1). Conversely, pitfall trap abundances and species numbers were highest during this period, which would explain why no seasonal variation was detected between collection periods. Incidentally, this collection period did not have the highest rainfall of the four collection periods. Since rainfall was not measured *in situ*, but rather at a research station 3 km away, it is difficult to be certain whether rainfall measurements accurately represent the collection area; there is the possibility that rainfall was not uniform across the forest.

Vegetation also appears to be responding to the greater moisture availability in the lower elevation plots. Gunatilleke *et al.* (2006) have observed greater cover of herbaceous species in lower elevation areas compared to woody species. They have also documented lower mean tree density and basal area compared to upper elevation sites. The presence of large canopy gaps in the lower elevation, where trees have appeared to die off in large clumps (I.A.U.N. Gunatilleke pers. obs.), may also have had an effect on ant species composition. Variable light conditions in canopy gaps alter plant community composition (Denslow 1987) and hence the invertebrate community that is dependent upon them. Ant assemblages in gaps appear to be more sensitive to seasonal variation in abiotic conditions (Feener & Schupp 1998), as are other arthropod groups (Richards & Windsor 2007). This may have contributed to differentiating the species composition of the lower plots from the upper plots.

Both the ant species and tree species assemblages responded significantly to differences in elevation within the plot, even though transect no. 2 (the middle transect) was on average only 60 m vertical distance from the lower transect (transect no. 3). Although earlier findings show a significant effect of elevation on ant assemblages (Chapter 3), forest type also had a considerable interaction as well. As this present study was carried out within undisturbed, primary forest, it provides further evidence that even very small elevation changes can influence ant species assemblage.

Ant species distribution was also very closely correlated with tree species distribution, demonstrating the similarity in response to topographical variation. It is difficult to comment on whether there are any interactive influences of ants on tree species distribution or vice versa, as this was not specifically tested in this study. It is of interest that one of the most common understorey trees in the FDP is a well known myrmecophyte (*Humboldtia*). Although it does not have the same symbiotic relationships found of other ant-plants (*Azteca–Acacia* (Longino 1991); *Crematogaster–Macaranga* (Fiala et al. 1989)), a consistent variety of ant species have been found to commonly inhabit the hollow internodes of the tree (Krombein *et al.* 1999). *Technomyrmex albipes* was by far the most commonly observed ant on the small trees in the SFR (N. Gunawardene, pers. obs). Though the ant was widespread, it was more abundant on the upper elevation plots than the lower plot. As *Humboldtia* is found in high densities in the upper elevation sites in the FDP (Gunatilleke *et al.* 2004b), analysis of the interactions between this plant and the ant communities that utilise it could be illuminating.

The structural components of the vegetation on the other hand do appear to be influencing the distribution of ant assemblages within the area surveyed. The constrained ordination showed the clumping together of the upper elevation plots and the variability in assemblages in the lower elevation plots. Percentage of plant ground cover, foliage density (0-50) and tree species richness all appear to have effects on the ant species assemblages in the lower elevation plots. The no. of stems on the other hand, appears to have an influence on the upper elevation plots. Medianero *et al.* (2007) also found higher abundances and species richness of litter arthropod fauna in sites with higher numbers of plant stems and higher basal area.

However, according to the ordination, over 60% of the variation in the species was not explained by the four plant variables. Elevation and topography may explain more of the variation in the ant assemblages, but the current study was limited in the number of plots analysed, making the dataset less robust to multivariate analyses. Future studies should sample further plots along the same slope using both collection methods and collecting just after the first rainy season of the year. Analysis of arboreal and shrub dwelling ants may also reveal clearer trends in terms of the relationship to tree species distribution. Ribas *et al.* (2003) found significant relationships between arboreal ant species richness and tree species and tree density in Brazilian cerrado. The 27 singleton ant species that were excluded from the analysis may provide further insight into the habitat relationships within the FDP. Even though most of these appear to be ground dwelling ants (*Pyramica*; *Cerapachys*), others are potentially arboreal ants (*Crematogaster*; *Camponotus*).

Overall results do suggest that structural changes associated with the shifts in vegetation composition from valley bottom to ridge top can significantly alter ant species composition. Sheltered upper elevation gullies can support high species richness and can potentially act as harbours of ant diversity in tropical forests in Sri Lanka. Conservation of forest fragments with high topographic variation in south-west Sri Lanka has the potential to protect a large proportion of ant species richness found in the country.

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6. Can matrix habitat type determine the invasibility of a forest edge? Assessing the effect of matrix habitat on forest edges using ants as indicator organisms

Abstract

Forest patches are no longer seen as islands of diversity in a sea of uninhabitable wasteland. An increasing number of studies now view the landscapes surrounding forest patches as heterogeneous sources and sinks of non-forest diversity. The habitats of the matrix (land surrounding a forest patch) can affect the internal dynamics of a forest patch by determining the degree to which edge effects penetrate. By looking at ant assemblages within forest edges bordered by different matrix habitats, significant differences were found between assemblages within the edges. Analysis of the ratios of disturbance tolerant ants to forest dwelling ants also varied with edge type and distance from forest/matrix edge. Generally, the ratio declined with distance from the forest/matrix edge but the forest adjacent to a matrix habitat with low structural similarity and high disturbance levels had much higher ratio values that did not decline to natural riparian edge levels, even up to 100 m from the border. It appears that even relatively large forest remnants can be affected by the surrounding matrix land uses and that encouraging the growth of structurally similar vegetation and minimising disturbance along the borders should attenuate the effect of the edge.

Key words: Formicidae, invasion, invasives, tropical forest, forest patch, disturbance, matrix habitat, edges, landscape heterogeneity

6.1 Introduction

Tropical forest remnants have often been viewed as habitat islands in an inhospitable sea of anthropogenically altered landscapes. However, over the last decade or so, studies have viewed the landscapes surrounding forests as a matrix of heterogeneous habitats rather than a homogeneous ‘desert’ or wasteland of unsuitable habitat (Ås 1999; Gascon *et al.* 1999; Ricketts 2001; Vandermeer & Carvajal 2001; Baum *et al.* 2004; Guirado *et al.* 2006; Kupfer *et al.* 2006; Lövei *et al.* 2006). Lindenmayer *et al.* (2008) suggested that forest patches with surrounding, often human-modified, matrix should be considered as parts of a mosaic rather than as independent units in a biogeographical context. It has been shown that land surrounding forest remnants (hereafter referred to as the 'matrix') differentially affects the biota within forest remnants (Åberg *et al.* 1995; Mesquita *et al.* 1999; Jules & Priya 2003; Kupfer *et al.* 2006). Thus, certain types of matrix can provide a source of animals and plants that can enter the forest remnant (patch), as well as food resources for patch dwellers (Janzen 1983). Cook (2002) found that in a successional landscape, 24% of patch diversity was shared with the matrix and that within natural, discrete edges, 'leakage' of species across the edge can reach up to 500 m into either habitat (Dangerfield *et al.* 2003). This 'spill-over' from the matrix into forest patches and vice versa, can have a variety of effects on patch-dependent species.

One of the main concerns of forest conservation and management is the maintenance of genetic diversity (Jennings *et al.* 2001). The remaining patches in a landscape require careful management, as they can be used as seed banks and source populations for newly rehabilitated land (Thebaud & Strasberg 1997). The structure and function of the matrix habitats can play an integral role in determining the integrity of a patch, and hence its long-term conservation viability (Gascon *et al.* 1999; Renjifo 2001; Ricketts 2001; Kupfer *et al.* 2006). Research has shown that matrices that have the most structurally similar vegetation to the forest patch tend to support a higher species diversity (Perfecto & Vandermeer 2002), can reduce tree mortality at the patch edge (Mesquita *et al.* 1999), and can facilitate the use of corridors and 'stepping stones' by patch dwellers to access distant patches (Baum *et al.* 2004).

Gascon *et al.* (1999) found that matrix which is structurally similar to the patches can reduce the abiotic and biotic changes brought about by edge effects (see reviews of edge effects by Murcia (1995), Fagan *et al.* (1999), Ries *et al.* (2004), and Harper *et al.* (2005)). These changes at the edge, such as altered microclimate, can be reduced if the patch is buffered by vegetation that has a similar structure to the patch (Kapos *et al.* 1997; Turton & Freiburger 1997). Majer *et al.* (1997), in their study of Atlantic rain forest in Brazil, suggested that the presence of similarly structured cocoa plantations at the edge of a reserve may have served to reduce the effect of the edge and hence the compositional differences in the ant community. Therefore, the structure and quality of the matrix habitat can act as a filter, either allowing the passage of species from habitat to habitat or isolating species within the forest patch (Åberg *et al.* 1995).

The existence of a structurally similar matrix habitat can also facilitate invasion of the patch by matrix dwellers. Janzen (1983) suggested that pristine forests surrounded by croplands could remain more ‘ecologically intact’ compared to those surrounded by secondary succession, as invasion by matrix-dwelling generalists would be reduced. Secondary succession could support populations of non-native species thus providing a source-population for invasion at the forest edge (With 2002). Patch edges with a distinct edge may develop an edge dwelling plant community which can insulate the patch from external physical conditions (Ranney *et al.* 1981; Schedlbauer *et al.* 2007). This vegetation would normally ‘seal’ the edges, effectively acting as a physical barrier to seed dispersal (Cadenasso & Pickett 2001; López-Barrera *et al.* 2007). Didham and Lawton (1999) found that patches with open edges had detectable changes in microclimate that extended two to five times further inwards than patches with closed edges. Thus, patch edges adjacent to similarly structured matrix may experience a reduction in edge–associated species and could become more porous and hence susceptible to invasion.

The degree of human disturbance in and around the patch, or the accessibilty of a patch, may also facilitate the incursion of invasive species (Fine 2002). Angelstam (1986) suggests that the steepness of the productivity gradient between the matrix habitat and forest patch can determine the degree of predation within the forest by matrix-dwelling predators. He describes a model in which an urban/forest gradient would allow the highest amount of predation when compared to a less-disturbed habitat/forest edge. Moffat *et al.* (2004) and Guirado *et al.* (2006) also found similar results, with forest remnants in urban areas being more prone to invasion by ‘synanthropic species’ (species adapted to living in human modified habitats) than forests adjacent to more rural landuses.

In the present study, ant assemblages within the edge of a large tropical forest patch in south-western Sri Lanka were analysed in relation to four surrounding matrix habitats. Each matrix habitat represented varying degrees of structural contrast and levels of anthropogenic disturbance. Penetration of the forest edge by matrix-dwelling (disturbance tolerant) ants was used to test the effects of the different landuses. The results from this study should assist the Sri Lanka Forest Department and other land management agencies to decide which type of land use can best protect the diversity of forest patches and provide guidance for the restoration of degraded and abandoned agricultural land surrounding these forest remnants.

6.2 Methods

6.2.1 Study site

Collections were carried out along the edge of Sinharaja Forest Reserve (SFR), an 11,000 ha reserve located in the Sabaragamuwa Province in Sri Lanka (6° 21’ N, 80° 21’ E) (Figure 6.1). Since patch size and shape can influence the degree to which different adjacent matrix habitats effect the patch (Ås 1999; Sobrinho & Schoereder 2007), collection was standardised by selecting sites that were located along the edge of this large forest patch. It is the largest remaining contiguous stand of lowland, mixed dipterocarp (*Mesua-Shorea* type) forest in the area, and covers a series of east-west running ridges. It receives between 4000 - 5000 mm of rain annually and is visited by two monsoon seasons during May to July (south-west monsoon) and during October to December (north-east monsoon). Temperature variability throughout the year is minimal, with an average daily temperature of 27°C (+/- 3 °C) (Ashton 1992).

6.2.1 Description of matrix types

Sites were located within forest edges bordering three of the main landuses surrounding the forest. These were pine plantation, chena fernlands and tea plantation. A naturally created riparian edge was chosen for comparison with these anthropogenically created edges. All sites had the same aspect, as this has been shown to affect the degree of edge effects (Palik & Murphy 1990).

The pine plantation is under the jurisdiction of the Sri Lanka Forest Department but is not patrolled by forestry officers. The pine is an exotic, *Pinus caribea,* which was planted by the Forest Department in the late 1970’s to protect slopes deforested by agriculture (Ashton *et al.* 1998). Originally planted for pulpwood, it is now used as part of a buffer zone to delineate the forest borders. The plantation was never thinned, so the trees are densely packed and reach to about 25 m in height. Most sections of the plantation are about 20 - 50 m in width and support some understorey growth.

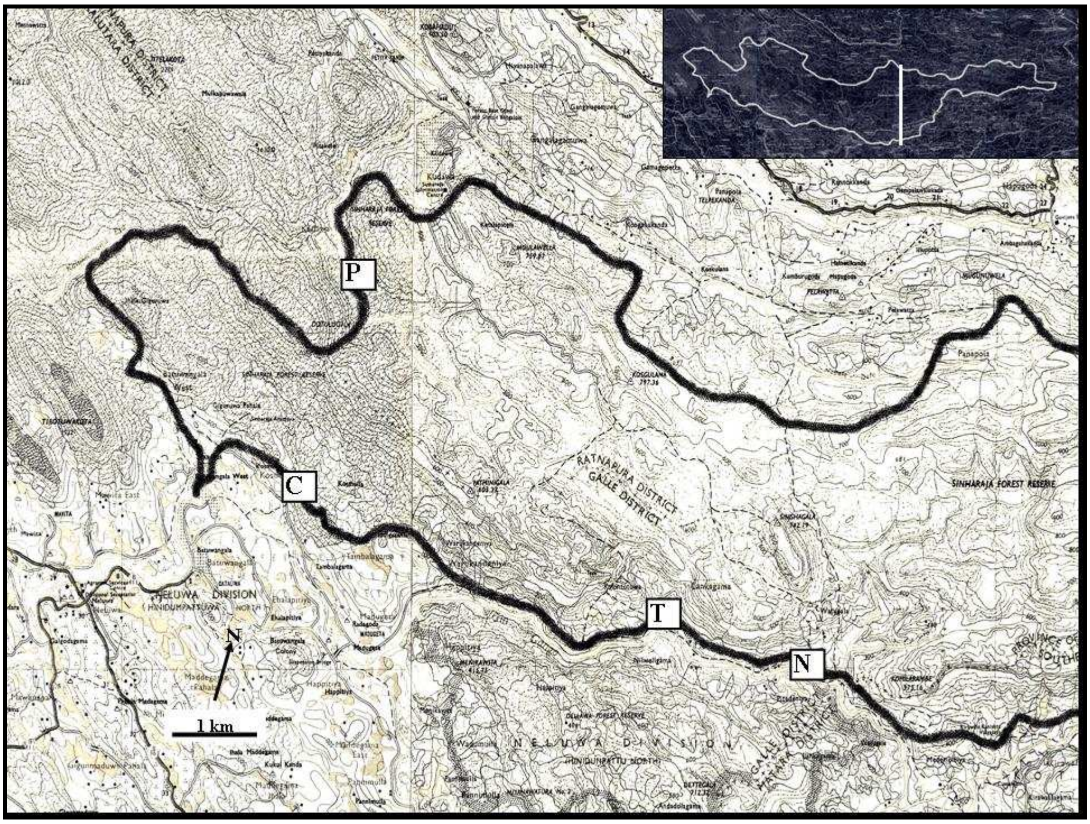

Figure 6.1. Collection sites are displayed on a Sri Lanka Survey Department map of the western half of Sinharaja Forest Reserve. The sites are located along the forest edge bordered by pine plantation (P), chena fernlands (C), tea plantation (T) and a natural river edge (N).

Fernlands commonly form in this region after shifting cultivation is abandoned and are often maintained by recurrent fires (Maheswaran & Gunatilleke 1988). The sites in the fernland (chena) are dominated by *Dicranopteris linearis* (Gleicheniaceae), commonly known as kekilla fern, which most likely established after shifting cultivation was banned along the forest borders in the early 1980s. *Dicranopteris linearis* grows to about 1 m in height and forms a dense cover under which a thick litter layer forms (Maheswaran & Gunatilleke 1988). This highly successful, exotic coloniser can often persist indefinitely in an area, effectively inhibiting forest regeneration (Cohen *et al.* 1995).

The forest bordered by pine and chena are adjacent to forest border villages and are used as entry points for collection of non-timber forest products by the villagers. Although the removal of timber is not permitted, there is some firewood collection in these areas (N.R. Gunawardene, pers. obs.).

The tea plantation is privately owned by a small holding landowner and is actively harvested. After establishment of the SFR as a protected area, only farms established more than 100 years previously were allowed to remain along the forest borders. While the land use may not always have been tea in this particular farm, it has been owned by the same family for at least two generations.

The natural edge is bordered by ripararian vegetation through which a small path passes. While this is traversed regularly by villagers, it is also the access path for a Forest Department station that is permanently staffed. This section of the river Gin Ganga is about 20 m in width. The land use on the opposite bank varies from farmland to secondary forest.

Collections were carried out in June 2005 (tea edge), December 2005 (pine edge), January 2006 (natural edge) and February 2006 (chena edge). Collections were also carried out during these times within four anthropogenically disturbed areas typical of the region (paddy field edge, rubber tree plantation, tea plantation and fallow farm land). These were at least 2 km from the SFR borders. This was done in order to assess which ant species are found in disturbed habitats within the vicinity of the reserve.

Samples were collected in two sites, 50 – 100 m apart, within each forest edge. In each site, five sampling points were laid out 5 m apart along five parallel transects (Figure 6.2). The transects ran parallel to the forest/matrix edge and were placed at 2 m, 10 m, 30 m, 60 m and 100 m from the edge. This exponential spacing of transects was done so as to maximise the potential for observing change at the forest matrix edge. A maximum of 100 m from the edge was deemed to be approaching forest interior conditions (Harper *et al.* 2005). Sampling was slightly altered for the disturbed areas; five sampling points were laid out 5 m apart along two transects within each of the disturbed areas.

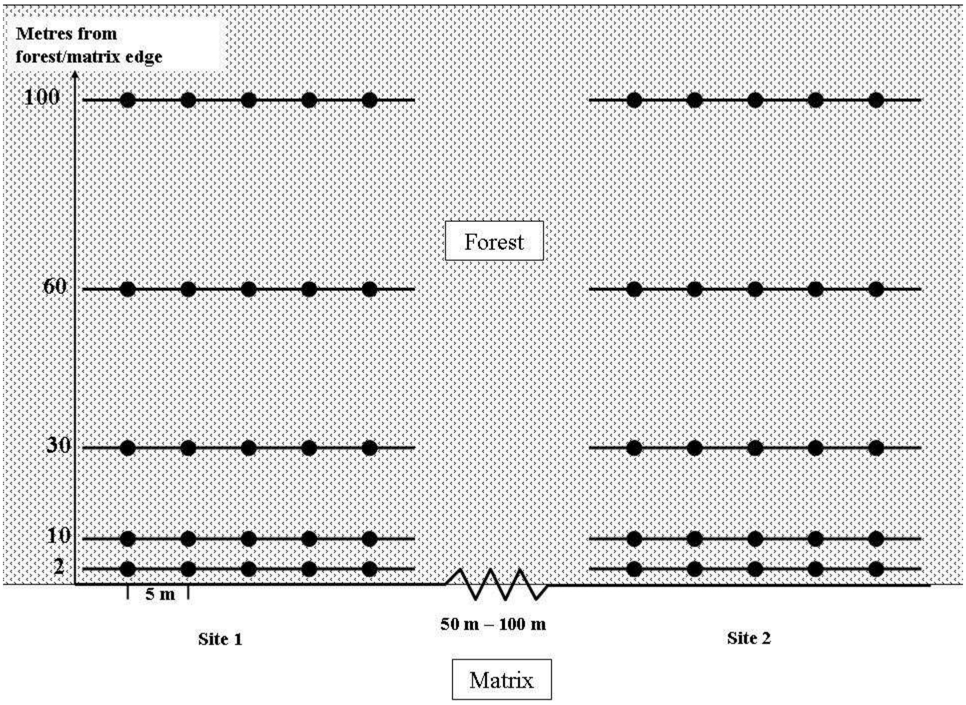

Figure 6.2. Layout of the 25 point sampling pattern in the two sites within each edge. All sites had similar aspects (south-west facing) and a gently rising slope gradient.

6.2.2 Ant sampling

Ants were sampled at each sampling point using two established methods for invertebrate collection, pitfall traps and Winkler extraction (Bestelmeyer *et al.* 2000). Ants were sampled using only pitfall traps in the disturbed areas since there was often no leaf litter to be collected. The pitfall trap consisted of a standard plastic drinking cup (7 cm diameter) which was inserted into the ground and filled with ~70 ml of methylated spirits. The pitfalls were then capped with another plastic cup with large triangles cut out of the sides to provide a lid to prevent rainfall from flooding the cup. After 72 hours, the material in the cups was collected and washed with fresh methylated spirits and returned to the lab.

In the forest sites, leaf litter was collected in a 1 m by 1 m quadrat and was sifted using a Winkler litter sifter. The sifted material was then hung inside a Winkler sack for 48 hours, with the leaf litter being removed and shaken after the first 24 hours. All material collected in the Winkler sack was then removed and stored in ethanol.

The material from the pitfall traps and Winkler sacks was then sorted in a laboratory and all invertebrates removed and stored in 70% ethanol. The ants were separated from the sample, point mounted and identified to morphospecies. Once a reference collection of point mounted specimens was created all excess ants were stored in 80% ethanol. Ants were identified to species where possible with certain genera being sent to specialists for confirmation of species. The wet and dry specimens are housed in Peradeniya University Entomology Museum, with a mounted representative collection stored in Curtin University of Technology Entomology Museum.

6.2.3 Environmental variables

At each sampling point, air temperature (1 m above ground level) was recorded using a Centre 310 RS-232 humidity/temperature meter. Ground cover characteristics of each point were quantified by estimating the percentage coverage by bare ground, leaf litter, large rocks, and plant stems in a 1 m^2 quadrat. Also, in the same quadrat, the number of dead branches and fallen tree trunks (>10 cm) were recorded and the depth of the leaf litter was measured using a ruler. Canopy cover was estimated using a GRS® densitometer five times around each point. Data from each sampling point were summed and averaged for each transect. Understorey foliage density was also estimated using a Levy pole (Majer 1981). The pole was divided into four intervals: 0 (ground)–50 cm; 51-100 cm; 101-150 cm; 151–200 cm; and the number of points where the pole was touched by vegetation was counted. At each interval, the number of plant touches for each of the four recordings was summed and divided by the total number of recordings taken for the transect (five points within a transect). Overall foliage density was then calculated for the transect by adding the values of the four intervals.

6.2.4 Data analysis

For each sampling point, the data from each pitfall trap and leaf litter sample were combined as the two methods are considered complementary (see Chapter 2). Then, the ants from the five points in each transect were combined and considered as representing one sample, henceforth called a distance sample. The sampling design ensured that these five distance samples were replicated in the second site (in each forest edge). The data from the two sites were then combined to get an overall ant species richness and abundance for each edge type and for each distance from the edge. The same procedure was carried out with the nine environmental variables. Species richness, abundance and all environmental variables were ln (x+1) transformed to reduce variance in the data. Levene's test for homogeneity of variance was run to test whether the transformations were adequate. Environmental variables were then tested for co-linearity by running two-tailed Spearman rank correlations. After co-linear variables were removed, a multivariate general linear model (GLM) was run on the transformed species richness, abundance and environmental data to test if there were significant differences between edge types and distances from the edge.

The ant data from each edge type were then transformed into a presence/absence matrix, which is a typical transformation for ant species data due to the tendency for ants to be spatially clumped (Longino 2000). The ant species assemblages in each edge were compared using two-way, crossed analysis of similarities (ANOSIM, Clarke & Warwick 2001)) using a Bray-Curtis similarity measure (Kruskal 1964). This enabled an assessment of significant differences between ant assemblages in each edge type and along each distance sample. A hierarchical cluster analysis (Clarke & Warwick 2001) using group-average linkage was then carried out to compare similarities in ant assemblages within each distance sample within each edge. ANOSIM and cluster analyses were carried out using the program Primer v.6.1.9 permanova+β18.

Each ant species was then designated as either: disturbance tolerant (D), if they occurred in the disturbed areas; forest interior inhabitant (F), if they were collected from the unlogged undisturbed forest (Chapter 3 and 4); or edge inhabitants (E), if they were not found in either the interior or the disturbed areas. Invasibility (I) was calculated as the sum of disturbance tolerant ants (D) divided by the total numbers of forest interior ants (F) and edge inhabitants (E) for each distance sample (j) using the equation

$$I_{(j)} = \sum D_{(j)} \,/\, (\sum F_{(j)} + \sum E_{(j)}).$$

Overall I for each edge type was calculated by subtracting I nearest the edge from I furthest from the edge. This would give an indication of the degree of change in I within each edge type. Invasibility of each distance sample was then projected onto a scatter-plot matrix against increasing distance from the edge and a R-squared linear regression line was fitted for each edge type. All tests were carried out using SPSS 15.0.

6.3 Results

6.3.1 Overview

Ant species collected in each edge type are shown in Table 6.1. The pine edge had the highest species richness, followed by the natural edge, tea edge and chena edge. Ninety eight species were caught in the forest edges combined, and a further 15 species were caught solely in the disturbed area pitfall traps. Overall abundance of individuals was highest in the natural edge (> 3500), followed by chena (>1900), pine (>1400) and tea (>1100).

6.3.2 Ant assemblages

The most abundant and frequently occurring ants were *Aneuretus simoni* and *Solenopsis* sp. SL113, which were four times more abundant than the next most commonly occurring ants, a myrmicine (*Solenopsis* sp. SL038), a ponerine (*Odontomachus* sp. nr *haematodes*) and a dolichoderine (*Technomyrmex bicolor*), all of these species were collected in especially high numbers in the natural edge site. Twenty four species were represented by only one specimen (singletons) and 32 species occurred in only one distance sample. Pine edge had the highest number of species unique to it (19), followed by natural edge (16); both tea and chena edge had no unique species. In terms of distance from the edge, the most abundant species all had their highest abundances in the 100 m distance samples.

The GLM analysis indicated that abundance and species richness were significantly different between edge types, but only abundance changed significantly with increasing distance from the edge (Table 6.2). This was also reflected in the two-way crossed ANOSIM, which showed that the ant assemblages in each edge type were significantly different at $P = 0.001$ (Global R = 0.656); all pairwise tests were significant ($P < 0.05$) except between tea and natural edges. This can be seen in the dendrogram from the cluster analysis, where the tea edge sites and the natural edge sites are grouped close to each other (Figure 6.3). However, tests for differences between distance samples did not yield any significant differences.

Table 6.1. All species collected in the study showing the presence/absence of species in each edge type: pine (P); chena (C); tea (T); natural (N); and in the disturbed area pitfall traps (D). Lighter shaded species are considered disturbance tolerant ants found within the forest, species shaded dark are edge inhabitants, and all others are either forest interior or disturbance dwellers.

Family	Genus	Species	P	C	T	N	D
Aenictinae	*Aenictus*	*binghami*				*	
Amblyoponinae	*Amblyopone*	sp. SL128				*	
Aneuretinae	*Aneuretus*	*simoni*	*	*	*	*	*
Dolichoderinae	*Bothriomyrmex*	*wroughtoni*			*		
	Dolichoderus	sp. SL089					*
	Tapinoma	sp. SL056	*			*	
	Tapinoma	sp. SL131					*
	Tapinoma	sp. SL156			*		*
	Tapinoma	sp. SL157			*		
	Technomyrmex	*albipes*	*		*	*	*
	Technomyrmex	*bicolor*	*	*	*	*	*
Formicinae	*Acropyga*	sp. SL203		*			
	Anoplolepis	sp. SL194		*			*
	Camponotus	sp. nr *infuscus*				*	
	Camponotus	sp. nr *angusticollis*				*	
	Camponotus	sp. SL083	*		*	*	*
	Camponotus	sp. SL138	*				
	Camponotus	sp. SL179				*	
	Camponotus	sp. SL187					*
	Lepisiota	sp. nr *capensis*	*				
	Lepisiota	sp. SL189					*
	Oecophylla	*smaragdina*	*	*			*
	Paratrechina	sp. SL001	*	*		*	*
	Paratrechina	sp. SL036		*	*	*	
	Paratrechina	*bourbonica*					*
	Paratrechina	*minutula* gp	*		*		
	Paratrechina	*minutula* gp				*	
	Paratrechina	sp. SL183				*	
	Plagiolepis	sp. nr *alluaudi*		*			
	Polyrhachis	*convexa*					*
	Polyrhachis	sp. (nr *hippomanes ceylonensis*)					*
Myrmicinae	*Acanthomyrmex*	*luciolae*	*				
	Cardiocondyla	*wroughtoni*					*
	Cardiocondyla	*nuda*		*			*
	Carebara	sp. SL012	*	*		*	*
	Crematogaster	sp. SL022				*	
	Crematogaster	sp. SL146	*		*		
	Crematogaster	sp. SL174			*		
	Crematogaster	sp. SL182				*	
	Crematogaster	sp. SL202		*			
	Meranoplus	*bicolor*					*
	Meranoplus	*rothneyi*		*			*
	Monomorium	*floricola* gp	*	*	*		*
	Monomorium	*hildebrandi* gp *M.* cf. australicum		*	*	*	
	Monomorium	*hildebrandi* gp *M.* nr *subcoecum*			*		
	Monomorium	*floricola*	*				*
	Myrmicaria	sp.A	*	*	*	*	*
	Pheidole	sp. SL006	*		*		
	Pheidole	sp. SL027	*	*	*		

Table 6.1 cont’d

Family	Genus	Species	P	C	T	N	D
Myrmicinae	*Pheidole*	sp. SL028	*	*		*	
(cont'd)	*Pheidole*	sp. SL030	*				
	Pheidole	sp. SL049	*				
	Pheidole	sp. SL063	*				
	Pheidole	sp. SL067		*	*		
	Pheidole	sp. SL070	*				
	Pheidole	sp. SL077					*
	Pheidole	sp. SL091	*	*	*	*	*
	Pheidole	sp. SL0ZA	*		*	*	*
	Pheidole	sp. SL0ZB	*	*	*	*	
	Pheidole	sp. SL0ZC	*	*			*
	Pheidole	sp. SL107				*	
	Pheidole	sp. SL142			*	*	
	Pheidole	sp. SL185					*
	Pheidole	sp. SL190					*
	Pheidologeton	sp. SL013	*		*	*	
	Pheidologeton	sp. SL141	*			*	
	Pristomyrmex	sp. nr *profundus*		*			*
	Pyramica	sp. SL159			*		
	Pyramica	sp. SL160			*		
	Pyramica	sp. SL167				*	
	Recurvidris	*pickburni* sp nv	*				
	Rhopalomastix	*rothneyi*	*			*	
	Solenopsis	sp. SL038		*	*	*	
	Solenopsis	sp. SL113	*	*	*	*	*
	Strumigenys	sp. sl-01	*		*	*	
	Strumigenys	sp. sl-02	*		*		
	Strumigenys	sp. SL109				*	
	Strumigenys	sp. SL180				*	
	Tetramorium	sp. SL002	*				
	Tetramorium	sp. SL015				*	
	Tetramorium	sp. SL020		*			
	Tetramorium	sp. SL054	*				
	Tetramorium	sp. SL055	*				
	Tetramorium	sp. SL058	*		*	*	
	Tetramorium	sp. SL059	*				
	Tetramorium	sp. SL05A	*				
	Tetramorium	sp. SL082					*
	Tetramorium	sp. SL118	*		*		
	Tetramorium	sp. SL123	*			*	
	Tetramorium	sp. SL127	*				
	Tetramorium	sp. SL134	*	*			
	Tetramorium	sp. SL162			*		
	Tetramorium	sp. SL184				*	
	Tetramorium	sp. SL191					*
	Tetramorium	sp. SL197					*
	Vollenhovia	sp. SL115			*		
	Vollenhovia	sp. SL177	*				
	Vollenhovia	sp. SL200		*			
Ponerinae	*Anochetus*	sp. nr *longifossatus*			*		
	Anochetus	sp. nr *nietneri*	*				
	Anochetus	sp. nr *longifossatus*		*			
	Cryptopone	*testacea*				*	
	Hypoponera	sp. SL016	*	*	*	*	
	Hypoponera	sp. SL051		*	*	*	
	Hypoponera	sp. SL052			*		
	Leptogenys	sp. SL125	*			*	

Table 6.1 cont'd

Family	Genus	Species	P	C	T	N	D
Ponerinae (cont'd)	*Leptogenys*	sp. SL155	*		*	*	*
	Leptogenys	sp. SL199		*			
	Odontomachus	sp. nr *haematodes*	*	*	*	*	*
	Pachycondyla	*melanaria*		*		*	
	Pachycondyla	*sulcata*	*				
	Pachycondyla	*jerdoni*	*	*	*	*	*
	Ponera	sp. SL048			*	*	
		Total	**52**	**34**	**41**	**47**	**37**

Table 6.2. Results of multivariate GLM analysis of edge type and distance from edge.

Source	Dependent variable	Type III SS	df	F	Sig.
Corrected model	Ant species richness	3.222	19	1.420	.221
	Ant abundance	14.223	19	1.292	.287
	% stone cover	3.322	19	.618	.851
	% plant cover	1.195	19	.892	.597
	No. of branches	.669	19	1.093	.422
	Litter depth	**3.367**	**19**	**5.292**	**.000****
	% canopy cover	.404	19	1.854	.090
	Air temperature °C	.517	19	1.030	.473
	Foliage density	1.741	19	1.392	.235
Edge type	**Ant species richness**	**1.871**	**3**	**5.224**	**.008****
	Ant abundance	**5.787**	**3**	**3.329**	**.040***
	% stone cover	.925	3	1.089	.377
	% plant cover	.185	3	.874	.471
	No. of branches	.058	3	.599	.623
	Litter depth	**.501**	**3**	**4.986**	**.010***
	% canopy cover	.030	3	.870	.473
	Air temperature °C	.117	3	1.480	.250
	Foliage density	.600	3	3.040	.053
Distance from edge	Ant species richness	1.042	4	2.182	.108
	Ant abundance	5.289	4	2.282	.096
	% stone cover	1.331	4	1.175	.352
	% plant cover	.159	4	.565	.691
	No. of branches	.178	4	1.380	.276
	Litter depth	**1.525**	**4**	**11.38**	**.000****
	% canopy cover	.081	4	1.771	.174
	Air temperature °C	.081	4	.770	.558
	Foliage density	.430	4	1.631	.206
Edge x Distance	Ant species richness	.309	12	.215	.996
	Ant abundance	3.148	12	.453	.920
	% stone cover	1.067	12	.314	.978
	% plant cover	.851	12	1.006	.478
	No. of branches	.433	12	1.121	.397
	Litter depth	**1.341**	**12**	**3.338**	**.008****
	% canopy cover	.293	12	2.128	.065
	Air temperature °C	.319	12	1.004	.479
	Foliage density	.711	12	.900	.563

* $P < 0.05$; ** $P < 0.01$

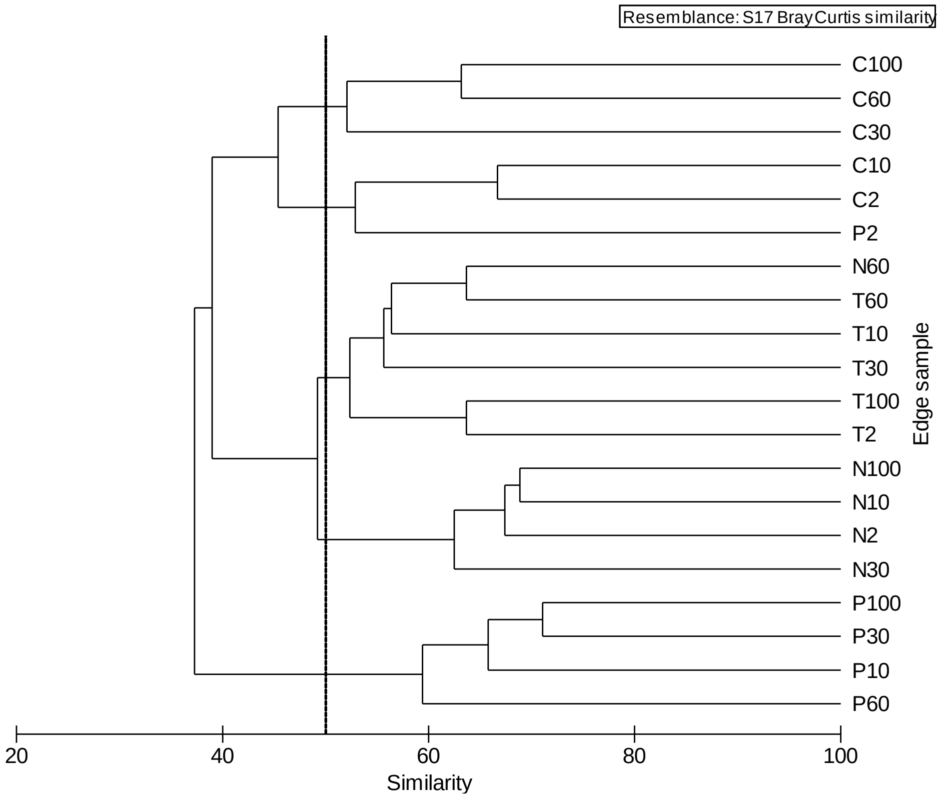

Figure 6.3. Dendrogram of distance samples within pine edge (P), chena edge (C), tea edge (T) and natural edge (N). The numbers indicate the distance from the edge where the sample was taken. The dendrogram shows grouping at the 50% similarity, which more or less splits the samples into the edge types. Only pine edge sample P2 was more similar to chena edge samples than to the other pine samples. Tea and natural edge samples were more similar to each other than to the other edges.

6.3.3 Environmental variability

Spearman rank correlation results showed % bare ground and % leaf litter cover were highly correlated ($P < 0.05$) with each other and with % stone cover, % plant cover and litter depth. These two variables were removed from the data matrix and the results of the GLM are shown in Table 6.2. Litter depth was the only environmental variable associated significantly with both edge type and distance from the edge.

The average values against distance from edge for four of the 12 measured variables are shown in Figure 6.4. These graphs show that mean litter depth was the highest at the border of the pine edge and was similar to the natural edge. Litter depth declined in the natural edge much more gradually than at the pine edge. Average temperatures in the chena and tea edges were slightly, though not significantly, higher than the other two edge types. This situation was reversed in terms of foliage density, with the pine and natural edges having denser understories. Pine edge had very high foliage densities at the border (2 m from matrix) but declined sharply by 10 m from the border.

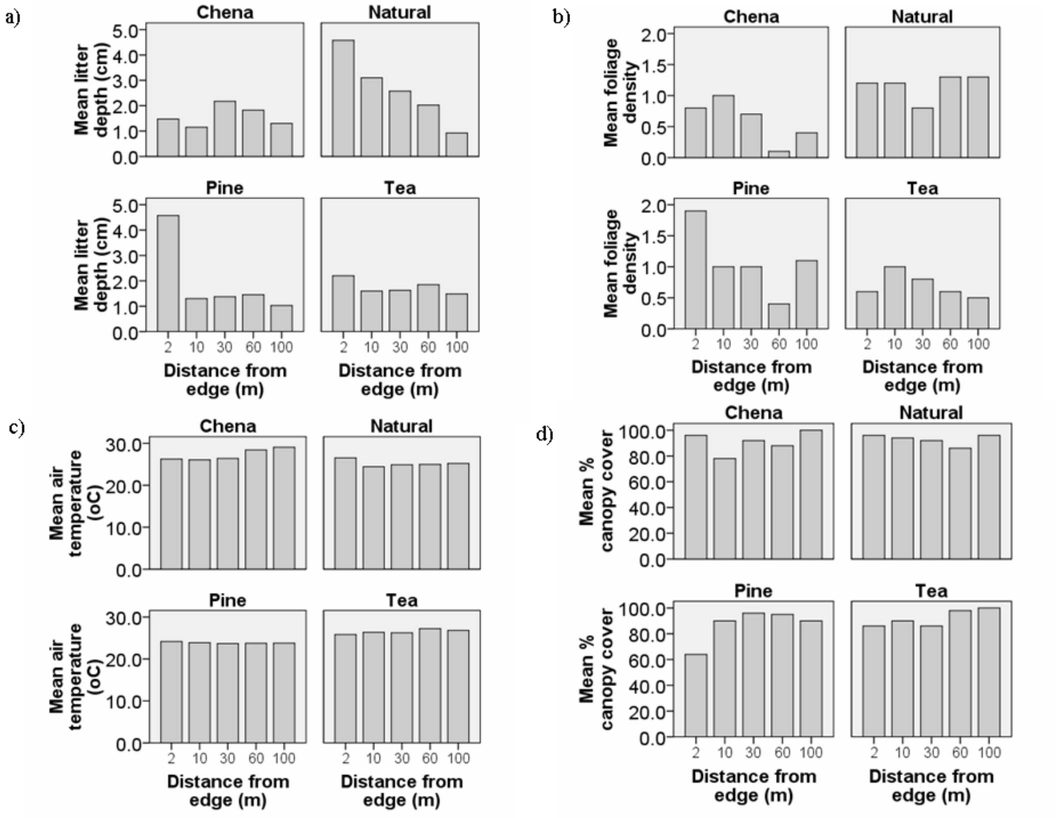

Figure 6.4. Changes in four of the nine environmental variables (a, mean litter depth; b, mean foliage density; c, mean air temperature; and d, mean %canopy cover) measured against distance from edge in each edge type.

6.3.4 *Invasibility*

Pine edge had the highest forest interior species richness as well as disturbance tolerant species. The natural edge had the highest proportion of edge dwelling species and the lowest number of disturbance tolerant species (Figure 6.5). Altogether, there were 22 species that were classed as disturbance tolerant. However, for eight of these species only one specimen was collected. These were *Aneuretus simoni*, *Carebara* sp. SL012, *Meranoplus rothneyi, Pheidole* sp. SL00ZA, *Pheidole* sp. SL091, *Tapinoma* sp. SL156, *Technomyrmex albipes,* and *Technomyrmex bicolor*. With the exceptions of *M. rothneyi* and *Tapinoma* sp. SL156, all the others were found in great abundances in the forest interior (see Chapters 2-5). These species were re-classed as forest dwellers since they were so low in abundance in the disturbed areas but proportionally in far greater numbers in intact forest. Out of the 18 species that were classed as edge dwellers, 10 were singletons.

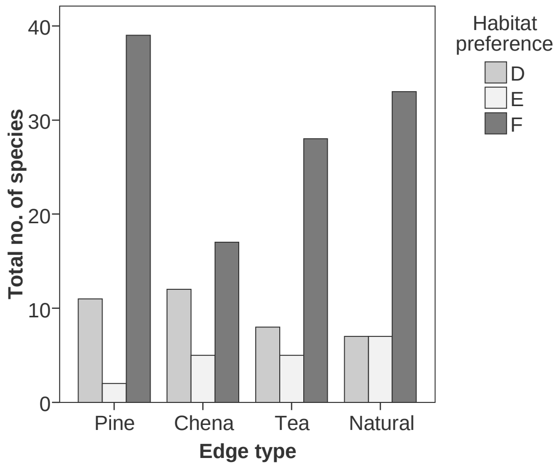

Figure 6.5. Total number of species showing proportions of disturbance tolerant (D), edge inhabitant (E) and forest interior inhabitant (F) ants occurring in each edge type.

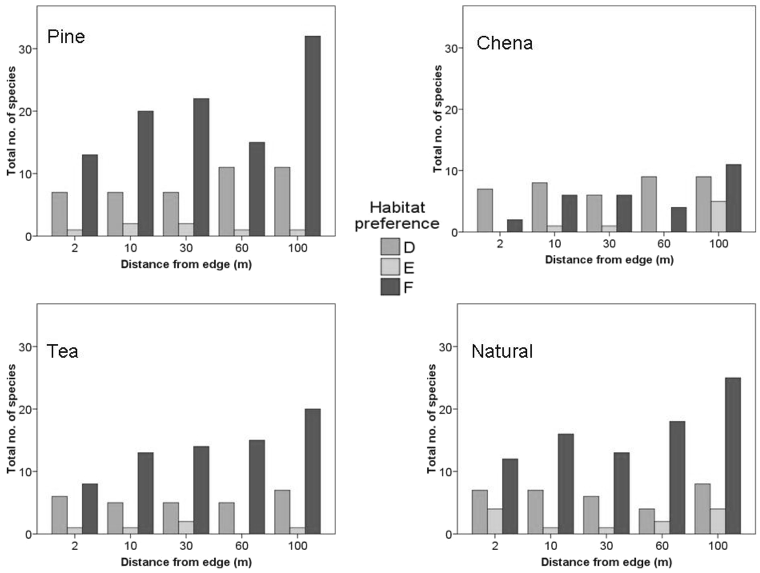

Figure 6.6. Proportions of disturbance tolerant (D), edge inhabitant (E) and forest interior inhabitant (F) ants with increasing distance from the edge within each edge type.

Overall, forest interior species richness increased for all edges, except chena, with increasing distance from the edge (Figure 6.6). Invasibility was highest in the chena edge (7.22), followed by pine (0.75) and tea edges (0.32), and lastly by the natural edge (0.22). In the scatter-plot matrix (Figure 6.7), the chena edge showed the most dramatic decline in invasibility with distance from the edge but still did not approach the relatively lower values of the other three edges. Tea edge and the natural edge were the most similar in demonstrating low levels of invasibility, with little change from edge to interior. Pine edge on the other hand had high invasibility at the edge but declined to similar levels as the natural edge with distance towards the interior.

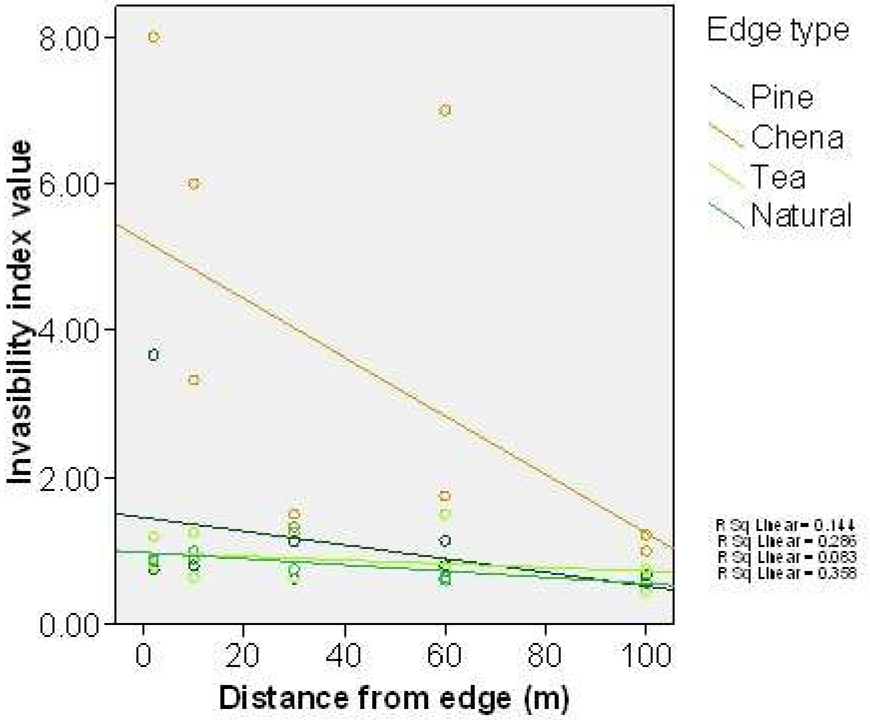

Figure 6.7. Scatterplot matrix of invasibility with increasing distance from the edge within each edge type. The R-squared linear coefficient (R sq Linear) is shown in the lower left hand corner of the figure.

6.4 Discussion

Conservation of tropical forest fragments is dependent on understanding the changes that occur when population dynamics and species interactions are altered as a result of edge creation. The study of edge effects in tropical forests is often carried out in the context of increasing fragmentation and the survival of species in increasingly small fragments. Yet, what constitutes a forest fragment can vary contextually and exploration of the effects of edges is dependent on the shape of the fragment and the scale of the taxa under study (Ewers & Didham 2007). Small patches are generally more prone to invasion by matrix dwelling species, but even relatively large fragments (> 40 sq km, just under half the size of the SFR) have been shown to have reduced diversity and increased tramp species presence compared to intact forest (Brühl *et al.* 2003).

However, large intact tracts of rainforest are not static, homogenous landscapes; tree falls and landslides create edges within the forest ecosystem and allow for a continuum of change. If these natural disturbances are adjacent to a pool of responding species that is different from those normally present (invasive colonists or exotics), then natural regeneration of the forest may be reduced, perhaps even obstructed (Hobbs & Huenneke 1992). Hence, if the degree of change that occurs as a result of the presence of an edge is greater than the natural variation that occurs within the forest, then the forest may start to lose its conservation value (Murcia 1995).

The present study adds to the growing body of research demonstrating how the matrix land use surrounding a forest can influence the degree of edge effect acting upon a forest patch. The results show that the composition of ant assemblages within forest bordered by different matrix land uses is significantly different and the degree of invasibility of the forest edge is potentially affected by the structure and level of disturbance of the forest/matrix edge.

The forest adjacent to pine showed a decrease in the ratio of disturbance tolerant ants to forest dwelling ants as distance from the edge increased, whereas forest bordered by tea showed low initial values but no real decline in the ratio as distance from the edge increased. Based on these results, the influence of the edge could be interpreted as greater in forest next to pine but these effects disappear after about 100 m. Forest bordered by tea, on the other hand, has a low invasion rate but the best fit line on the scatter-plot matrix could be extrapolated to mean the effects of the edge could potentially extend much further into the forest interior. Forest bordered chena, though having high invasion ratios overall, showed declines in invasion levels as distance from edge increased, but also showed that the influence of the edge could extend beyond 100 m from the edge.

Out of the human-made edges, pine plantation could be considered the most structurally similar to the forest. Contrary to expectations, there was high foliage density and low canopy cover at the border of the pine/forest edge. This could be due to the fact that there was difficulty in assessing the location of the border between the pine and forest as compared with the other three edges. It is possible that the space between the last pine row and the forest, once filled with gap specialists, is now in the process of succession and the forest border has become diffuse. The tall pine trees would nonetheless offer a windbreak and a degree of canopy cover that may allow the growth of forest interior understorey vegetation. In the SFR, experiments that tested the use of pine trees as a nurse species for late seral tree species during regeneration have shown that the pine trees can provide a protective canopy for these shade tolerant trees. However, thinning of the pine stands has to be carried out since the pine stands would compete for resources with the seedlings, and dense beds of pine needles can also create allelopathic conditions (Ashton *et al.* 1997).

However, the physical variables that were measured displayed minimal differences between the edge types. It is possible that the physical variables measured did not adequately measure the influence of the edge and so it is difficult to ascertain what factors the ant species are actually responding to. Only litter depth was significantly different between edge types and with increasing distance from the border. Litter dwelling ants and surface active ants may be responding to the availability of litter, which varies according to the vegetation composition at the edge. Maheswaran and Gunatilleke (1988) found significant differences between decomposition rates of forest tree litter and *D. linearis* litter within the forest, this could influence nesting patterns of litter dwelling ant species.

The pine/forest edge was adjacent to a border village. During field work for this study, villagers were observed walking through the forest to collect non-timber forest products (NTFP), and evidence of small tree/fuelwood removal was also observed. These minor disturbances could be contributing to the presence of disturbance tolerant ants all the way through the forest edge. Generally, large intact tracts of rain forest are thought to be less susceptible to invasion by exotic species, as long as human disturbance is minimal (Fine 2002). If there has been continuous disturbance to vegetation by humans in this edge, forest dwelling ant species may have gradually retreated from the area. Thus, the subsequent resource release may have allowed disturbance tolerant and/or invasive ants to colonise the area (Davis *et al.* 2000)

This could explain the lower levels of invasion in the tea/forest edge. The tea plantation was regularly harvested by the plantation owners, so the forest behind it was less accessible to other villagers. This did not necessarily mean that NTFPs were not being harvested. However, there was no evidence of it in the sampling sites. The chena/forest edge, on the other hand, did show evidence of recent palm sugar tapping. Also, a very small patch of chena fernlands was observed about 80 m in from the forest edge (outside the study sites), which could indicate a localised past disturbance or tree fall area that has been colonised by the ferns. This points to the alarming potential for the fern to invade deeper into the forest interior using tree falls as ‘stepping stones’ and preventing normal forest regeneration.

If only disturbance tolerant ants are examined, none of the four edge types showed a decline in these species. Two potential reasons could be inferred: disturbance tolerant ants have invaded the forest edge to greater than 100 m and therefore the extent of edge effects is potentially further reaching than examined or disturbance tolerant ants are naturally pervasive throughout the forest at low background levels and are only common in disturbed areas outside the forest due to reduced competition from forest dwelling ants. Carvalho and Vasconcelos (1999) found that ant communities in forest sites more than 300 m from an edge were significantly different from those communities found within 200 m from the edge.

Of the 22 disturbance tolerant species found inside the forest, there were six species that were deemed to be forest generalists rather than truly disturbance tolerant, as they were collected in the undisturbed forest interior. There is the possibility that the remaining 16 ant species are originally forest dwelling species that have managed to colonise disturbed habitats outside the forest and are not actually invasive. Perhaps only species such as *Anoplolepis gracilipes, Cardiocondyla nuda, Oecophylla smaragdina*, and *Odontomachus* sp. nr *haematodes* can be confidently classed as originally non-forest dwelling, as confirmed by their presence in the Colombo metropolitan area (N. Gunawardene pers. obs.). Due to the lack of data available on the biogeography of Sri Lankan ants, it is difficult to confidently class the other ants as truly invasive or just highly adaptable ants. In the future, it would also be interesting to look at the composition of forest dwelling ants in order to quantify the percentage of endemic species present in the edge. Wijesinghe and Brooke (2005) found that endemic birds and small mammals in the SFR did not utilise disturbed habitats and were generally confined to forest sites. Umetsu and Pardini (2007) found similar patterns with endemic small mammals in Brazilian Atlantic rain forest.

There is the potential that the differences in ant species richness and assemblage between the edges could be due to intrinsic patchiness of the SFR. Studies on the distribution of dominant tree species within the forest have shown habitat specialization relating to topography and canopy disturbance (Gunatilleke *et al.* 2006). Vasconcelos *et al.* (2003) also found ant species in the Amazon to be related to topographical variation. Hence, it is possible that the ants in the edges are responding to topographical differences within the edges. Since these were not quantified in the study, it is difficult to eliminate them as possible determinants of ant species distribution. Replication was also an issue in this study, as there were only two sites per edge type which reduces the interpretive power of the dataset. This was a result of difficulty in finding sites within edges that were uniform in aspect, elevation, and vegetation, since all these factors would contribute to increasing within-edge variability and potentially cloud any between edge patterns. Multiple collections from the same plots would increase the power of the dataset and allow for more in-depth analysis of patterns.

The findings from this study do provide a stepping stone towards understanding the responses of a particular taxon to different edge conditions. Around the SFR, pine plantations act as a good buffer against edge effects, but disturbance needs to be kept at a minimum to prevent disturbance tolerant ants from colonising the area. Tea/forest edges would be the next choice, as reduced accessibility to the forest would minimize anthropogenic disturbances and allow for the edges to seal naturally protecting the forest edge communities. Chena/forest edge should be rehabilitated to allow secondary succession to occur. If unchecked, this fern has the potential to permeate the forest and cause irreparable damage to the forest ecosystems.

For patches that are surrounded by agricultural land that will most likely not be restored or reforested in the future, allowing the edge to seal so that there is minimum invasion by matrix dwellers may be a more appropriate form of management for maintaining the biological integrity of the forest. In this case, it would be better to maintain a land use that would allow for edge-oriented plant species to seal the edge and reduce anthropogenic disturbance within the fragment. However, for areas where forest will eventually be encouraged to regenerate, it will be more beneficial to have analog forest, or land uses with vegetation that is more structurally similar to the forest so that animals can flow across the borders and recolonise regenerating areas.

6.5 References

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7. Synthesis

7.1 Overview- findings and conclusions

Species diversity appears to be declining in all biomes of the world. The degree of loss in biodiversity can only be estimated if baseline information is available on existing species (Pimm *et al.* 1995). This study represents the first comprehensive collection of ground dwelling ants in the Sinharaja Forest Rerserve (SFR), one of the last few relatively undisturbed forest remnants in a biologically diverse zone of Sri Lanka. The Wet Zone of Sri Lanka harbours the highest animal and plant diversity for the whole island (Erdelen 1996); one third of the plant species (845 species) is confined to this zone (Ashton & Gunatilleke 1987). Dias (2002) lists 246 Sri Lankan ant species curated in the Kelaniya University and Colombo Museum collections; the fact that 173 species were found in small sections of the western half of SFR alone demonstrates the high ant diversity of the reserve and its potential to harbour a high proportion of the ant diversity of the entire island.

Perhaps the fact that the reserve is an important biological storehouse does not need to be re-iterated by ants. However, this study provides a baseline for the future monitoring of the forest and its ant diversity. Without such baseline studies, changes in the community may not be detected. The role of ants in ecosystem functioning is well known (Wilson & Hölldobler 2005); they fill multiple roles as major predators and scavengers and in some cases, as herbivores. Loss of major predators in a forest ecosystem can cause a ‘trophic cascade’ of increased herbivory, the consequence of which is a reduction in overall biodiversity (Terborgh *et al.* 2001).

Gauging the ant diversity present in this reserve also provides a standard for which smaller fragments in the region can be compared to. The distinct assemblages of ants within the three main collection areas inside the reserve and along its edge demonstrate the potential for further diversity to be harboured in smaller fragments. The two main methods (Winkler extraction and pitfall trapping) utilised in this study allowed the collection of a large proportion of the estimated species richness and enabled the comprehensive analysis of species assemblages across its variable topography. The change in ant assemblages from low to mid elevation on the slopes of western SFR further emphasized the need to conserve entire gradients within forest reserves. Also, the fact that logged forest assemblages of ground dwelling ants were significantly different from the adjacent unlogged forest drove home the point that this entire forest may have been permanently altered, had logging not been terminated in 1977.

The findings from the thesis also demonstrate the external influences along the forest borders and the effects of the different land uses in the matrix surrounding the forest. Ant assemblages revealed the detrimental presence of chena fernlands along the forest edge. The results add to studies that have shown that regeneration of forest is arrested due to dominance of invasive shrubs in forest clearings (Schrumpf *et al.* 2007).

7.2 Critique and future directions

The major disadvantage in the statistical robustness of the data set was the number of sites studied. Since four collections were carried out in each site in order to account for possible seasonal effects, collections in more sites were not feasible as man-power was limited. Since seasonal differences in rainfall and temperature did not appear to affect overall ant capture rates, multiple collections in one site did not appear to be necessary. In the future, ant collections in this region need only occur once, and at most twice, in one year in one collection area.

Even at such high intensity of collection, as was carried out in each plot in the three main forest areas, relatively high numbers of singletons were collected. It points to an overall rarity and patchiness of ant species, perhaps emulating the rarity and patchiness of particular tree species. The rarity of so many species in the collection perhaps increases the resistance of the reserve to invasion by exotics. Lyons and Schwartz (2001) have demonstrated, using experimental thinning of grassland species, that removal of rare species, as opposed to abundant species, increases susceptibility to invasion by exotics.

It could also point to the presence of a component of the biota that was not effectively collected by the sampling methods. There were a number of ants that were incidentally collected either on tree falls or from simply dropping out of the canopy (see Appendix). For example, five *Polyrhachis* species (*Polyrhachis aculeata gibbosa, Polyrhachis yerburyi, Polyrhachis thrinax, Polyrhachis rastellata,* and

Polyrhachis aedipus) were collected solely by hand collection and therefore were not included in any of the analyses. Other commonly canopy dwelling ant genera, such as *Dilobocondyla* and *Cataulacus*, were also caught by opportunistic collection. Future studies in western SFR should look at canopy dwelling ants, as they may have a closer relationship with tree species distribution. Collection in eastern SFR would also be necessary to gain a better perspective of the total species diversity of the reserve. Eastern SFR has a longer elevation range, with some of the upper slopes being dominated by monotypic stands of *Shorea garneri*. This difference in topography and vegetation indicates the potential for a much greater ant species diversity to exist.

As this was a study focusing on SFR, there is the potential that it is not representative of the remaining forest patches in the region. The SFR is relatively well protected and the public are not permitted past a certain point in the forest. Surrounding forest patches could contain a very different set of ants as many of the patches are disturbed or degraded. Further study should be carried out in these patches and comparative studies made to assess the status of the ant communities. Another potential factor that was not analysed was slope aspect. Gunatilleke *et al.* (2006) make reference to the differences in tree species distribution in relation to aspect within the Forest Dynamics Plot. All sites in this study had a south west facing aspect; it would be of interest to see whether there are significant differences in ant assemblages on north facing slopes of the reserve.

Another issue was that multiple year comparisons were not made. In retrospect, collections should have been made in twice in one year and twice in the following year, rather than four times in one year. However, as the SFR is a dipterocarp dominated forest, the potential issue with multiple year study in the SFR is the mast fruiting events that occur every few years. Increased resource availability and hence increased ant activity would potentially cloud any spatial distribution patterns. Unfortunately, current research points to a variety of causes of mast fruiting events, making its predictability difficult.

It would be a great boon to understanding spatial distribution of ants in Sri Lanka if similar high density collections were to occur in forested areas in other parts of the country. Large tracts of dry forest occur in the Dry Zone of the country. Thus, comparisons of ant species diversity along a north to south gradient would provide further information on the factors that influence spatial distribution of the ant species in Sri Lanka

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8. Appendix.

Table 8.1. List of ant species collected in western Sinharaja Forest Reserve, Sri Lanka showing their occurrence (*) in the different collection areas: Logged forest (L); Unlogged forest (U); Forest Dynamics Plot (FDP); Edge sites (E); Disturbed areas (D); and hand collected species (H). Species were determined by taxonomist (far right column) or by author using available keys. Highlighted species were not included in analyses.

Subfamily	Genus	Species	Code	L	U	FDP	E	D	H	Keys used	Det. by
Aenictinae	*Aenictus*	*binghami* Forel	SL014	*	*	*	*		*	Bingham 1903	N.R. Gunawardene
	Aenictus	sp. nr *punensis* Forel	SL124		*	*			*	Bingham 1903	N.R. Gunawardene
Amblyoponinae	*Ambylopone*	sp. nr *amblyops* Karavaeiev	SL128	*			*			Wu 2001	N.R. Gunawardene
	Myopopone	Head only maybe *M. castanea* Smith	head only						*	Bingham 1903	N.R. Gunawardene
Aneuretinae	*Aneuretus*	*simoni* Emery	SL008	*	*	*	*			Bingham 1903	N.R. Gunawardene
Cerapachyinae	*Cerapachys*	sp. *dohertyi-cribrinodis* gp. sensu Brown 1975	SL011	*							M. L. Borowiec
	Cerapachys	sp.	SL026	*	*	*					
	Cerapachys	sp.	SL074	*	*						
	Cerapachys	sp.	SL101	*	*	*					
	Cerapachys	sp.	SL104	*		*					
	Cerapachys	sp.	SL106	*	*	*					
	Cerapachys	sp.	SL111		*						
	Cerapachys	*fragosus* (Roger)	SL130	*							M. L. Borowiec
	Cerapachys	sp.	SL144		*						
	Cerapachys	sp.	SL152		*						
	Cerapachys	sp.	SL165			*					
	Cerapachys	*typhlus* (Roger)	SL173			*					M. L. Borowiec
	Cerapachys	sp.	SL217						*		
	Cerapachys	sp.	SL215						*		
	Cerapachys	sp.	SL216						*		

Table 8.1 cont'd

Subfamily	**Genus**	**Species**	Code	**L**	**U**	**FDP**	**E**	**D**	**H**	**Keys used**	**Det. by**
Dolichoderinae	*Bothriomyrmex*	*wroughtoni* Forel	SL158				*			Bingham 1903	N.R. Gunawardene
	Dolichoderus	sp.	SL075	*							
	Dolichoderus	sp.	SL089	*		*	*	*			
	Tapinoma	sp.	SL056	*	*		*				
	Tapinoma	sp.	SL131	*			*	*			
	Tapinoma	sp.	SL147			*					
	Tapinoma	sp.	SL156				*				
	Tapinoma	sp.	SL157				*				
	Technomyrmex	*albipes* (Fr. Smith)	SL004	*	*	*	*			Bingham 1903	N.R. Gunawardene
	Technomyrmex	*bicolor* Emery	SL007	*	*	*	*			Bingham 1903	N.R. Gunawardene
Ectatomminae	*Gnamptogenys*	*laevior* gp. sp.nr *delta* sp nv or *lacunosa* sp nv	SL110		*					Lattke 2004	N.R. Gunawardene
	Gnamptogenys	*coxalis* gp sp nr *binghami* Forel	SL171			*				Lattke 2004	N.R. Gunawardene
Formicinae	*Acropyga*	sp.	SL093	*		*					
	Acropyga	*acutiventris* Roger	SL203				*			Bingham 1903	N.R. Gunawardene
	Anoplolepis	*gracilipes* (Smith)	SL194				*			Bingham 1903	N.R. Gunawardene
	Camponotus	sp.	SL034	*	*		*				
	Camponotus	sp.	SL060	*	*	*	*				
	Camponotus	sp.	SL083	*	*	*	*		*		
	Camponotus	sp.	SL138	*	*		*				
	Camponotus	sp.	SL169			*					
	Camponotus	sp.	SL172			*					
	Camponotus	sp.	SL179				*				
	Camponotus	sp.	SL187				*	*			
	Camponotus	sp.	SL213						*		
	Camponotus	sp.	SL212						*		
	Forelophilus	sp.	SL092	*							
	Lepisiota	*(Acantholepis)* sp. nr *capensis* (Mayr)	SL126		*		*			Bingham 1903	N.R. Gunawardene

Table 8.1 cont'd

Subfamily	**Genus**	**Species**	Code	**L**	**U**	**FDP**	**E**	**D**	**H**	**Keys used**	**Det. by**
Formicinae	*Lepisiota*	sp.	SL189				*	*			
cont'd	*Myrmoteras*	*binghami* Forel	SL039		*	*				Bingham 1903	N.R. Gunawardene
	Oecophylla	*smaragdina* (Fabricius)	SL178				*			Bingham 1903	N.R. Gunawardene
	Paratrechina	sp.	SL001	*	*	*	*				
	Paratrechina	sp.	SL036	*	*	*	*				
	Paratrechina	*bourbonica* (Forel)	SL088	*			*	*			Dr. S. Shattuck
	Paratrechina	*minutula* (Forel) gp.	SL105	*		*	*				Dr. S. Shattuck
	Paratrechina	*minutula* (Forel) gp.	SL181				*				Dr. S. Shattuck
	Paratrechina	sp.	SL183				*				
	Plagiolepis	sp. nr *alluaudi* Wetterer	SL198				*				N.R. Gunawardene
	Polyrhachis	*(Myrmhopla) hippomanes ceylonensis* Emery	SL068		*						Dr.R. Kohout
	Polyrhachis	*(Hemioptica) bugnioni* Forel	SL069	*	*	*					Dr.R. Kohout
	Polyrhachis	*(Myrma) illaudata* Walker	SL085	*							Dr.R. Kohout
	Polyrhachis	*(Myrma) convexa* Roger	SL192				*	*			Dr.R. Kohout
	Polyrhachis	*(Myrmhopla)* sp. (nr *hippomanes ceylonensis*)	SL195				*	*			Dr.R. Kohout
	Polyrhachis	*(Myrma) aculeata gibbosa* Forel	SL204						*		Dr.R. Kohout
	Polyrhachis	*(Myrma) yerburyi* Forel	SL205						*		Dr.R. Kohout
	Polyrhachis	*(Myrmothrinax) thrinax* Roger	SL206						*		Dr.R. Kohout
	Polyrhachis	*(Cyrtomyrma) rastellata* (Latreille)	SL208						*		Dr.R. Kohout
	Polyrhachis	*(Myrmhopla) aedipus* Forel	SL209						*		Dr.R. Kohout
	Pseudolasius	*familiaris* (Smith)	SL140		*	*				Bingham 1903	N.R. Gunawardene
Leptallininae	*Protanilla*	sp.	SL080						*		
	Protanilla	sp.	SL108	*							
	Protanilla	sp.	SL129		*	*					
Myrmicinae	*Acanthomyrmex*	*luciolae* Emery		*			*			Moffett 1986	N.R. Gunawardene

Table 8.1 cont'd

Subfamily	**Genus**	**Species**	Code	**L**	**U**	**FDP**	**E**	**D**	**H**	**Keys used**	**Det. by**
Myrmicinae	*Cardiocondyla*	*nuda* Mayr		*	*		*	*		Bingham 1903	N.R. Gunawardene
cont'd	*Cardiocondyla*	*wroughtoni* Forel					*			Bingham 1903	N.R. Gunawardene
	Carebara	Subgenus *Oligomyrmex*		*	*	*	*				N.R. Gunawardene
	Carebara	Subgenus *Oligomyrmex*		*							N.R. Gunawardene
	Cataulacus	*latus* Forel	SL024	*	*					Bolton 1974	N.R. Gunawardene
	Cataulacus	*simoni* Emery	SL120							Bolton 1974	N.R. Gunawardene
	Crematogaster	sp.	SL022	*		*	*				*Crematogaster*
	Crematogaster	sp.	SL062	*	*	*					currently
	Crematogaster	sp.	SL119		*	*					being
	Crematogaster	sp.	SL136	*							determined by
	Crematogaster	sp.	SL146				*				Dr. S. Hosoishi
	Crematogaster	sp.	SL148			*					
	Crematogaster	sp.	SL174		*		*				
	Crematogaster	sp.	SL182				*				
	Crematogaster	sp.	SL202				*				
	Dilobocondyla	sp.	SL214						*		
	Meranoplus	*loebli* sp nv	SL018	*						Shodl 1998	N.R. Gunawardene
	Meranoplus	*bicolor* (Guérin-Méneville)	SL188				*	*		Shodl 1998	N.R. Gunawardene
	Meranoplus	*rothneyi* Forel	SL196				*			Shodl 1998	N.R. Gunawardene
	Monomorium	*floricola* gp.	SL023	*	*	*	*				Dr. B. Heterick
	Monomorium	*hildebrandti* gp sp. cf. *australicum* Forel	SL025	*	*	*	*				Dr. B. Heterick
	Monomorium	*destructor* gp.	SL137	*		*					Dr. B. Heterick
	Monomorium	*hildebrandti* gp sp. nr *subcoecum* Emery	SL161				*				Dr. B. Heterick
	Monomorium	*floricola* Jerdon	SL170			*	*				Dr. B. Heterick
	Myrmecina	*curtisi* Donisthorpe	SL116		*					Tiwari 1994	N.R. Gunawardene
	Myrmicaria	*brunnea* Saunders	SL032	*	*	*					N.R. Gunawardene

Table 8.1 cont'd

Subfamily	**Genus**	**Species**	Code	**L**	**U**	**FDP**	**E**	**D**	**H**	**Keys used**	**Det. by**
Myrmicinae	*Myrmicaria*	sp. A (Bolton)	SL043		*	*	*				N.R. Gunawardene
cont'd	*Pheidole*	sp.	SL006	*	*	*	*				*Pheidole*
	Pheidole	sp.	SL019	*	*	*					currently
	Pheidole	sp.	SL027	*	*	*	*				being
	Pheidole	sp.	SL028	*	*	*	*				determined by
	Pheidole	sp.	SL029	*	*						Dr. K. Eguchi
	Pheidole	sp.	SL030	*	*	*	*				
	Pheidole	sp.	SL049		*	*	*				
	Pheidole	sp.	SL063	*	*	*	*				
	Pheidole	sp.	SL064		*						
	Pheidole	sp.	SL067	*	*	*	*				
	Pheidole	sp.	SL070	*	*	*	*				
	Pheidole	sp.	SL077	*	*	*	*	*			
	Pheidole	sp.	SL090	*							
	Pheidole	sp.	SL091	*	*	*	*				
	Pheidole	sp.	SL099						*		
	Pheidole	sp.	SL0Za	*	*	*	*				
	Pheidole	sp.	SL0Zb	*	*	*	*				
	Pheidole	sp.	SL0Zc	*	*	*	*				
	Pheidole	sp.	SL107	*			*				
	Pheidole	sp.	SL142	*		*	*				
	Pheidole	sp.	SL185				*	*			
	Pheidole	sp.	SL190				*	*			
	Pheidologeton	sp.	SL013	*	*	*	*				
	Pheidologeton	sp.	SL141		*	*	*				
	Pristomyrmex	sp. nr *profundus* Wang	SL017	*	*	*	*			Wang 2003	N.R. Gunawardene
	Pyramica	sp.	SL143	*							*Pyramica*
	Pyramica	sp.	SL159			*	*				currently

Table 8.1 cont'd

Subfamily	**Genus**	**Species**	Code	**L**	**U**	**FDP**	**E**	**D**	**H**	**Keys used**	**Det. by**
Myrmicinae	*Pyramica*	sp.	SL160				*				being
cont'd	*Pyramica*	sp.	SL163			*					determined by
	Pyramica	sp.	SL164			*					Dr. B. Fisher
	Pyramica	sp.	SL167				*				
	Recurvidris	*pickburni* sp. nv	SL095	*	*	*	*			Bolton 1992	N.R. Gunawardene
	Rhopalomastix	*rothneyi* Forel	SL133	*		*	*			Xu 1999	N.R. Gunawardene
	Rhopalothrix	sp.	SL102	*		*					
	Rogeria	sp.	SL057	*							
	Solenopsis	sp.	SL038	*	*	*	*				
	Solenopsis	sp.	SL113		*		*				
	Strumigenys	sp. sl-01	SL003	*	*	*	*				Dr. B. Fisher
	Strumigenys	sp. sl-02	SL044	*	*	*	*				Dr. B. Fisher
	Strumigenys	sp.	SL098	*	*	*					
	Strumigenys	sp.	SL109	*			*				
	Strumigenys	sp.	SL180				*				
	Tetramorium	sp.	SL002	*	*	*	*				*Tetramorium*
	Tetramorium	sp.	SL015	*	*		*				currently
	Tetramorium	sp.	SL020	*	*		*				being
	Tetramorium	sp.	SL054	*	*	*	*				determined by
	Tetramorium	sp.	SL055	*	*	*	*				Dr. S. Yamane
	Tetramorium	sp.	SL058	*	*	*	*				
	Tetramorium	sp.	SL059	*			*				
	Tetramorium	sp.	SL05A	*	*	*	*				
	Tetramorium	sp.	SL05B	*	*	*					
	Tetramorium	sp.	SL082	*	*	*	*	*			
	Tetramorium	sp.	SL117	*	*	*					
	Tetramorium	sp.	SL118		*	*	*				
	Tetramorium	sp.	SL123	*	*	*	*				

Table 8.1 cont'd

Subfamily	**Genus**	**Species**	Code	**L**	**U**	**FDP**	**E**	**D**	**H**	**Keys used**	**Det. by**
Myrmicinae cont'd	*Tetramorium*	sp.	SL127	*		*	*				
	Tetramorium	sp.	SL134	*		*	*				
	Tetramorium	sp.	SL135	*							
	Tetramorium	sp.	SL162			*	*				
	Tetramorium	sp.	SL184				*				
	Tetramorium	sp.	SL191				*	*			
	Tetramorium	sp.	SL197				*	*			
	Tetramorium	sp.	SL210						*		
	Tetramorium	sp.	SL211						*		
	Tyrannomyrmex	sp. nv	SL151			*					Dr. G. Alpert
	Vollenhovia	sp.	SL033	*	*	*					
	Vollenhovia	sp.	SL115	*	*	*	*				
	Vollenhovia	sp.	SL149			*					
	Vollenhovia	sp.	SL177				*				
	Vollenhovia	sp.	SL200				*				
Ponerinae	*Anochetus*	sp. nr *longifossatus* Mayr small	SL035	*			*			Brown 1978	N.R. Gunawardene
	Anochetus	sp. nr *nietneri* (Roger)	SL037	*	*	*	*			Brown 1978	N.R. Gunawardene
	Anochetus	sp. nr *longifossatus* Mayr big	SL042	*	*	*	*			Brown 1978	N.R. Gunawardene
	Anochetus	sp. nr *nietneri* (Roger)	SL168			*				Brown 1978	N.R. Gunawardene
	Cryptopone	*testacea* Emery	SL010	*	*	*	*			Bingham 1903	N.R. Gunawardene
	Discothyrea	sp.	SL050		*	*					
	Harpegnathos	*saltator* Jerdon	SL071		*	*			*	Bingham 1903	N.R. Gunawardene
	Hypoponera	sp.	SL016	*	*	*	*				*Hypoponera*
	Hypoponera	sp.	SL051		*		*				currently
	Hypoponera	sp.	SL052		*		*				being
	Hypoponera	sp.	SL066	*		*					determined by
	Hypoponera	sp.	SL114	*	*	*					Dr. T. Varghese
	Leptogenys	sp.	SL041		*						

Table 8.1 cont'd

Subfamily	**Genus**	**Species**	Code	**L**	**U**	**FDP**	**E**	**D**	**H**	**Keys used**	**Det. by**
Ponerinae cont'd	*Leptogenys*	sp.	SL065	*	*	*					*Leptogenys* currently being determined by Dr. T. Varghese
	Leptogenys	sp.	SL072		*	*					
	Leptogenys	sp.	SL125		*	*	*				
	Leptogenys	sp.	SL155				*				
	Leptogenys	sp.	SL175			*					
	Leptogenys	sp.	SL176			*					
	Leptogenys	sp.	SL199				*				
	Myopias	*amblyops* Roger	SL132	*						Bingham 1903	N.R. Gunawardene
	Odontomachus	sp. nr *haematodes* Linnaeus	SL153				*	*		Bingham 1903	N.R. Gunawardene
	Pachycondyla	*(Bothroponera) rufipes* Jerdon	SL046	*	*	*				Bingham 1903	N.R. Gunawardene
	Pachycondyla	*(Mesoponera) melanaria* Emery	SL053	*	*	*	*			Bingham 1903	N.R. Gunawardene
	Pachycondyla	*(Bothroponera) sulcata* Frauenfeld	SL096			*	*			Bingham 1903	N.R. Gunawardene
	Pachycondyla	*(Ponera) truncata* Smith	SL100	*	*	*				Bingham 1903	N.R. Gunawardene
	Pachycondyla	*(Brachyponera) jerdoni* Forel	SL154				*			Bingham 1903	N.R. Gunawardene
	Ponera	sp.	SL048	*	*	*	*				
Pseudomyrmicinae	*Tetraponera*	*difficilis* (Emery)	SL121	*						Ward 2001	N.R. Gunawardene
	Tetraponera	*attenuata* F. Smith	SL166			*				Ward 2001	N.R. Gunawardene