Leaf litter ant communities in tropical lowland rain forests in Sabah, Malaysia: effects of forest disturbance and fragmentation

vorgelegt von
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'At last they reached the primeval forest, huge trees swathed in luxuriant creepers, an inextricable tangle, and awe descended upon them. They cut their way through the undergrowth. They walked in twilight and only now and then caught through the dense foliage above them a glimpse of sunshine. They saw neither man nor beast, for the denizens of the jungle are shy and at the first sound of footsteps vanish from sight.'

William Somerset Maugham, *Neil MacAdam*

Für meine Eltern

1 Introduction

A general increase in species richness can be detected in most animal and plant groups moving from the temperate latitudes to the tropics, culminating in the terrestrial ecosystem where most living organisms of Earth are resident: the evergreen tropical rain forests. The determinants and primary causes of this gradient and the mechanisms responsible for the maintenance of this high diversity are manifold and widely discussed (Blackburn & Gaston, 1996; Colwell & Hurtt, 1994; Connell, 1978; Flenley, 1993; Gaston, Blackburn & Spicer, 1998; Linsenmair, 1995; 1997; MacArthur, 1969; Paine, 1966; Rhode, 1997; Willig & Lyons, 1998) since noticed by the first naturalists (Wallace, 1869). The lowland tropical rain forest is the most species rich terrestrial ecosystem harbouring more than 50-75% of all living organisms on ca. 6-7% of the land area (Linsenmair, 1990; Wilson, 1992).

Invertebrates contribute most to the high biodiversity of tropical rain forests. An unexpected high species richness of arthropods which even resulted in new global estimations of biodiversity was recorded in studies of the rain forest canopy (Basset, 1991; Basset, Aberlenc & Delvare, 1992; Basset & Kitching, 1991; Erwin, 1982; 1995; Floren & Linsenmair, 1994; Gaston & Hudson, 1994; May, 1988; Stork, 1987; 1991) and was also confirmed for the forest floor layer by studies of different insect groups (Brühl, Gunsalam & Linsenmair, 1998; Fittkau & Klinge, 1973; Hammond, 1990; Stork, 1988). Apart from the preservation of a huge amount of the world's overall biodiversity, tropical rain forests are of a unique importance due to their ecosystem services for climate stabilisation as major carbon stores, for erosion prevention and for the global and local water balance (Laurance, 1998; Linsenmair, 1997).

Tropical rain forests are disappearing from the surface of the Earth at fast rates. It has been estimated that by 1990 24% of the lowland tropical rain forests on Earth had been cleared (Turner & Corlett, 1996) and estimates for actual global rates of rainforest loss approach an area larger than Poland per year. The relentless deforestation of tropical forests driven on a vast scale by logging highly valuable tropical timber together with the extent of fragmentation of forests and their conversion to plantation has given rise to great international concern about the potential loss of biodiversity and our global responsibility was conceived at the UNCED conference in Rio in 1992 (Holloway, Kirk-Springs & Chey, 1992; Linsenmair, 1997; Lovejoy, 1994; Schminke, 1997).

Although extinction rates are difficult to determine, recent calculations suggest that in tropical rain forests the absolute rate of species loss is now on the order of 1 000 to 10 000 times before human intervention (Edwards & Abivardi, 1998; Vitousek et al., 1997). Every year 27 000 animal species go extinct as a result of the continuing deforestation of tropical forest (Wilson, 1992). As we simply do not know how important species diversity is for the long term stability and function of ecosystems (Cardinale, Nelson & Palmer, 2000; Emmerson & Raffaelli, 2000; Lawton, 1994; Linsenmair, 2000; Mawdsley, 1996; Naem et al., 1994; Rainey et al., 2000; Symstad et al., 1998) if for no other reason, prudence would urge the preservation of as much diversity as possible (Edwards & Abivardi, 1998). Unfortunately few tropical nations have large areas of undisturbed lowland rain forests remaining and only 5% of their forested area is sufficiently protected today (Aide et al., 2000; Turner & Corlett, 1996). Therefore logged-over forests and forest fragments will become increasingly important

in economical as well as ecological planning in the near future (Chazdon, 1994, 1998; Lugo, 1995; Saunders, Hobbs & Margules, 1991).

The urgent need of sustainable management of natural forests including the maintenance of biodiversity, economic viability and sustainability of timber yields (Bawa & Seidler, 1998), has been recognised (Porritt, 1993; Uebelhör & von der Heyde, 1993), but only a few forests in the world are managed in a way that merits this attribute (Linsenmair, 1997). The efficacy of the developed concepts for a sustainable forest management is mostly based on models that include only a few commercial tree species. This neglects the fact that the continuity of a tropical forest ecosystem largely depends on complex interactions between many animals and plants as obvious in processes like decomposition or pollination (Didham, 1996; Miller, 1993). Long-term economically sustainable forest management will therefore only be possible if the conservation of a large proportion of biodiversity is simultaneously guaranteed although the compatibility of the two is questionable (Ehrlich & Daily, 1993; Hilborn & Ludwig, 1993; Ludwig, 1993; Ludwig, Hilborn & Walters, 1993; Mooney & Sala, 1993). So far not many studies on biodiversity included the remaining systems of logged over and regrowth secondary forests or forest fragments of different sizes in their inventory program (Chazdon, 1994), although these habitats will be the target areas for future conservation and management concepts.

The tropical rain forests of Southeast Asia are recognised as one of the oldest living ecosystems of the planet. Fossil records show that they have existed in more or less their present form for 70 to 100 million years (Whitmore, 1984). The forests of Borneo are especially species rich in their floral and faunal composition consisting of many endemic species (MacKinnon *et al.*, 1996) with a recognised hotspot of biodiversity in the north-western part of the island, in Sabah, a federal state of Malaysia (Kitching, 2000; Myers, 1988; Wilson, 1992). Although Sabah has about 45% (33 486 km² in 1992) of its land under natural forest, the forest cover is disappearing at a fast rate (Chey, Holloway & Speight, 1997). Today Sabah has almost depleted its primary forests outside conservation areas because of the commercial value of its dipterocarp rain forests (Chung *et al.*, 2000). 40% of the state area is designated commercial forest reserve, supposed to be managed on a sustainable basis (Marsh *et al.*, 1996). In practice, little evidence exists to suggest that this is the case (Marsh *et al.*, 1996) and most forests are instead mined for their timber (Putz, Dykstra & Heinrich, 2000). More than two thirds of the commercial forest reserves have been turned into second growth forests of low standing volume by a combination of resource rents, accelerated timber production, inappropriate logging methods and a lack of stand compatible silviculture (Uebelhör & von der Heyde, 1993). 3.5% of the production forests are selectively logged annually. (Lambert, 1992).

One measurement to counteract deforestation is to invest in timber plantation: by 1999 about 138 400 ha (around 2% of Sabah's land area) had been planted with forest plantation species, thereof 57 000 ha with *Acacia mangium*, a fast growing exotic tree species (Chung *et al.*, 2000). Many logged over and regenerating forests are threatened by conversion to other land uses because they are close to the agricultural frontier and of relatively easy access (Bawa & Seidler, 1998). In the last decades 1 Mio ha of forest land have been converted into large scale monocultures of oil palm plantations, a major cash crop for the state economy.

Plate 1:
Large tracts of primary lowland rain forest remain in only a few locations in Sabah. The Danum Valley Conservation Area on the east coast with its 438 km² is one of the two semi-protected parks.

Today 40% of Sabah's land area is designated commercial forest reserve. More than two thirds have been turned into highly disturbed logged over forests with a drastically altered stand structure.

Oil palm plantations are forming the picture of the landscape today. The vegetation remaining after the clear cut catches fire easily especially in dry ENSO years.

The first timber concession in Sabah was issued in 1879. Since then log production has increased constantly reaching its highest peak in 1978 when the volume exceeded 13 Mio m³ (Kleine & Heuveldop, 1993). With the start of the timber boom in the 1960s, economic pressure led to cutting cycles between 20-30 years and with the change to heavy machinery logging damage increased at an alarming rate (Whitmore & Sayer, 1992).

Forestry in Sabah involves harvesting all healthy, commercially viable trees with a girth of 60 cm, which occur on slopes of < 20° (Marsh & Greer, 1992). The logs are usually extracted by skidding to the roadside with bulldozers or a log landing from which they are removed by trucks. During the first logging operation an average of 8-12 trees are harvested per logged hectare, yielding 80-150 m³ha^{-1} of timber (Healey, Price & Tay, 2000; Lambert, 1992). Although only 3-7% of trees are extracted, over 50-80% of trees > 30 cm can be destroyed by logging and road building (Lambert, 1992; Marsh et al., 1996), 40-70% of the residual trees are damaged and 15-40% of the logged area is traversed by bulldozers leaving open spaces, compacting soils and displacing topsoil (Healey, Price & Tay, 2000; Pinard, Barker & Tay, 2000). These levels of extraction and damage are higher than in most other tropical regions due to the dominance of large dipterocarp trees in these forests (Johns, 1992a). Additionally Sabah is among the three countries where forests were clear felled for wood chips (Johns, 1992a). After logging there remains a mosaic of vegetation types: relatively undisturbed forest, especially on slopes or ridges, areas dominated by pioneer trees (e.g. *Macaranga, Octomeles, Duabanga*), open areas with grasses, ferns, vines and climbing bamboo (*Dinochloa*) and exposed and compacted mineral soil with little or no vegetation cover (Bawa & Seidler, 1998; Willott et al., 2000).

Regrettably, there is little information available concerning the response of many species groups to forest disturbance and fragmentation and the insights gained from studies in the Neotropics or with a more severe disturbance gradient are not easily transferable to the situation in Sabah. Current views are biased by the reactions of larger animals which are only a part of the total biological diversity of the forests (Johns, 1992a). In birds the effects are variable, certain guilds are hit hard by logging and especially the insectivores usually decline (Gascon, 1998; Johns, 1992a; Jullien & Thiollay, 1996; Lambert, 1992; Mason, 1996; Stouffer, 1998; Stouffer & Bierregaard, 1995; Styring & Ickes, 2001). The data on mammals also indicate responses to logging and fragmentation, ranging from withdrawal and local extirpation to increases in the abundance of some species (Chiarello, 2000; Laidlaw, 2000). On the response of primates to logging, more data are available than on any other mammal group, but consistent trends are hard to pick out (Johns, 1992b; Laidlaw, 1996). Invertebrate targets are often butterflies and moths (Beck &Schulze, 2000; Chey, Speight & Holloway, 1992; Chey, Holloway & Speight 1997; Hamer & Hill, 2000; Hill et al., 1995; Schulze, 2000; Shahabuddin & Terborgh, 1999; Willott et al., 2000). They usually show a reduced species richness and abundance in logged forests as compared with primary forests. Although data on certain invertebrate taxa are increasing (Eggleton et al., 1997; Vasconcelos, 1999), there remains a critical deficiency of information on the impact of logging on this first tier of forest-inhabiting animals at the community level (Bawa & Seidler, 1998; Kim, 1993).

Ants are an insect group standing out in terms of its biomass, number of individuals and ecological relevance in tropical rain forests. 15% of the entire animal biomass of the Amazonia terra firme rain forests is composed of ants, with each hectare of soil containing more than 8 Mio ants (Fittkau & Klinge, 1973; Hölldobler & Wilson, 1990). They thrive in all strata of the forest (Brühl, Gunsalam & Linsenmair, 1998), use a wide variety of food resources (Hölldobler & Wilson, 1990; Kaspari, 2000) and contribute to species richness by their manifold interactions with other organisms (Schultz & McGlynn, 2000). Generally 45-50% of all macro invertebrates in the leaf litter are ants (Adis et al., 1989; Brühl, 1996; Burghouts et al., 1992; Lavelle & Kohlmann, 1984; Olson, 1994). The local diversity of ants is also very high: 524 species were recorded in about 4 km² of rain forest in Sabah and thereof 139 species were collected in only 60 m² of leaf litter (Brühl, Gunsalam & Linsenmair, 1998). All ants living in soil and leaf litter layer can be classified as ecosystem engineers (Jones, Lawton & Shachak, 1994). This is due to their effects on soil structure and processes which indirectly affect the flow of energy and material in ecosystems as well as the habitat of other species (Folgarait, 1998). Worldwide, they turn and enrich more soil than earthworms (Wilson, 2000) enhancing the mineralisation of nutrients (Gunadi & Verhoef, 1993) and microbial activity in the soil (Dauber & Wolters, 2000). In tropical rain forests ground-dwelling ants are especially recognised in their role as the most important invertebrate predators which exert a structuring influence on the arthropod community (Carroll & Janzen, 1973; Hölldobler & Wilson, 1990).

Knowledge of ant communities and their ecological functions are critical for the understanding of tropical ecosystems. The stationary nesting habit of these social insects with their unique pattern of resource control add a distinctive life form to the taxa studied in biodiversity monitoring programs so far. The sessile part of their way of life and their low mobility compared to other animal groups also guarantees a tighter habitat connection. Additionally, their taxonomy is fairly robust and well known (Bolton, 1995; Brown, 2000). Identification to genus level is comparatively easy because an excellent key is available (Bolton, 1994) and the sorting of specimens to morphospecies needs only relatively little training (Alonso, 2000; Andersen, 1997). Furthermore, ants of the leaf litter can be collected in a standardised and quantitative way with established sampling methods like the litter extraction with Winkler sacks (Bestelmayer et al., 2000; Besuchet, Burckhardt & Löbl, 1987; Brühl, Mohamed & Linsenmair, 1999; Delabie et al., 2000; Olson, 1991).
Ants have been found to overlap with other taxa in their richness or diversity and their responses to environmental change in many studies in different habitats (Alonso, 2000; Lawton et al., 1998). They have successfully been used as bioindicators in Australia or Brazil for many years (Andersen, 1993; Majer, 1996; Majer et al., 1984). Together with their relative stability, moderate diversity and sensitivity to microclimate the ground-dwelling ant community fulfils all criteria of a potential taxon for the measurement of biodiversity (Hammond, 1994; Kremen, 1992; Kremen et al., 1993; Lawton et al., 1998; Pearson, 1995). Experts on leaf litter ants are now forming a worldwide network with standardised collecting methods and a database which will allow the comparison of community patterns on a global scale (Agosti et al., 2000).

Plate 2: Ants of the leaf litter are recognised as important predators of the ground-dwelling arthropod community (1. *Harpegnathos spec.;* 2. + 3. *Letogenys spp.;* 4. *Odontomachus rixosus).* The soil turning activity of ants recently led to their identification as ecosystem engineers with a substantial impact on nutrient cycling (5. + 6.).
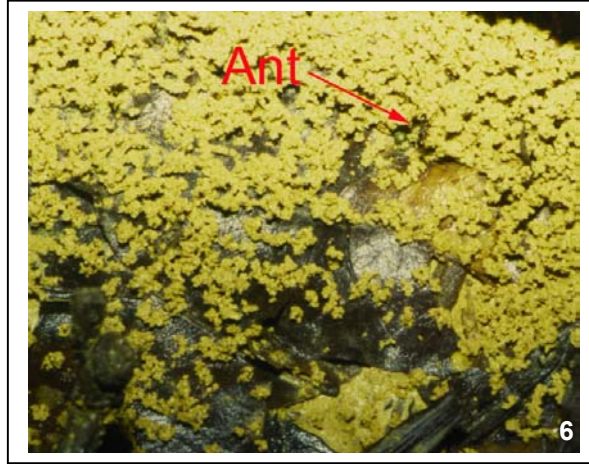
Leaf litter ants are expected to react towards logging as the microclimate is altered due to the opening of the forest canopy and the use of heavy machinery during timber operations has a direct impact on the soil and forest floor. I initially planned to study the effects of different logging methods (conventional, reduced impact logging, cable harvesting) on the leaf litter ant community. Due to logging operations with different extraction rates before the experimental harvesting, comparisons between treatments were impossible and this project could therefore not be realized.

This thesis focuses on the effects of anthropogenic disturbance and fragmentation of lowland rain forests on leaf litter ant communities in Sabah and considers the following principal questions:

- How does forest disturbance affect species richness, diversity and community composition of leaf litter ants?

- Which effect does forest fragmentation have on the same aspects of the leaf litter ant community?

- Is the leaf litter ant community of forest fragments isolated by the surrounding matrix?

- Which environmental parameters exert causal influences on the leaf litter ant community?

I would like to point out that most chapters of this thesis are about to be published in journals and therefore some redundancy could not be avoided.

2   Study Sites

Sabah, the second largest state of Malaysia, is situated in the north-east of Borneo and is accounting for a total land mass of approximately 7.37 Mio ha. It falls into the intertropical convergence zone free from hurricanes; its climate is marine equatorial with an average temperature of 26°C and regional distributions of rainfall range from 1 700 to 5 100 mm per year.

Research plots were established in four study sites in the lowland rain forests on the east coast namely in the Danum Valley Conservation Area (DVCA), the Sepilok Forest Reserve (SFR), the Kebun Cina Forest Reserve (KCFR) and the Deramakot Forest Reserve (DFR) (Fig. 1). Distances between the four study areas are displayed in Tab. 1.
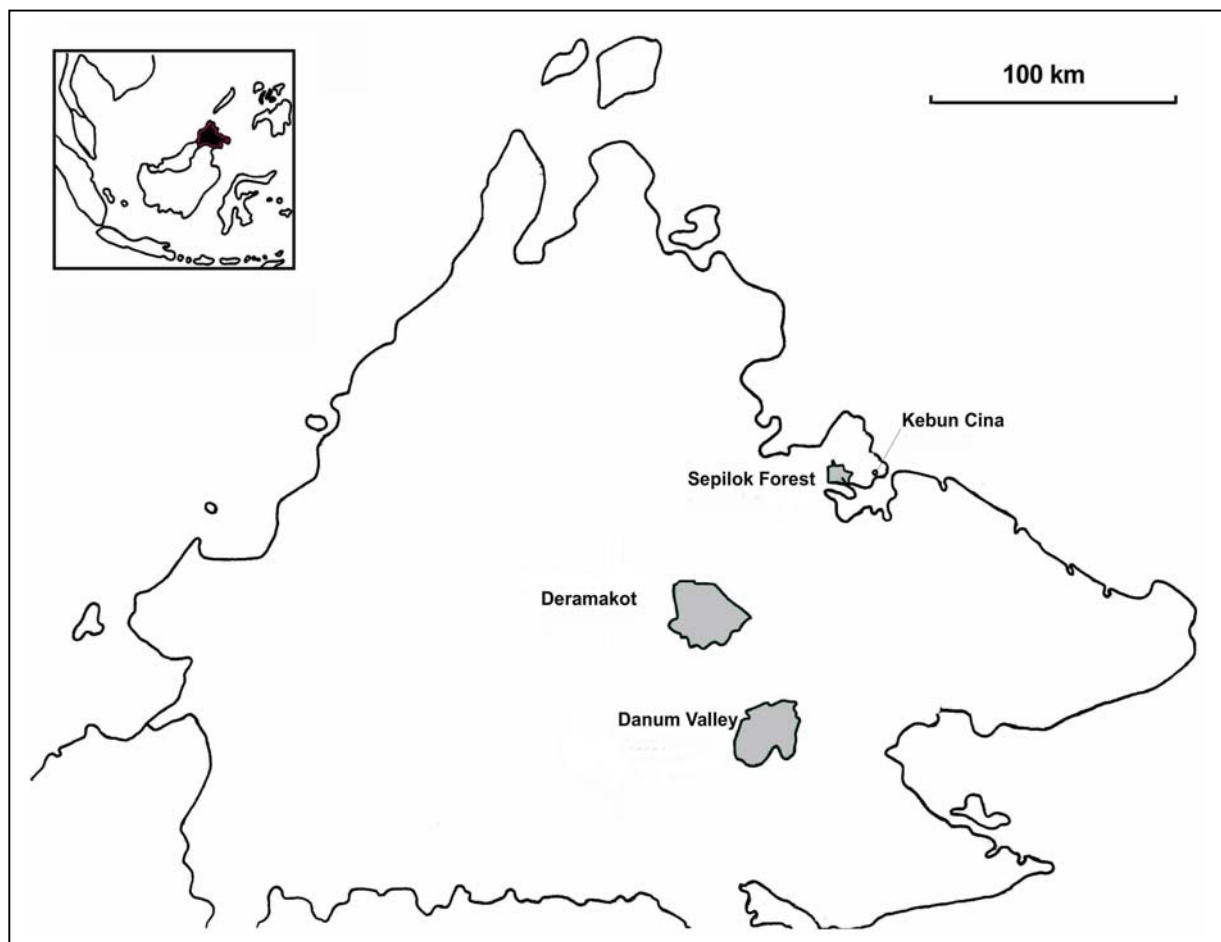
Fig. 1 Map of Sabah with the four study sites (grey). In the insert the location of Sabah in SE Asia is rendered in black.

Tab. 1 Distances between the four study sites

	Danum Valley	Deramakot	Sepilok	Kebun Cina
Danum Valley		70 km	100 km	100 km
Deramakot	70 km		70 km	85 km
Sepilok	100 km	70 km		15 km
Kebun Cina	100 km	85 km	15 km	

2.1   Danum Valley Conservation Area (N 4°50'-5°00' and E 117°35'-117°45')

2.1.1   Location

The Danum Valley Conservation Area is situated about 60 km west of the town of Lahad Datu and includes 43 800 ha of currently uninhabited, mostly lowland forest of the *Parashorea malaanonan* Type A (Marsh & Greer, 1992). The Segama River, of which the Danum River is a major tributary, forms its eastern and southern boundary. Most of the area (90.4%) occupies rugged terrain at moderate elevations (below 760 m a.s.l.) with three summits within: Gunung (Gn., Malay for mountain) Danum (1 093 m a.s.l.), Gn. Nicola (917 m a.s.l.) and Gn. Tribulation (861 m a.s.l.). A rolling plateau at about 300 m elevation is found in approximately a fifth of DVCA on the western side in the 10 km² bowl west of the Danum Valley Field Center (DVFC).

2.1.2   Geology and soils

The main geological formations are: Crystalline Basement, Chert-Spillite and Kuamut. The Crystalline Basement are the oldest rocks in the region of Lower Triassic or older age. The areas with comparatively low relief, as around the DVFC, are mostly occupied by the Lower to Upper Miocene Kuamut Formation. The formation consists of a sandstone, radiolarian chert, shale and siltstone Volcanic rock and charcoalified wood are also found in the melange. Altogether the area encompasses seven different soil associations, but more than 85% of the DVCA is covered by just two: the Mentapok and Bang associations. Around the Field Center the Bang association is prominent, which is developed over rocks of the Kuamut formation. The majority of these soils are Orthic Acrisols developed on sand- and mudstone. These soils vary in colour and clay percentages range from 30% to 60% with an acidity between pH 5.3 to 4.

2.1.3   Climate

The running annual rainfall average at DVFC for thirteen years of record (1986-1998 incl.) stands at 2 662 mm (+/- 409 mm std. dev.) which is drier than most northern parts of Sabah east of the Crocker Range (Chappell, 2000). Normally the winter NE monsoon is the dominant rainfall regime in the area with January and October being the wettest months (302 mm and 297 mm respectively). April is usually the driest month with 120 mm on average and has the most variable rainfall total. The highest daily rainfall recorded is 162.5 mm. There are ca. 220 days with measurable rain in the year. Variation in rainfall is considerably high between rain gauges 2 km apart, reflecting the local passage of thunder cells. Rainfall was measured at the DVFC on meteorological hill (data kindly provided by Nick Chappell, Hydrology project, Royal Society South East Asia Research Programme (RS SEARP) (Fig. 2). 1997-1998 was the driest two year period on record caused by the El Niño Southern Oscillation (ENSO). The drought was followed by the wettest year on record: in 1999 rainfall totalled in 124% of normal rainfall. Atypically, April received the most rainfall while September had the least. One effect of these changes was a reduction in seasonality. The mean annual temperature is 26.7°C (mean max: 30.9°C, mean min: 22.5°C) at the meteorological station DVFC, which is found in a large clearing. Within the forest, mean maximum and minimum were 28.4°C and 21.2°C (measured over a two year period) (Marsh & Greer, 1992).
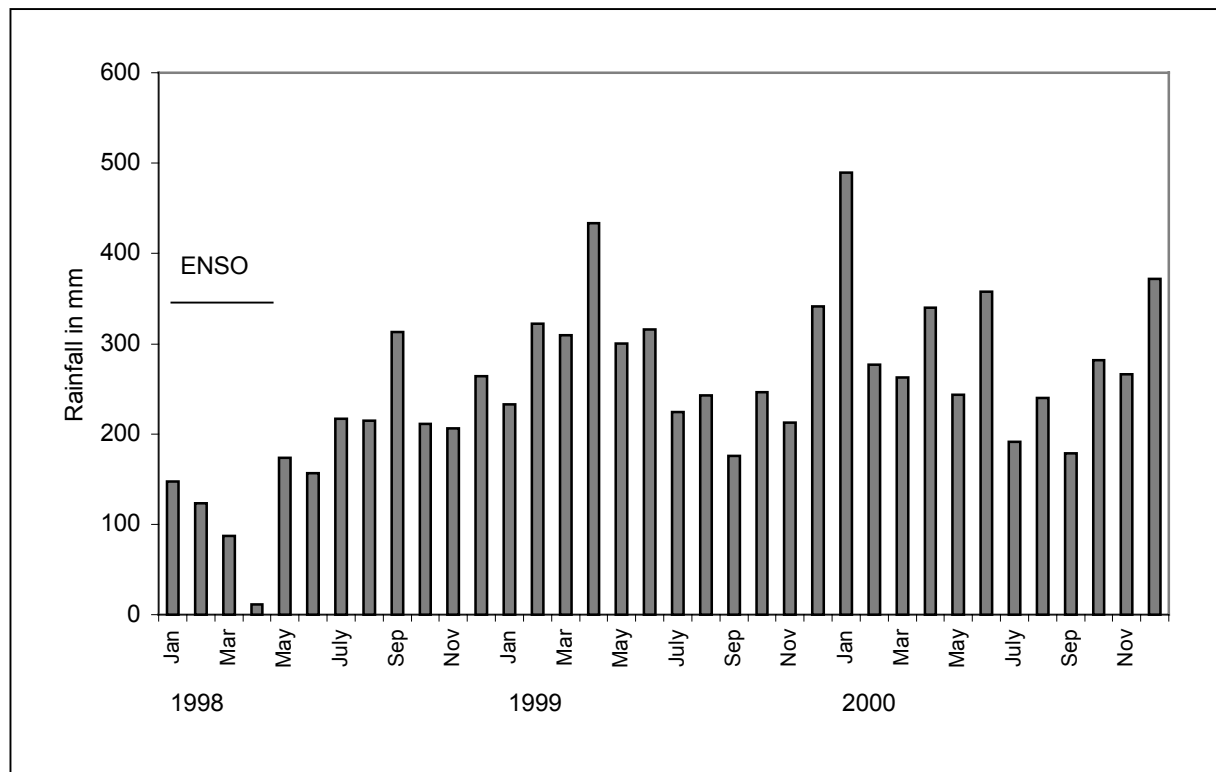
Fig. 2 Rainfall in Danum Valley (1998-2000) measured at DVFC, meteorological hill (data kindly provided by Dr. Chappel, Hydrology project, RS SARP).

2.1.4 Forest type

The forest around the Field Center is dominated by *Parashorea malaanonan and P. tomentella* (white Seraja group) together with *Shorea johorensis* and other *Rubroshorea sp.* (red Seraja group) with a very distinguished high proportion of Euphorbiaceae and Meliaceae found in two long term study sites (Newbery *et al*., 1992).

2.1.5 Research plots

Two research plots were established around the DVFC (N 4°57.7', E 117°48.2'): one is situated along the West Trail (Plot L: W10-W16, ca. 250 m a.s.l., Fig. 3) and the other after about 1.5 km on the Waterfall trail in eastern direction (Plot M, ca 270 m a.s.l) (Anonymous, 1997).
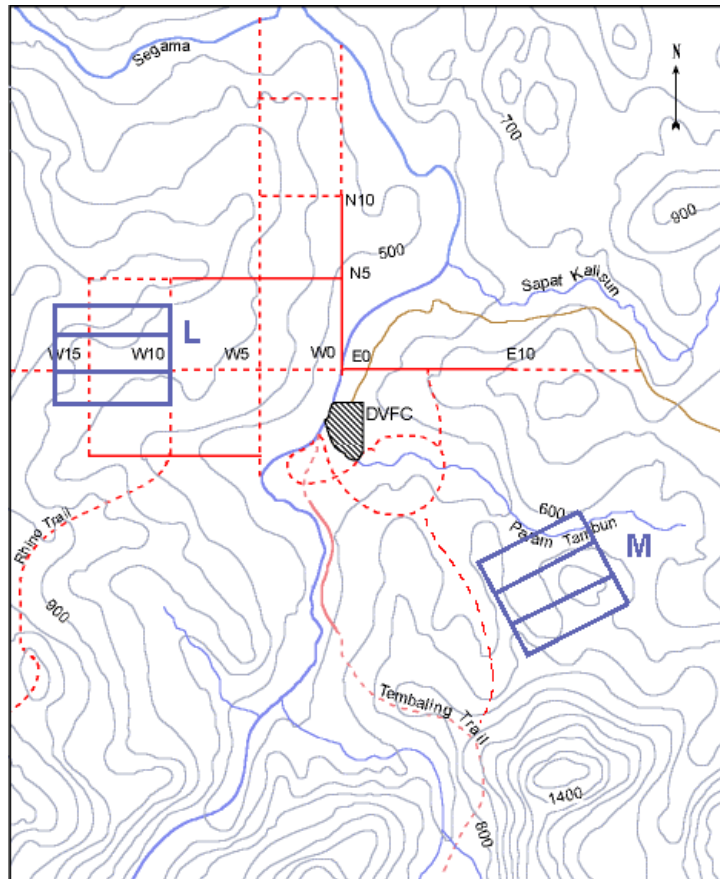
Fig. 3 Research plots in DVCA: plot L on West 10 and plot M along the short cut to Tembaling trail. Altitudes are in feet a.s.l.

2.2 Sepilok Forest Reserve (N 5°54', E 118°04')

2.2.1 Location

The Sepilok Forest Reserve is situated 24 km west of Sandakan on the east coast of Sabah. It is a lowland rain forest reserve of 4 294 ha not including the Mangrove Forest of Sepilok Mangrove Forest Reserve bordering the sea. Lowland rain forest is found between 20-120 m a.s.l. The Reserve is surrounded by different types of plantations (fruit trees, old rubber and oil palm plantations) in the east, north and west and by mangrove forests and the sea in the south (Fig. 5). The main rivers in Sepilok Forest (Kabili, Pakis, Sepilok Kecil and Sepilok Besar) are draining to the south. The area is intersected by sandstone ridges. (Fox, 1969; 1973).

2.2.2 Geology and soils

The Sandakan geological formation consists of mudstone (50%), sandstone (40%) and some siltstone of the Upper Miocene. Four soil associations are recognised in the Reserve: soils on sandstone ridges, soils on sandstone cuestas, soils on low mudstone and alluvial flats and soils on coastal swamps (Fox, 1973).

2.2.3 Climate

The mean annual rainfall measured at Sandakan Airport (1951-1998 incl.) was 3 017.4 mm. The wettest months were December (463.9 mm) and January (420.3 mm), the driest and highest in monthly rainfall variation was April (107.5 mm). Rainfall at Sandakan is largely influenced by the north-east monsoon which is generally experienced between November and mid-February.

Rainfall data of Sepilok Forest Reserve (measured at the Forest Research Center (FRC), 1997-1998) were kindly provided by the Hydrology project, FRC (Fig. 4). The ENSO drought effect is clearly visible when comparing the measured rainfall with the mean monthly rainfall data of Sandakan Airport.
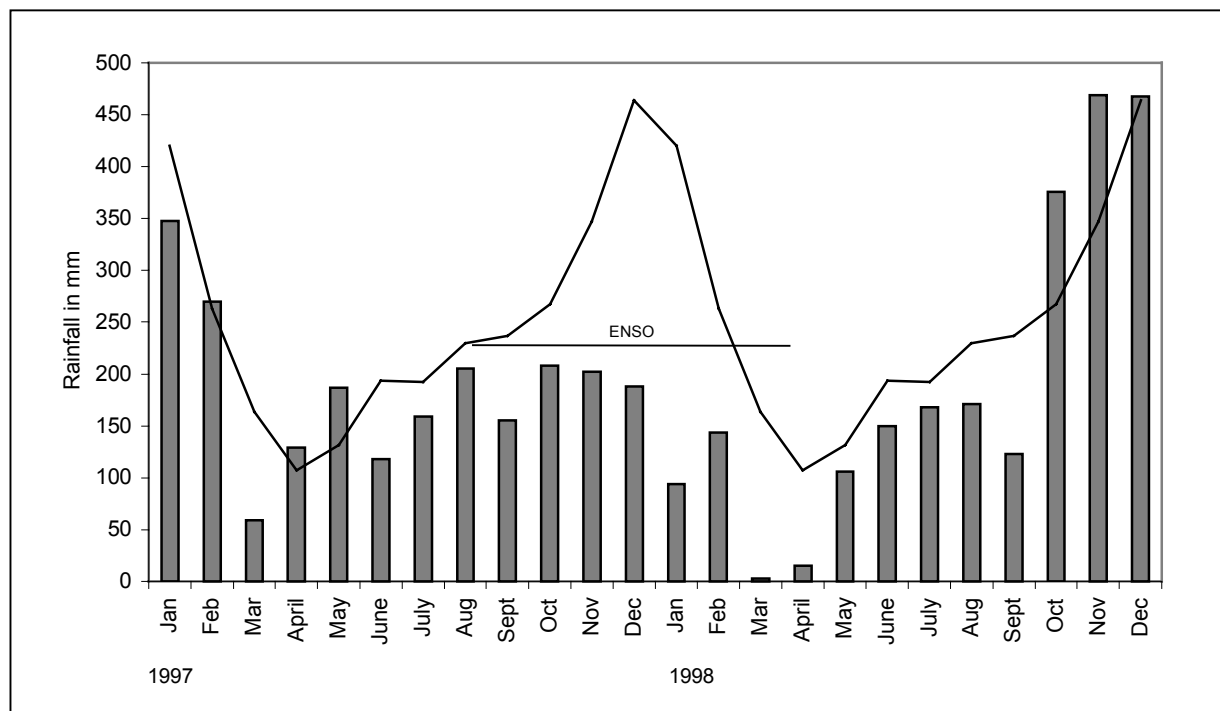
Fig. 4 Rainfall in SFR (1997–1998, data kindly provided by Hydrology project, FRC). Mean monthly rainfall of Sandakan Airport (1951-1998) is displayed as a line.

2.2.4 Forest type

In terms of its flora Sepilok is the best known area in the state of Sabah. About 450 different tree species are estimated to occur here. 40% (54 spp.) of all known dipterocarps in Sabah are recorded in the reserve. Sepilok is dominated by a mixed dipterocarp lowland forest of the *Parashorea tomentella-Eusideroxylon zwagleri* type, with interspersed keranga forest on the sandstone ridges and mangrove forest in the south.

2.2.5 Management history

Along the lower Kabili Forest existed a coffee plantation which was abandoned in 1910. Additionally some of the lower areas close to the sea were logged 90-100 years ago on a highly selective basis. There are also records of low impact logging from 1919-56, some of the area also being under silvicultural treatment as implemented in the Malaysian Uniform

System. In 1967 illegal logging is recorded. The area most affected by logging activities is situated in the south-west of the reserve (Fox, 1973; Payne, 1988).

2.2.6   Research plots

Two research plots were established in the previously unlogged area of SFR: one following the Waterfall Trail in about 1 km distance from the Orang Utan Rehabilitation Center (Plot K, ca. 60 m a.s.l., (Fig. 5)). The other plot was accessed through Kampung Sepilok and an abandoned oil palm plantation also examined in this study, following a trail to the sandstone ridges in the south-west (Plot K*, ca. 60 m a.s.l.). For both plots distance to the forest edge was at least 400 m. Plot K was first sampled in 1998 and resampled in 1999 to account for yearly variation. Plot K* was sampled in 1999 for spatial replication.
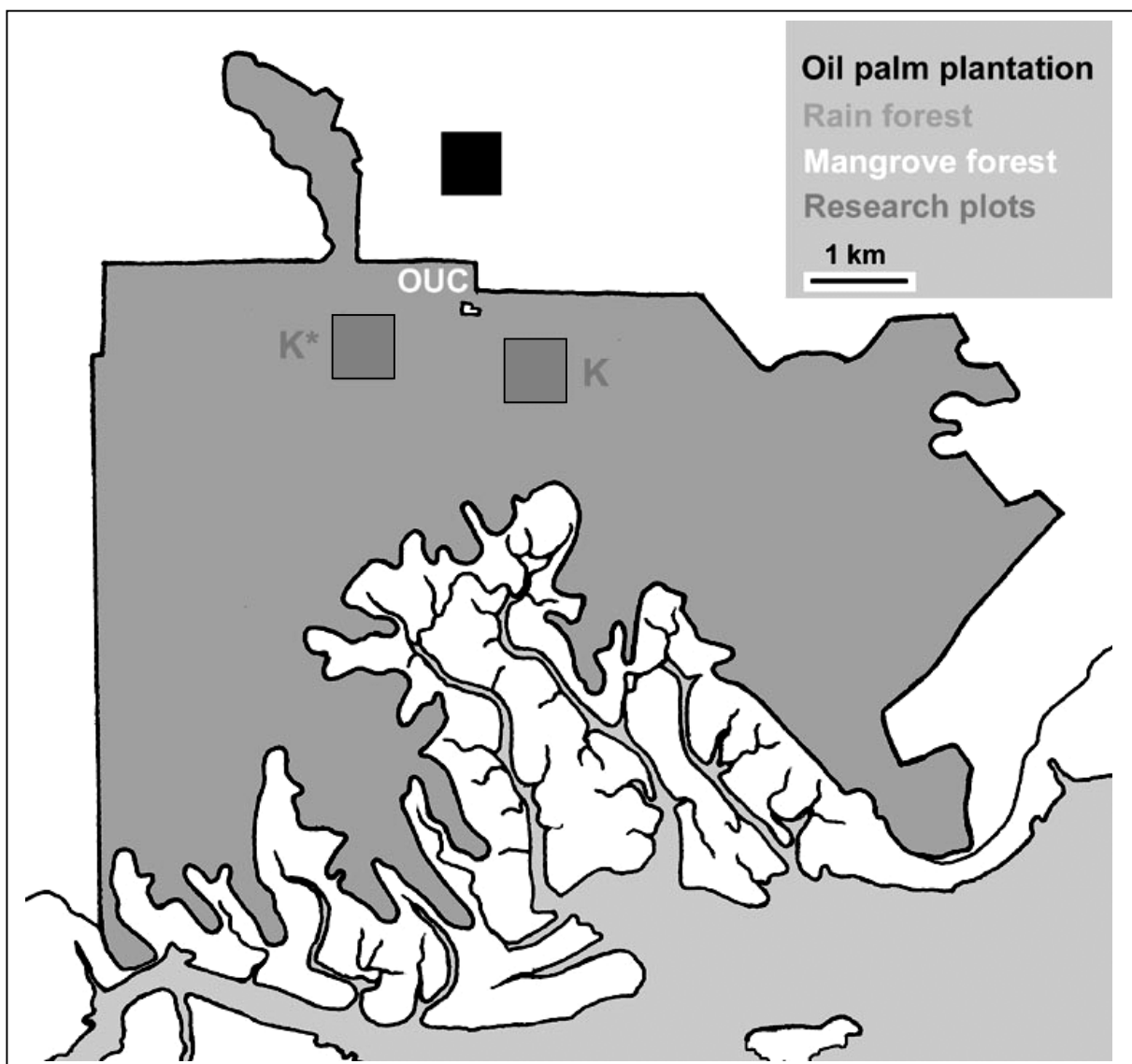
Fig. 5   Map of SFR, (after Fox, 1973). OUC: Orang Utan Center.

2.3   Kebun Cina Forest Reserve (N 5°52', E 118°05')

2.3.1   Location

Kebun Cina Forest Reserve (Malay for Chinese gardens, KCFR) is situated 3 km west of Sandakan harbour. The Reserve is 146 ha in size and covered with *Parashorea tomentella-Eusideroxylon zwagleri* primary forest typical of the Sandakan area. The geology, soils and climate are also comparable to Sepilok Forest, which is in a distance of about 15 km. The reserve is surrounded by houses in the north and east and old rubber plantations in the west and south. No detailed information about the history of the forest fragment and time since isolation was available alhough the rubber trees are at least 30 years old. Today the area serves as a water catchment for Sandakan town with water tanks situated close to the reserve entrance.

2.3.2   Research plots

The only transect line of 500 m in length followed the main trail (Plot O, ca. 90 m a.s.l.). As the reserve is hardly visited it is assumed that disturbance along the trail has been minimal. Sampling was undertaken in at least 5 m distance from the trail inside the forest in March 2000. The plot was established to get data from a smaller forest fragment after first results indicated a decreased species richness in the SFR ant community.

2.4   Deramakot Forest Reserve (N 5°19'-5°20' and E 117°20'-117°42')

2.4.1   Location

The Deramakot Forest Reserve, a commercial class II permanent forest estate is located about 50 km south of Telupid. It has been established as a model forest area to test the implementation of sustainable forestry practices in Sabah (Kleine & Heuveldop, 1993; Uebelhör & Nydegger, 1996). Apart from the logging camp and the settlement of Kampung Balat at the banks of Kinabatangan River the forest is uninhabited at present. DFR extends over an area of 55 083 ha. The forests of Deramakot occupy parts of the basin formed by five rivers which all drain into the Kinabatangan River which marks the reserve's southern border. The area is between 20-120 m a.s.l. in elevation forming an undulating landscape with slopes of varying steepness in almost 80% of the area.

2.4.2   Geology and soils

The geology of DFR is dominated by tertiary sediment formations with mud- and sandstone being the prominent types. The soils derived from these rocks are easily erodible and rather infertile with limited stocks of plant-available nutrients. Acrisols (Kapilit and Paliu) prevail (91.1%) while Leptosols and other soil types are patchily distributed. Due to past logging activities 85% of the area is affected by erosion. While only 42% can be considered not compacted, strong compaction is found on 13% of the area (Chai & Amin, 1994).

2.4.3   Climate

Long term rainfall data were only available from different villages in the vicinity: Tangkulap (30 a), Batu Bajau (21 a), Tulit (31 a) and Bukit Garam (48 a): average yearly rainfall was

2 347 mm with minimum values in March and April. Between 1998-1999 rainfall was additionally measured in DFR at the base camp (Fig. 6). The drought in 1998 caused by a severe ENSO event was evident with six months below 100 mm of rainfall (Chai & Amin, 1994). The mean annual temperature available from the forestry station at Telupid in about 60 km distance to the base camp was around 27°C with an average minimum of 23°C and an average maximum of 31°C.
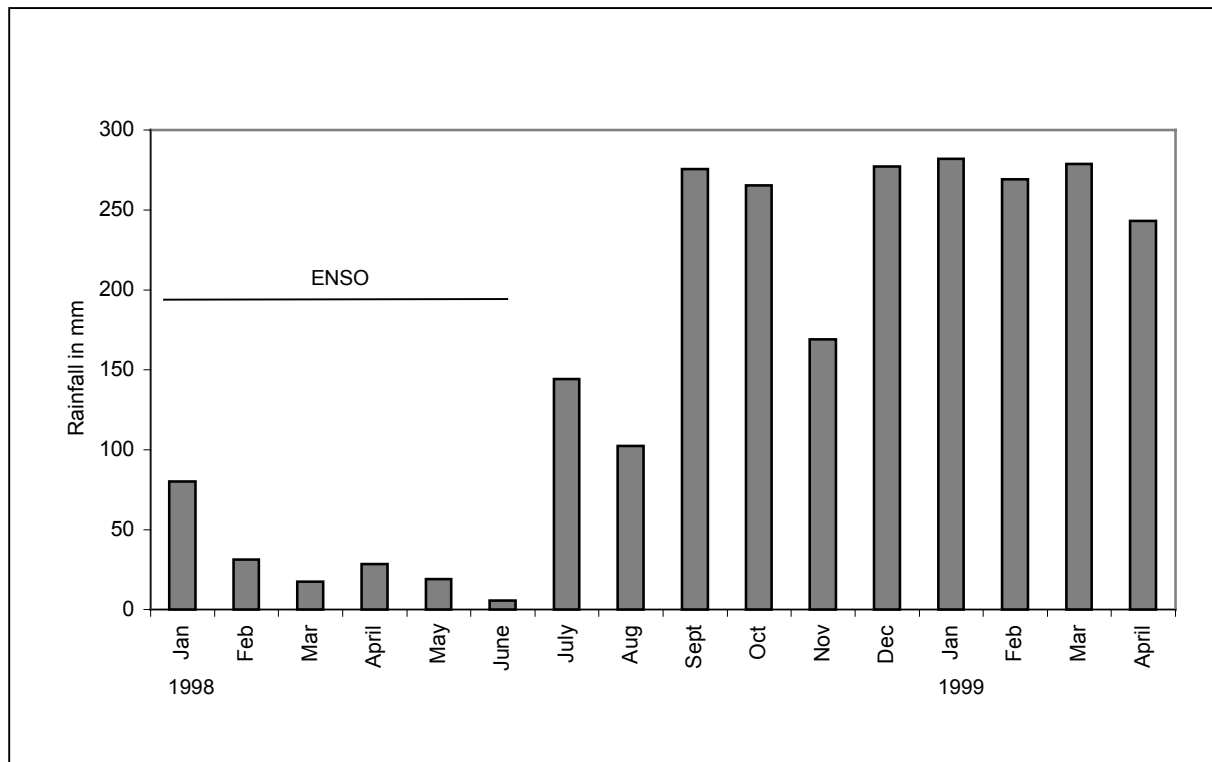
Fig. 6   Rainfall in DFR (1998-1999) measured at the base camp.

2.4.4   Forest type

Deramakot consists of mixed dipterocarp lowland forest of the *Parashorea tomentella-Eusideroxylon zwagleri* type which covers much of the Sandakan area. The forest is dominated by *Parashorea* (20%) with associated species such as *Shorea leptoclados, Dryobalanops lanceolata* and *Dipterocarpus caudiferus*. Together these four dipterocarp tree species account for about 40% of the large trees (Chai & Amin, 1994).

2.4.5   Management history

In Deramakot logging started in 1956 from the Kinabatangan River and logged area per year increased tremendously during the 60ties and 70ties. Timber production rose from 74 065 m³ in 1961 to a peak of 467 757 m³ in 1973. The average production between 1962 and 1968 was 110.6 m³ha^{-1}. The forest was logged under the Modified Malayan Uniform System, which included silviculture treatment as poison girdling (Sodium Arsenite) and control of climbers and did not allow felling trees under 60 cm diameter at breast height (dbh.) (Johns, 1992; Udarbe *et al*., 1993; Uebelhör & Nydegger, 1996; Uebelhör & von der Heyde, 1993). Some parts in the south were logged twice after 1976 and between 1987-88 the northern parts of the

reserve were illegally logged up to two times. During the El Niño drought of 1983 fire additionally destroyed some parts of the remaining stands in the south. Due to the past management the forest structure in the reserve has become extremely heterogeneous with a wide range of structural features, from open gaps to dense stands (Chai & Amin, 1994). This heterogeneity can be inferred from the stratum map (Fig. 7), which gives a coarse image of the real situation as it is based on aerial photographs.

2.4.6   Research Plots

For management reasons the Deramakot Forest Reserve is subdivided into 134 compartments. The research plots in DFR refer to these compartment numbers (see Fig. 7). The Stratum map of DFR provides a rough information on the distribution of forests of various degrees of disturbance. The classification of the strata is based on the number of emergent trees per ha counted on aerial photographs (Stratum 1: < 5 trees; stratum2: 5-8 trees; stratum 3: 9-16 trees; stratum 4: >16 trees) which is useful for forest management planning. However, the situation of forest disturbance is different on ground-level especially in the north of DFR, where the area was heavily logged a few times (see Forest Structure).
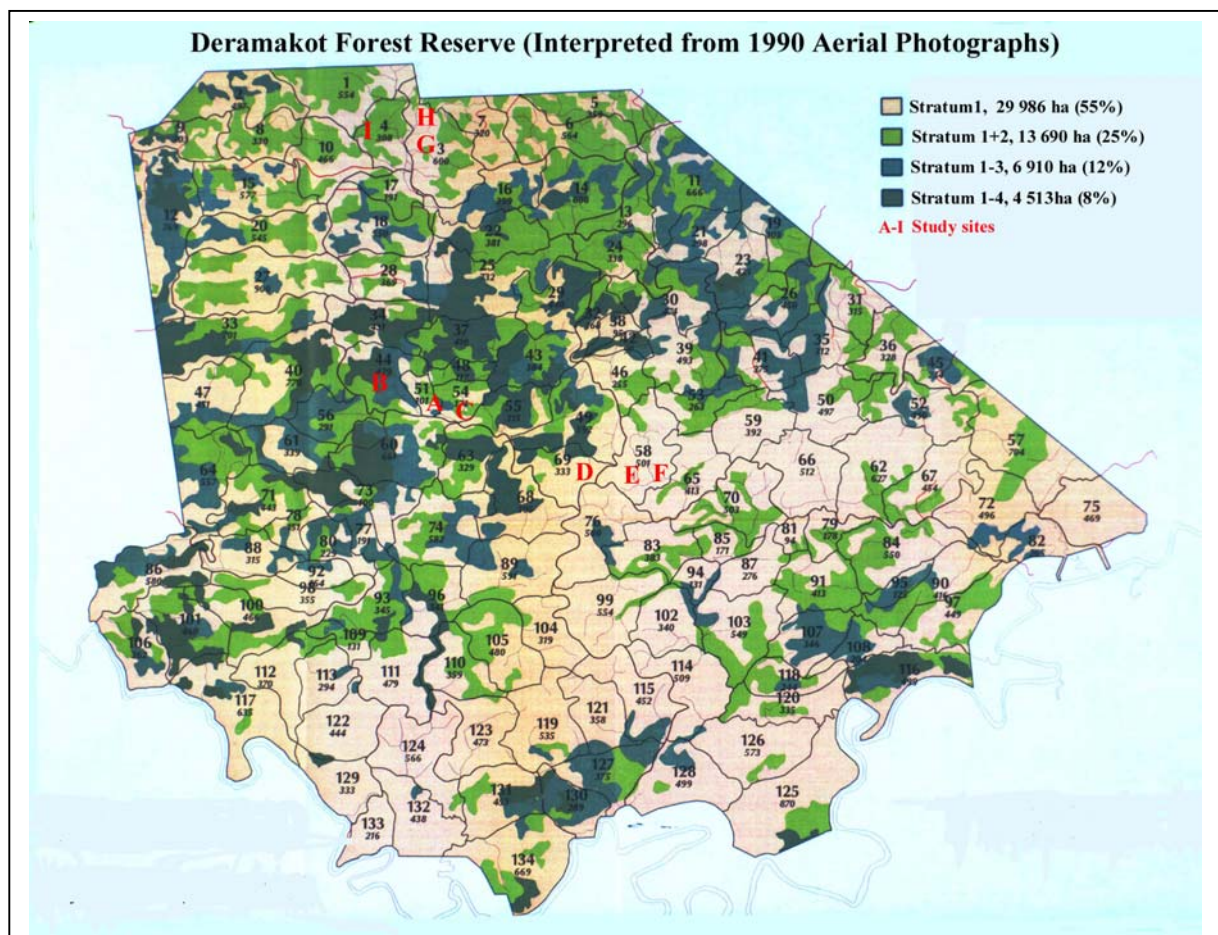
Fig. 7 Stratum map of DFR showing the compartment numbers and forest composition in the reserve based on aerial photographs (Forestry Department, Sandakan, 1993). Strata are defined by the number of emergent trees per ha. Statum 1: < 5 trees; 2: 5-8 trees; 3: 9-16 trees, 4: > 16 trees.

For this study three different forest types were selected and termed good, regenerated and disturbed for simplification.

1. Good logged over forest (ca. 250 m a.s.l.):
Plots of this forest type are situated close to the base camp. The area was logged between 1974 and 1976 with low timber extraction rates.

- Plot A: Compartment 51
- Plot B: Compartment 44
- Plot C: Compartment 54

2. Regenerated logged over forest (ca. 250 m a.s.l.):
Plots are located about 30 km south of the camp in direction to Kampung Balat, situated at the banks of the Kinabatangan river. The area was logged heavily between 1968 and 1970 with a much higher extraction rate than in the good logged over forest plots.

- Plot D: Compartment 69
- Plot E & F: Compartment 58

3. Disturbed logged over forest (ca. 85 m a.s.l.):
The plots are situated ca. 35 km north of the camp. This area was logged for the first time between 1980 and 1982. Illegal logging occurred in 1983, 1985 and 1989 with an almost total extraction of large and valuable timber trees. The stand is now characterised by a single layered canopy, to a high proportion consisting of pioneer trees of the genus *Macaranga* and heavy infestation of climbing bamboo *(Dinochloa* spp.*)*.

- Plot G & H: Compartment 3
- Plot I: Compartment 4

All plots were sampled in 1998. Resampling for temporal replication took place in one plot per forest type in 1999 (plots A, E and H).

3   General Methods

3.1   Sampling and specimen processing

3.1.1   Research plots

The different research plots in the forest types along the disturbance and forest size gradient were supposed to be replicates in space. For site selection of the plots in the different logged over forests I referred to the available stratum map of Deramakot (Fig. 7), aerial photographs as well as maps on topography and geology of the forest reserve. The logging history was also taken into account, although precise data on extraction rates were not available. The replicate plots of a forest type had to be similar in all these variables. As the stratum map produced only a very coarse picture of the situation in the forest and aerial photographs are difficult to read for a beginner, ground surveys were undertaken. A transect grid was established, when I was convinced of the similarity of the forest structure within plots. It also had to be taken into account, whether access to the plots was possible. Old logging roads in DFR were partly difficult to access, especially in the wetter months of December and January and some of the research plots could only be reached by foot after a one hour hike.

3.1.2   Transects

A transect grid system was established in the selected research plots for the recording of forest structure and the sampling of ants. Four parallel transects lines of 600 m length were marked in the forest, enclosing an area of 600 x 600 m (Fig. 8).
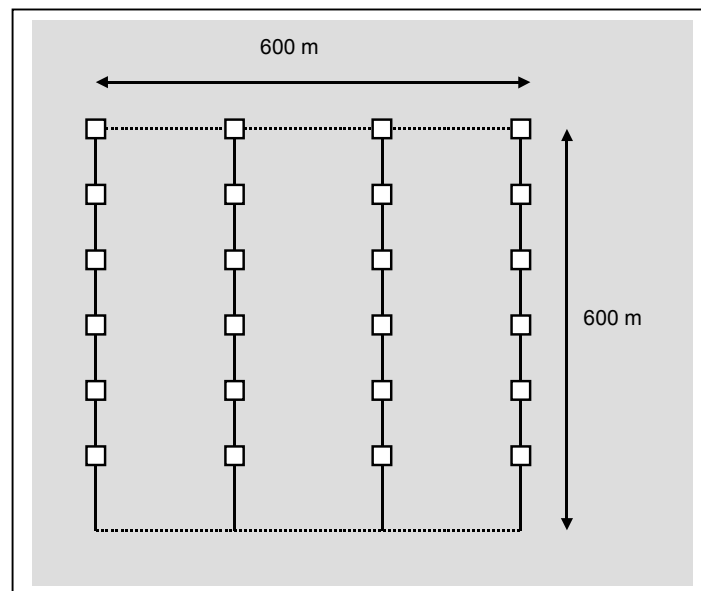
Fig. 8 Grid system (600 x 600 m) consisting of four transects with six sampling sites every 100 m.

The lower vegetation along transect lines was cut to allow easy access and trees were marked for orientation. In total, a transect system of around 50 km length was established. Distance to logging roads was 100 m. Sampling sites were situated every 100 m to collect data for the forest type classification (see Forest Structure). Along one of the intermediate transects sampling of the ants of the leaf litter was conducted. The collection of leaf litter samples took

place at six separate sites along a line with a distance of 100 m between the centers of the sampling sites. This sampling design proved to be the most efficient regarding sampling effort and collected species of the total estimated species pool (see Sampling Efficiency).

In all forests except Kebun Cina, two to three spatial replicates were studied for each forest type (see Study Sites). All plots in Danum Valley and the Deramakot logged over forests were sampled for the first time in 1998 as well as plot K in Sepilok Forest. To account for seasonality and temporal variability in the ant community I resampled plot L of Danum Valley as well as A, E and H of the Deramakot forests in 1999. Plots K and K* in Sepilok were also sampled in 1999, plot O in Kebun Cina in 2000.

3.1.3 Winkler litter sifting

Around the center of each sampling site, ten one square meter samples of leaf litter were collected on a single occasion, situated at least 3 m apart from each other. Three meters is a distance which exceeds the foraging range of most litter inhabiting ants (pers. observ., Carvalho & Vasconcelos, 1998; Kaspari, 1993). Therefore in most samples foragers of different nests were collected. The square meters were chosen randomly within a circular area with a radius of 15 m to the center of the sampling site. Each selected square meter of litter was enclosed by a metal frame to prevent the escape of ants during the sampling process (Fig. 9). The litter within the frame was sifted on the spot using a sieve with 1 x 1 cm mesh size. Litter is defined as the layer of leaves and detritus which can easily be scraped from the more compact soil. During the sifting process twigs and branches were broken to collect ants nesting therein. The fine leaf litter obtained after sifting was collected in numbered plastic bags adjusted below the sieve. The bags were used for transportation to the base camps and always kept in cool places to avoid overheating of the samples.

Sampling was undertaken at least two days after heavy rains, thus assuring that small arthropods would not stick to leaves and could reliably be extracted by the method. Sifting was conducted between 9:00 h and 14:00 h. This time frame was adjusted to the local environment: before 9:00 h the litter layer is too humid due to night fog or rain and after 14:00 h the chances of rain are increasing (Brühl, 1996).

At the base camp the litter samples were immediately filled into mesh bags (4 x 4 mm mesh size). For extraction they were left in the mini Winkler apparatus (Fig. 10) (Besuchet, Burckhardt & Löbl, 1987) in a shady place for three days (Fig. 11). Three days is a recommended time frame in which most of the species in a sample can be collected (Bestelmayer *et al*., 2000; Brühl, 1996; Ward, 2000). The arthropods remaining in the litter migrate from the mesh bags into the Winkler sack and eventually fall in a collection jar filled with 70% industrial spirit suspended below the funnel of the sack. Finally the extracted arthropods were stored in vials in 70% alcohol. In their recently published book Bestelmayer and co-workers (2000) give a very detailed description on standardised methods for monitoring the diversity of leaf litter ants. The difference between my sampling and the described method is that I used a simple sieve instead of a Winkler sifter with its heavy and bulky cotton cover (Bestelmayer *et al*., 2000) and the square meter frame to enclose the leaf litter sample on the forest floor.

Fig. 9   The fine leaf litter of one square meter of forest floor enclosed by a metal frame is collected by sieving (wire mesh 1 x 1 cm).
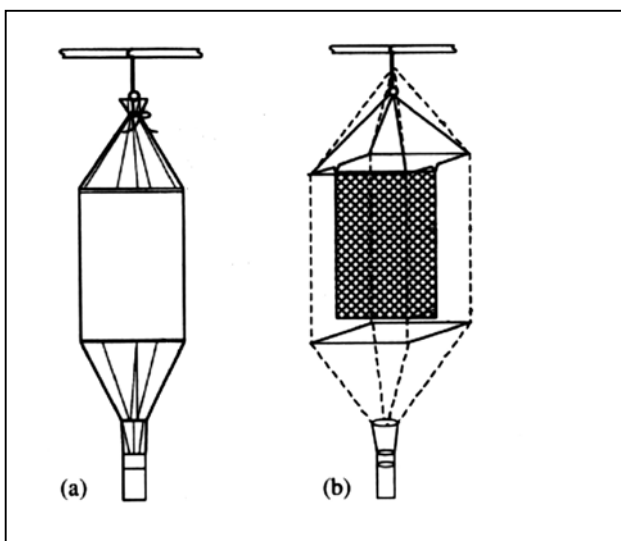
Fig. 10   The mini Winkler sack:

(a) external view of the outside made of cotton cloth.

(b) construction of the apparatus with the wire supports for the mesh bag (4 mm grid size) and the plastic cup below the funnel for collecting the extracted arthropods.

(After Bestelmayer et al., 2000).

Fig. 11   120 mini Winkler sacks running in the shade for three days in Danum Valley.

3.1.4   Sorting of the samples and species identification

A first sorting took place in Sabah. Staff of the DVFC and the Entomology Section of the FRC was trained to separate ants from the remaining arthropods and debris. In Germany all samples were checked again for overlooked ants, but generally the error rate was low and only some ants were found in the debris of a few samples. The alcohol ant samples were subsequently presorted to genus level under a dissecting microscope (Leica Wild M3 B, 10 x 21) and then mounted on cardboard pins, following the convention of Bolton (1994). Genus identification was checked again on the mounted specimen using the key of Bolton (1994). Finally morphospecies were designated based on external morphological characters of the worker class (Leica MZ 8, 16 x 14). The processes of sorting, mounting and first identifications are excellently described by Lattke (2000). In case of the genus *Pheidole* I additionally included characters of the major workers for morphospecies designation as suggested by Seiki Yamane and Euguchi Katsujuki, Kagoshima University, Japan. Various genera were examined by established experts and the morphospecies numbers were replaced by valid species names where possible. *Gnamptogenys* was inspected by John E. Lattke, University of Davis, USA, *Lophomyrmex* by Fabrizio Rigato, Italy, *Strumigenys*, *Pyramica* and *Kyidris* by Barry Bolton, Natural History Museum, London, UK, *Pheidole* by Euguchi Katsujuki, Kagoshima University, Japan, *Myrmecina* by Okido Hirofumi, Kyushu University, Japan, and *Polyrhachis* by Rudy Kohouts, Queensland Museum, Australia. Several species of other genera could be identified with the help of Seiki Yamane, Kagoshima University, Japan. Additionally, taxonomic revisions and recent new descriptions were used for species identifications in some genera (Bolton, 1986; 1992; 1999; Eguchi, 1998; 1999; Rigato, 1994; Taylor, 1967; Yamane & Hashimoto, 1999).

So far, the applied morphospecies concept did not yield a smaller or larger number of species in a genus compared to the confirmed valid species in the analysed genera. As all species in the species rich genera of *Pheidole* and *Strumigenys* have been verified I am confident that the error in the morphospecies classification is low, especially as most genera included only one to four species (see Forest Disturbance and Forest Size).

3.1.5   Species included in the analysis

For the analysis of the leaf litter ant community of different forests only species that could be quantitatively collected by the Winkler method and species typical of the stratum leaf litter were included. Therefore some species collected in a few samples were excluded from the analysis. These were large species which would not fit through the 4 mm mesh bag of the Winkler apparatus and could therefore not be collected systematically. Species larger than 15 mm usually possess a diameter that prevents them from moving through the mesh bag. Excluded species are: *Odontomachus rixosus*, *Odontoponera transversa*, *Meranoplus mucronatus* species of *Diacamma*, *Leptogenys*, *Cerapachys* and *Pachycondyla*. These large species are mostly foraging on the litter and in the lower vegetation and are therefore not recognised as typical leaf litter inhabitants by some specialists (B. Bolton, pers. comm.). Generally, leaf litter ant species are minute ranging from 1-5 mm in length. Therefore the Winkler method collects the majority of leaf litter ants reliably.

With the Winkler method one regularly collects a certain number of ant species which is foraging in or on the leaf litter, but is generally rare on the forest floor or not nesting there.

From previous studies on ants in Sabah, information on the stratification of ants was available (Brühl, 1996; Brühl, Gunsalam & Linsenmair, 1998). Some ant species typical for deep soil were collected in the litter and only one individual was recorded in some species. Species of the genera *Protanilla* and *Aenictus* were therefore excluded from the analysis. The same is the case for typical vegetation or canopy ant genera as *Camponotus*, *Polyrhachis*, *Dolichoderus*, *Echinopla* and some species of *Cataulacus* and *Cerapachys*. *Monomorium floricola*, a tramp species associated with human disturbance (Schultz & McGlynn, 2000) contaminated all Winkler samples in Deramakot from big colonies present in the base camp; therefore it had to be excluded from the analysis. In total, 72 species of ants were not considered in the following comparison of leaf litter ant communities.

3.1.6   Discussion

The sampling procedure used in this study is in most aspects identical with the methods and procedures as described by Agosti and co-workers (2000). However, there are some differences which need further explanation.

Considering the distance of about 3 m between samples it should be said that ant colonies often exist in the form of multiple nests covering a large area (Hölldobler & Wilson, 1990). For the giant jungle ant of Borneo, *Camponotus gigas* Pfeiffer (1996) could demonstrate a territory of more than 8 500 m² covered by 11 nests. I observed multiple nests in some leaf litter ant species, e.g. in *Pheidole* species and especially in *Lophomyrmex bedoti* in baiting experiments, but the majority of leaf litter ant species had only one nest. However, one has to closely inspect patterns emerging from Winkler data if one considers a species as very abundant at a sampling site (10 m²). Therefore I compared species numbers only between sampling sites, because the established distance of 100 m (Fig. 8) exceeds foraging ranges of all leaf litter species and most probably also the area covered by multidomous colonies. The largest foraging distance I recorded in baiting experiments was 35 m by *Meranoplus mucronatus*, a species not included in the analysis (see above), while general foraging ranges are around 1-3 m (pers. observ., Carvalho & Vasconcelos, 1999).

Another detail different from Agosti and co-workers (2000) is the use of a metal frame to enclose the selected sample square meter. The frame not only has the function of keeping all arthropods in the sampling area, but also to sample a complete 1 m² section of the forest floor. In my experience the frame helps tremendously in the scraping process as it forms a stable border. If one uses a rope to measure the square meter boundaries get blurred during the sifting process which is especially unfortunate since the time needed for measuring the one square meter area is considerable. I have to admit though that it is quite tedious to carry a metal square through the dense undergrowth of a tropical rain forest.

A last point to mention is the exclusion of some ants from the analysis. It could be argued that the term leaf litter ant species should include all ant species sampled by the Winkler method even if they only occasionally forage there (D. Agosti, pers. comm.). I excluded these species for the biological reasoning above, but also, because there would be another drawback if one included all species sampled by the method: these species were only present in some samples leading to the impression that they were actually among the rarest in the forest litter. Compared with the ants of the lower vegetation studied by M. Gossner (1999) at the same sites I understood that most of these rare litter species were actually very abundant in the

vegetation but just rarely collected with the sifting method on the forest floor. Including these species in the analysis would therefore lead to a false perception of the litter ant community composition and blur the picture in comparisons between communities.

3.2 Statistical methods

3.2.1 Data entry

The presence and absence of ant species in the samples were arranged in a data matrix. I did not include abundance data as ants are social organisms and the presence of many individuals may be simply due to collecting a nest or a column of foragers (Chung & Maryati, 1996). As some analyses assume that within a spatially and temporally defined community all individuals in the sampling have an equal probability of being sampled, which is not the case for the highly aggregated ants, the presence - absence approach is to be preferred (Folgarait, 1998; Longino, 2000). To get an estimate of the relative abundance of a species I therefore collected many samples and used the presence in samples as an indication of abundance (= pseudo abundances): A common ant species is present in most of the 60 samples of a forest plot, whereas a rare species is found in only a few samples. The use of presence - absence counts of ant species also has the advantage that sorting time is limited as one doesn't have to count all individual workers in the sample, which takes a considerable amount of time, if a nest with a few thousand workers is collected. With presence - absence counts we therefore save time which then allows the processing of a large number of samples.

3.2.2 Species richness estimators

Community species richness is among the most important criteria used to determine the conservation value of an ecosystem (Chichilnisky, 1996; Johns, 1992; Kremen *et al.*, 1993; Williams, Vane-Wright & Humphries, 1993). To obtain a reliable estimate of species richness is an important goal. Because my sampling is based on area (1 m²) there is an increase in sampled area with increasing sampling. This is a species - area phenomenon and species richness might be described as an ever increasing function of sampled area (Rosenzweig, 1997). However, it might be more appropriate to treat communities as though they were discrete. This approach is taken by Colwell and Coddington (1994). They propose that biodiversity is partitioned into two parts: the species richness of the local community and the complementary among these communities. With this assumption, the species accumulation curves rise owing to increasingly accurate sampling, not to species - area effects and species richness is considered a finite community parameter (Longino, 2000). Only a high sampling effort with the species accumulation curve reaching an asymptote and the species richness estimators following this pattern will yield a reliable estimate of the total species richness of the community (Soberon & Llorente, 1993). Therefore it is very important that sampling is profound and large sample sizes are collected (Longino, 2000; Peterson & Slade, 1998). The various estimators of species richness used are described in Appendix (for a more detailed description of the mathematical background or applied examples see Beck, 1998; Butler & Chazdon, 1998; Coddington, Young & Coyle, 1996; Colwell, 1997; Colwell & Coddington, 1994; Dobyns, 1997; Lawry, 1991, 1992). Species accumulation curves and estimators were calculated using the computer package EstimateS 5.0 (Colwell, 1997) randomising the data

100 times. General statistical tests like ANOVA, Scheffe post-hoc test, regression and correlation analysis follow Sokal and Rohlf (1981), calculated with STATISTIKA 5.5. (StatSoft, 2000). ANOVA and Scheffe tests were only applied if all prerequesites were met.

3.2.3   Alpha-diversity indices

Alpha-diversity describes the variety of organisms occurring in a particular place or habitat and is therefore often called local diversity (Swingland, 2001). To compare community diversities I calculated different α-diversity indices based on the pseudo abundances (occurrence in number of samples) of all present species at a site. Magurran (1988) gives a detailed account of the terminology, calculations and limitations of the different indices. I used some of the most common diversity indices: the parametric Fisher's α and the nonparametric indices Shannon-Wiener H', Simpson's D and Eveness J. The performance of all these indices and their advantages and disadvantages are discussed in the literature and often show a lack of consistency. The main limitations are based on their dependence on sampling effort, total species number and dominant species in the samples (for detailed reviews of the performance of the different indices see Bulla, 1994; Hurlbert, 1971; Lande, deVries & Walla, 2000; Mouillot *et al.*, 2000; Rennolls & Laumonier, 2000; Robinson, 1998; Taylor, 1978; Wilsey & Potvin, 2000; Wolda, 1981, 1983). Nevertheless, I applied the indices as they are widely used and especially practical for a comparison with other ant community studies (e.g. Andersen, 1993; Chung & Maryati, 1996; Roth & Perfecto, 1994). A description of the calculations is found in Appendix.

To compare the diversities of the different forests randomisation tests (Solow, 1993) were performed (10 000 runs) using the Species Diversity & Richness 2.3 software (Henderson & Seaby, 1998). Another method for the ranking of α-diversities is presented by the Renyi family of diversity ordering. The Renyi family is closely related to the Hill Series (a log transformation of Renyi) now commonly in use (Legendre & Legendre, 1998; Rennolls & Laumonier, 2000; Wolda, 1983). By varying the scale parameter α we generate a range of diversity measures (for calculation of the Renyi index H(α) see Appendix), including H' and D. If a community displays higher values over the whole range it is more diverse, if two communities cross they are non-comparable. The Renyi series was calculated using Species Diversity & Richness 2.3 (Henderson & Seaby, 1998).

3.2.4   Beta-diversity index

For β-diversity or the variety of organisms within a region arising from turnover of species between habitats (Swingland, 2001), there are many indices to choose from, although their quality of performance is very different (see Wolda, 1983; 1987, Magurran, 1988). As the data obtained were not real abundance data but pseudo abundances (see above) I could not use a quantitative similarity measure as the widely recommended NESS index (Wolda, 1983). Because pseudo abundances are at maximum 60 (= total number of square meters sampled in one plot) and at minimum 1, the difference between common and rare species is not very distinct and the NESS index is unable to separate communities. The possibility of using the commonly used Sørensen index was ruled out as this index performs best with presence - absence data and the data are of a more quantitative nature (Legendre & Legendre, 1998; Wolda, 1981, 1983). Therefore I followed the suggestions of Faith, Minchin and Belbin ((1987) in Legendre & Legendre, 1998) for the analysis of species count data. The data were

standardised by dividing each value by the maximum abundance for that species in the data set and the Steinhaus similarity measure was used (see Appendix for calculations). This strategy yielded the most informative ordination results in simulations (Faith *et al*., 1987). The Steinhaus similarity measure is one component of the Bray-Curtis index (Legendre & Legendre, 1998), which is now included in standard ecological computer packages like Species Diversity & Richness 2.3 (Henderson & Seaby, 1998).

3.2.5   Multidimensional scaling

Multidimensional scaling (MDS) is at present the recommended ordination method for community analysis (Dufrene & Legendre, 1997; Golden & Crist, 2000; Minchin, 1987; Pfeifer *et al*., 1998) as it has some advantages over other ordination methods: MDS is not limited to Euclidean distance matrices; it can produce ordinations of objects from any distance matrix and, contrary to PCA, PcoA or CA, which are eigenvector methods, MDS calculations do not maximise the variability associated with individual axes of the ordination (Legendre & Legendre, 1998). I followed the protocol of (Legendre & Legendre, 1998) using a stepwise approach in the reduction of dimensions. For MDS I used the available package in STATISTIKA 5.5. (StatSoft, 2000). MDS has already been applied in ant studies and produced robust results (Carvalho & Vasconcelos, 1998; 1999; Golden & Crist, 2000; Vasconcelos, 1999; Vasconcelos, Vilhena & Caliri, 2000).

3.2.6   Cluster analysis

Another way of grouping similar objects is the cluster analysis (Fry, 1993; Krebs, 1989). For the obtained data set I used the 1 - Steinhaus dissimilarity values (= Bray-Curtis index) and used the common cluster algorithms Unweighted Arithmetic Average (UPGMA) and Single Linkage (SL). UPGMA fuses clusters when the similarity reaches the mean intercluster similarity value and is recommended for a collection of objects obtained by systematic sampling. SL contracts the space between clusters and is a combinatorial method for ordination methods (Legendre & Legendre, 1998). For calculations I used the cluster analysis package in STATISTIKA 5.5. (StatSoft, 2000).

4   Forest Structure

4.1   Introduction

Forest structure is the three-dimensional arrangement of trees and other plants in combination with non-living spatial elements such as soils, slopes and hydrology. Structure includes such characteristics as canopy and understory geometry, continuity or fragmentation of canopy cover, homogeneity or patchiness of species distribution through the landscape and species composition and age structure of the forest stands (Seidler & Bawa, 2001). Forest structure influences forest biodiversity directly through the formation of microhabitats as well as the determination of large scale habitat characteristics although this relationship is complex and not well understood.

Since it is part of this study to describe the patterns of changes in community composition of leaf litter ants along a disturbance gradient it has to be certain that (1) the different study sites really form a disturbance gradient and (2) the plots within one forest type are similar to each other in their degree of disturbance. It was not my aim to record all parameters of forest structure and exceeded our possibilities and therefore I concentrated on stand structure as one determinant. I conducted ground surveys in the established research plots and measured tree size distribution as a parameter of forest structure additional to the data I obtained from the study of maps and aerial photographs (see General Methods). Only few studies attempt to quantify stand structure with an appropriate sampling design and replication (Cannon *et al.*, 1994) and they are especially scarce if time since logging exceeds 10 years (Finegan, 1996).

4.2   Methods

Data on forest structure were obtained for all research plots in the different forest types in Deramakot and the two plots established in Sepilok Forest and Danum Valley. I measured the tree size distribution using angle-count sampling with a custom-made Spiegel relaskop (Schreuder, Banyard & Brink, 1987). I took individual counts with basal area factor four every 100 m along the transects in the research grids (see Fig. 8, General Methods). All in-trees above a diameter at breast height (dbh.) of 5 cm were counted and divided in five dbh.-classes: 5-15 cm, 15-30 cm, 30-60 cm, 60-100 cm, and trees above 100 cm. In addition, I separately recorded trees of the pioneer genus *Macaranga* which includes ca. 250 species (Whitmore, 1984). Trees of this genus can be easily recognised by their leaf form and bark structure. Common species in the logged over forests in Deramakot are *M. hypoleuca, M. gigantea* and *M. pearsonii* (B. Fiala, pers. comm.).

4.3   Results

For a statistical analysis the primary forest sites of Danum Valley and Sepilok Forest were combined and consecutively tested for effects of forest type on tree diameter distribution (Fig. 12) using ANOVA (with four levels of disturbance: primary and the three levels of disturbed forests of DFR described above). The differences in the variables tested were significant: the skewness of the diameter distribution (N = 14, df = 3, F = 4.98, p < 0.05), the total number of large trees above 60 cm dbh. (df = 3, F = 15.65, p < 0.001) and the total number of

Fig. 12 Tree size distribution in the different forests. ■ *Macaranga*
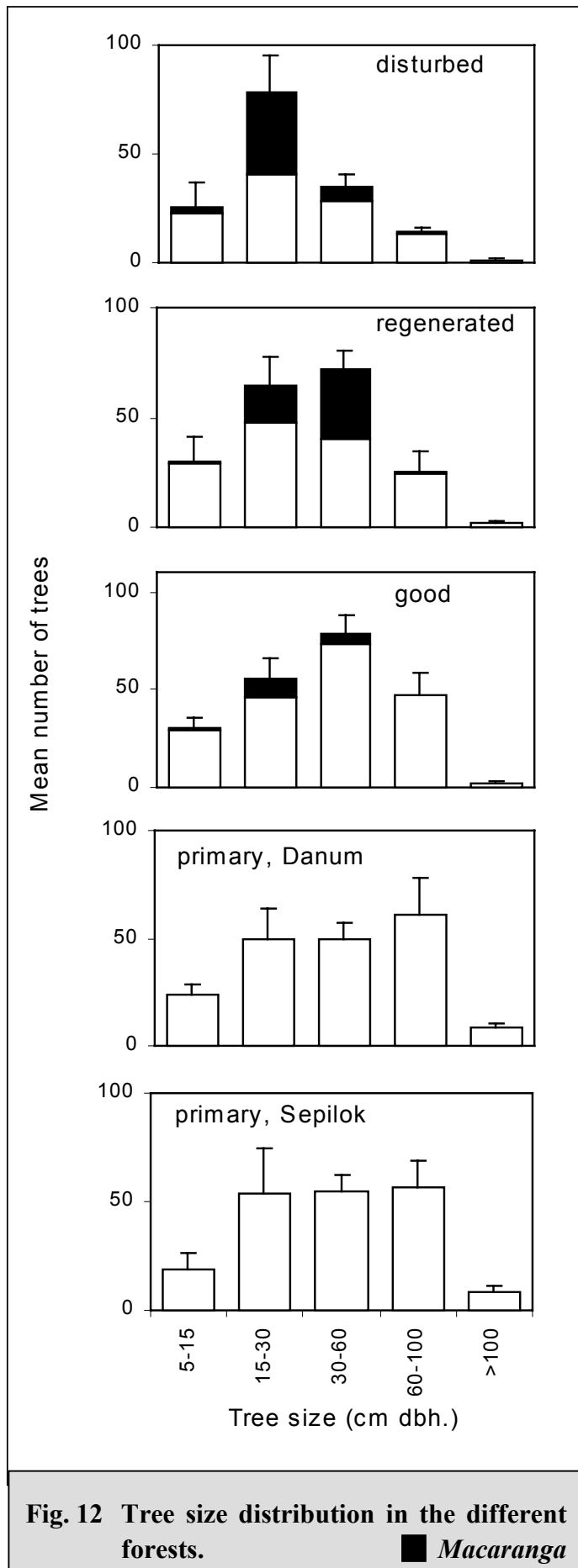
Macaranga trees (df = 3, F = 24.3, p < 0.001). The presence of larger trees and *Macaranga* spp. decreased from primary forests towards more heavily and more recently disturbed sites. The primary sites of Danum Valley and Sepilok showed very similar distributions.

4.4   Discussion

The analysis of the three parameters confirmed that the research plots established in the four forest types were different from each other and followed a gradient of disturbance. The low standard deviation in Fig. 12 within forest types and the results of the ANOVA indicated that forest structure of the replicates was more similar than between forest types. Thus, the analysis of structural parameters justifies the selection of the chosen research plots and the grouping into the four forest types.

Generally, the predominance of larger trees decreased along the disturbance gradient (primary > good > regenerated > disturbed), whereas the presence of *Macaranga* pioneer trees increased in the same order. *Macaranga* trees were absent in the four primary forest plots in Danum Valley and Sepilok. In Deramakot *M. hypoleuca* makes up a huge proportion of the pioneer trees and tends to form almost pure stands of a similar age resulting in a single layered canopy, particularly evident in the most disturbed sites.

The regenerated forest had a lower density of larger trees and higher numbers of *Macaranga* spp. trees than the good forest, logged six years earlier but with a higher extracted timber volume. Therefore it becomes evident that the amount of extracted timber and the related damage during logging operations is even more important for the description of the forest structure than time since logging. Differences in stand structure compared to a primary forest were clearly visible even after a regeneration time of 25 years.

Although the impact of logging is widely recognised, studies on the alteration of species composition or forest structure after logging are scarce (Cannon, Peart & Leighton, 1998). A comparison of forests one and eight years after logging in Kalimantan showed alarming results: tree density was severely affected especially for trees > 20 cm dbh., which fell by 41% (Cannon *et al*., 1998). Although forest structure in logged forests was very different from primary forests, it has been implied that tree species number was similar (Cannon *et al*., 1994). I did not record the species composition in the studied forests, however the situation in the area studied by Cannon and co-workers must have been very untypical, as they found only two *Macaranga* trees in the logged forest plots. A reason for their astonishing results might be the short time since logging in the research plots. As mentioned above, *Macaranga* trees are dominant in the disturbed forests of Deramakot and account for 38% of all trees > 30 cm dbh. in Peninsular Malaysia (Johns, 1992). In Kalimantan, *Macaranga* was especially dominant in burnt forests but also moderately common in the overstorey of a 15 year old selectively logged forest affecting the tree species composition considerably (Slik, 2001).

The regenerated forest in Deramakot was logged between 1974-76. Even 25 years after logging, forest structure was markedly different and the proportion of pioneer trees was higher. A similar picture was revealed by a study in an abandoned pepper plantation in Kalimantan where little recruitment of primary forest trees was obvious and the most common trees belonged to *Macaranga* spp. (MacKinnon *et al*., 1996). Model simulations of a dipterocarp forest in Peninsular Malaysia came to the conclusion that even 110 years after logging forest structure will be nowhere near its primary forest state (Bossel & Krieger, 1994). There evidently is a need for detailed studies on tree species composition and forest structure in logged over forests before management and conservation decisions based on small and obviously local data sets become established.

5 Environmental Parameters

5.1 Introduction

Structural changes in the forest due to logging activities may cause changes in a series of abiotic and environmental factors. Especially temperature and humidity are among the most important physical factors affecting ecological processes within the forest ecosystem. They have influences on plant growth rate and survival, seedling establishment, physical soil properties, microbial activity and occurrence of insects (Brown & Whitmore, 1992; Burghouts, Campbell & Kolderman, 1994; Muhamad & Kamaruzaman, 1987; Nussbaum, Anderson & Spencer, 1995). Although climate measurements exist for most of the tropical areas and also in Sabah, these measurements are generally obtained at airports or on open ground and are thus not reflecting the climate of the forest interior. With an increasing effort in the study of the arthropod community of tropical forest canopies a growing body of data exists for climatic stratification within primary tropical forests (Parker, 1995). However, investigations on the effects of logging on temperature and humidity changes in tropical forests are scarce (Verhaag, 1991) and the only quantitative data set for Malaysia includes mostly measurements of soil temperatures over a very limited period of time at two study sites (Muhamad & Kamaruzaman, 1987). As the distribution of litter ants might be influenced by microclimatic conditions (Kaspari, 1993; 2000; Levings, 1983; Levings & Windsor, 1984; Torres, 1984) temperature and humidity measurements of various forest floor habitats were taken in the different forests.

5.2 Temperature

5.2.1 Air temperature

5.2.1.1 Methods

Air temperature was recorded in the different forests of Deramakot (Plot A, good forest, Plot E, regenerated Forest, Plot H, disturbed forest) and Sepilok (Plot K). A Celsi pick$^{©}$ temperature logger was fixed to a pole at 1 m above ground level. An aluminium wok cover (diameter 80 cm) was used to shelter the logger from rain and direct sun light but left it completely exposed to the air. All logging stations were situated under dense vegetation inside the forest to collect shade temperature values. Temperature was recorded for 13 days (March 27-April 8, 1999) in 16 min intervals in all forests simultaneously (total of 1 118 measurements). The weather during this period was mostly cloudy and rainy with some short intervals of sunshine.

5.2.1.2 Results

From the measured air temperature data I calculated a mean daily temperature curve for all the different plots (Fig. 13). The temperatures were similar in plots A and E in Deramakot over the course of a day, cooling down to identical night temperatures and displaying comparable daily temperatures, with E being a bit cooler than A. The temperature in plot H in the disturbed forest of Deramakot was cooling down at night to a similar level as the two other Deramakot forests but was heating up considerably during the day. The Sepilok primary forest displayed a similar temperature behaviour as the two Deramakot logged over forests A
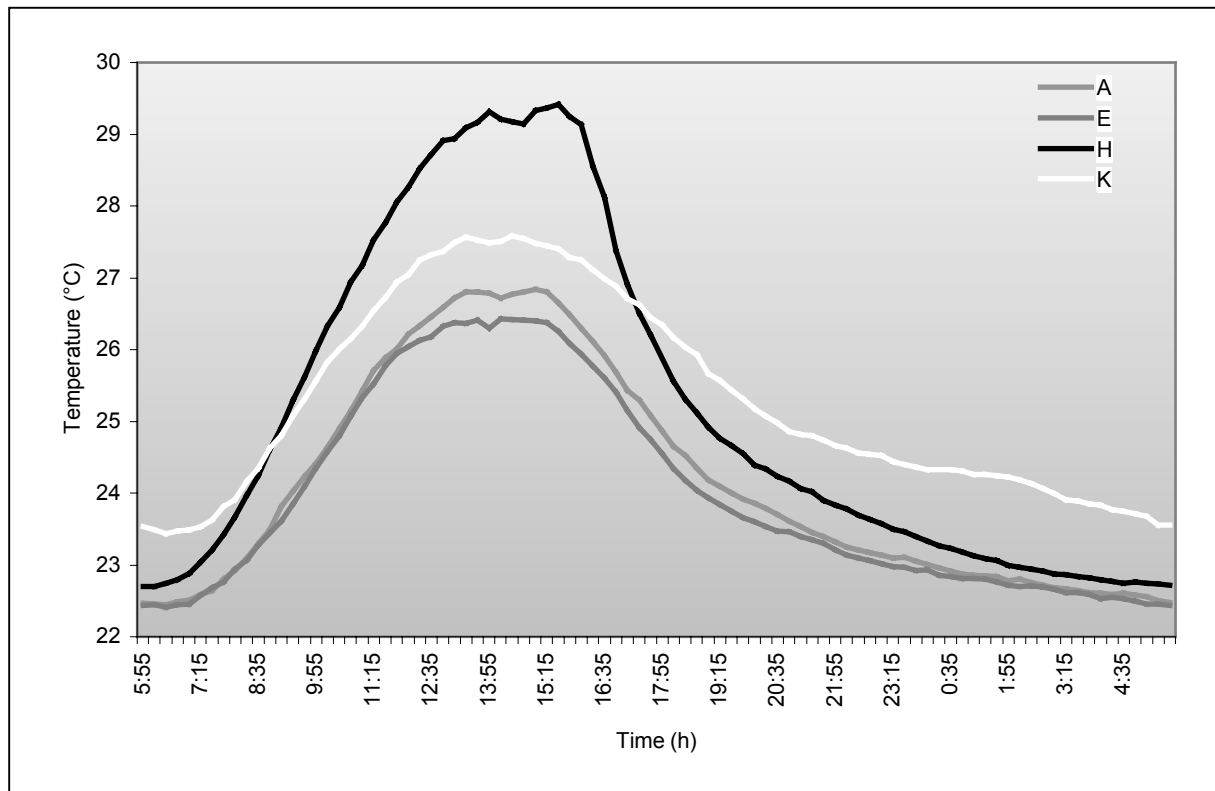
Fig. 13   Daily air temperature curves (mean of 13 days) in the different forests of DFR (A, E, H) and the primary forest of SFR (K).

and E as the curve was almost parallel, but shifted to a 1°C higher temperature level. Sepilok forest was therefore not only during day but also night times one degree hotter than the Deramakot forests of the good and regenerated type. This difference in the temperature curves was also obvious when comparing temperature values as total mean, range, minimum and maximum values (Tab. 2).

Tab. 2   Mean, range, maximum and minimum air temperature values (in °C) of 13 days of simultaneous measurements in the different forests.

Forest Plot	Deramakot good A	Deramakot regenerated E	Deramakot disturbed H	Sepilok primary K
Mean	24.0	23.8	25.0	25.0
Range	7.9	7.9	13.9	6.4
Minimum	21.3	21.3	21.3	22.3
Maximum	29.1	29.1	35.2	28.8

Mean temperatures were similar in A and E, and also in H and K. Whereas A and E were identical in all other values, I found a higher range in H and a slightly lower range in K. The minimum temperature recorded in Sepilok was 22.3°C, in Deramakot it was – independent of forest type – 21.3°C. Sepilok had a lower value in the maximum temperature than A and E. The disturbed forest of Deramakot (H) showed the highest maximum recorded with 35.2°C being more than six degrees higher than that of the other forests.

Air temperature at Sandakan Airport:

As the air temperatures in the forests were only recorded in 1999 I was also interested in the yearly variation of temperature in Sabah. As described above there are no long term records available for forest interior temperatures but these do exist for airports in Sabah. The Meteorological Services of Malaysia kindly provided me with temperature recordings from Sandakan Airport from 1968 to 1998. In Fig. 14 the annual values of highest maximum, mean maximum, daily mean, mean minimum and lowest minimum recorded are displayed. The correlation of temperature with time was significant in daily mean temperatures ($p \ll 0.001$; $r^2 = 0.597$), mean minimum ($p \ll 0.001$; $r^2 = 0.831$) and lowest minimum ($p = 0.004$; $r^2 = 0.251$). Whereas the maximum values of the recorded air temperatures did not change over the observation period, there was a significant increase in mean and minimum temperatures noticeable.
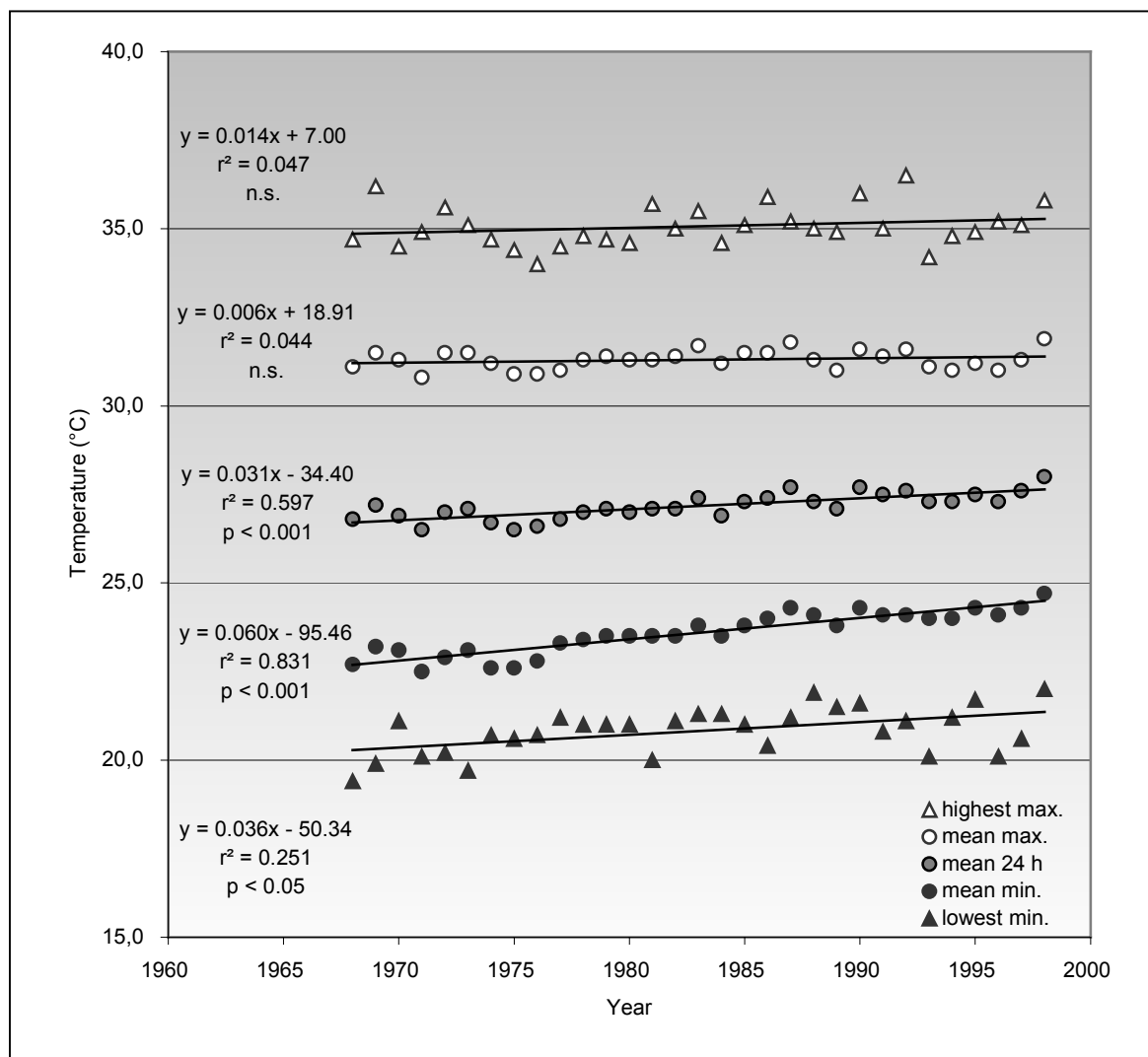
Fig. 14   Air temperature at Sandakan Airport (1968-1998): annual values of highest maximum, mean maximum, daily mean, mean minimum and lowest minimum. Regression lines are fitted to the data and equations, r² and significance levels are given.

In the 31 years of the record the annual mean daily temperature increased by 0.96°C resulting in a yearly rate of 0.03°C. The mean daily temperatures for May, which is among the hottest

months in Sabah, showed an even higher rate of 0.04°C per year leading to a total increase of 1.27°C from 1968 to 1998.

5.2.2 Leaf litter temperature

5.2.2.1 Methods

The temperature in the leaf litter was measured using Celsi pick© temperature loggers. The loggers were placed on the ground in the leaf litter. They were enclosed in plastic bags and nailed to the ground to protect them against humidity and to avoid removal by animals. Leaf litter temperature was recorded between 11:00 h and 13:00 h in all plots in 5 min intervals (March 15-April 14, 1999). The weather during the measuring period was mostly cloudy and rainy. The loggers were placed under dense vegetation to avoid direct sunlight along the Winkler transect at the six sampling points. Leaf litter temperature was measured in Danum Valley (plot L, 6d, N = 33), in Sepilok Forest (plot K, 3d, N = 18), and the Deramakot forests (good forest: plot A, 6d, N = 34; regenerated forest: plot E, 3d, N = 17; disturbed forest: plot H, 4d, N = 23). The number of measurements differed due to malfunction of some loggers and bad weather conditions not allowing access to the sites.

5.2.2.2 Results

The mean of the recorded temperatures of each measuring event was calculated. The mean temperatures recorded in the leaf litter of the different forests were significantly different (ANOVA: df = 4, F = 12.99, p << 0.001, Fig. 15).

Fig. 15   Box-Whisker plot of the leaf litter temperature in the five different forests: DVCA (L), SFR (K), DFR: good (A), regenerated (E), disturbed (H); (ANOVA: df = 4, F = 12.99, p << 0.001).

A Scheffe post-hoc test revealed a significant difference between the temperatures recorded in L and K and L and H (p < 0.001). The temperatures in plots A and E were also significantly different from the ones recorded in H (in both cases p < 0.01). The temperatures in the primary forest of Danum Valley (L), the good (A) and regenerated forest (E) of Deramakot were lower than in Sepilok Forest (K) and the disturbed forest of Deramakot (H). L displayed a broader range than A and E and H showed a broader range of temperatures than K. When comparing the means a difference of almost 2°C was found between Danum Valley and the disturbed forest H and a 1.5°C difference to the smaller primary forest of Sepilok (Tab. 3). The minimum leaf litter temperature was lowest in Danum Valley and highest in the Sepilok Forest.

Tab. 3 Maximum, minimum and mean leaf litter temperatures (°C) of the different plots.

Forests Plots	Danum Valley primary L	Sepilok Forest primary K	Deramakot good A	Deramakot regenerated E	Deramakot disturbed H
Maximum	30.4	28.0	28.0	27.2	29.8
Minimum	22.7	26.4	24.9	25.1	26.0
Mean	25.6	27.1	26.2	26.0	27.5

5.2.3 Soil temperature

5.2.3.1 Methods

This part of the project was carried out together with Thomas Reinfelder, student of Geography, University of Würzburg during his practical field course in 1999. Soil temperature was measured in the different forests using the DIGI SENSE© soil temperature probe of Cole & Parmer. This probe is recording temperature over the total length of the sensor (15 cm). Measurements took place in Danum Valley (L), in Sepilok Forest (K), and the Deramakot forests (good (A), regenerated (E), disturbed (H) in April 1999 using the six sampling sites of the transects. Temperature was measured in the morning (9:30-12:00 h) and afternoon (13:30-15:30 h) of three days yielding 36 temperature records in total. Due to heavy rains we could only record the afternoon temperatures in plots L, K and H on two days.

5.2.3.2 Results

The morning, afternoon and total data were analysed separately. There were significant differences in soil temperature between the different plots in all three categories (ANOVAs morning: df = 4, F = 16.92, p << 0.001; afternoon: df = 4, F = 28.70, p << 0.001; total: df = 4, F = 30.25, p << 0.001). In Fig. 16 the means, standard errors and standard deviations of the temperature are displayed for the complete data set (morning and afternoon measurements).

Fig. 16   Box-Whisker plot of the soil temperature in the five different forests: DVCA (L), SFR (K), DFR: good (A), regenerated (E), disturbed (H); (ANOVA: df = 4, F = 30.25, p << 0.001).

A Scheffe post-hoc test revealed significant differences in the soil temperature between L and H, L and K, K and E, H and A, H and E and E and A (in all cases $p \ll 0.001$). The temperatures could be grouped as follows: K and H showed higher and L and E lower values. The temperature in Plot A could not be assigned to any of the groups due to the great variance displayed. The means of L and E (low temperature) and K and H (high temperature) were very similar and showed a difference of about 1°C (Tab. 4). Regarding the minimum values, there was no difference between Danum Valley (L) and Sepilok Forest (K) but a great difference to the disturbed forest of Deramakot (H). The maximum soil temperature in Danum Valley is about 1°C lower than in E, about 1.5°C lower than in K and A and almost 2°C lower than in H.

Tab. 4   Maximum, minimum and mean soil temperatures (°C) of the different plots.

Forests Plots	Danum Valley primary L	Sepilok Forest primary K	Deramakot good A	Deramakot regenerated E	Deramakot disturbed H
Maximum	25.6	26.9	27.1	26.5	27.4
Minimum	23.9	23.9	24.4	24.2	25.0
Mean	25.1	25.9	25.4	24.8	26.2

As maximum temperatures may have an influence on the survival of ants the hotter afternoon temperatures were compared with each other as well. After the significant differences in the ANOVA (see above) a Scheffe post-hoc test was performed: L was significantly different

from H and K, K and H were different from A and E (in all cases p < 0.001). As obvious from Fig. 17 two groups of temperature were obtained: Danum Valley (L), Deramakot good (A) and regenerated (E) with lower and Sepilok Forest (K) and the Deramakot disturbed forest (H) with higher afternoon soil temperatures.

Fig. 17   Box-Whisker plot of the afternoon soil temperature in the five different forests: DVCA (L), SFR (K), DFR: good (A), regenerated (E), disturbed (H); (ANOVA: df = 4, F = 28.70, p << 0.001).

The maximum, minimum and mean temperatures in the afternoon are displayed in Tab. 5: again there was a 1°C difference of Danum Valley to Sepilok Forest and 1.5°C to the disturbed forest of Deramakot in the mean temperatures. Sepilok Forest showed the highest minimum temperature in the afternoon and Danum Valley the lowest maximum recorded.

Tab. 5   Maximum, minimum and mean afternoon soil temperatures (°C) of the different plots.

Forests Plots	Danum Valley primary L	Sepilok Forest primary K	Deramakot good A	Deramakot regenerated E	Deramakot disturbed H
Maximum	25.6	26.9	26.4	26.5	27.4
Minimum	24.5	25.6	24.7	24.8	25.0
Mean	25.2	26.2	25.6	25.1	26.6

5.3   Humidity

5.3.1   Soil humidity

5.3.1.1   Methods

Soil humidity was measured in the different forests of Deramakot (Plot A: good forest, Plot E: regenerated forest, Plot H: disturbed forest) in Sepilok (Plot K) and Danum Valley (Plot L). The soil humidity Theta probe$^{©}$ of Delta T was used to collect humidity measurements along the Winkler transects at the six sampling sites. From March 15-April 14, 1999 soil humidity was recorded in each of the plots at three different days. Three measurements at each sampling site (6 sites x 3 measurements x 3 days = 54 measurements per plot) were taken in the morning (9:30-12:00 h) and afternoon (13:30-15:30 h). Unfortunately, rain interrupted the data collection in the afternoon of one day in plots K and L (therefore: N = 36 measurements) and also during measuring in H (N = 33). Since the weather during this period was very rainy the soil was always showing high humidity values which made the collection of humidity data very difficult. The data were collected at least one day after heavy rains to allow surface water to vanish. All measurements are weight % H_2O (thereafter written as %H_2O).

5.3.1.2   Results

The morning, afternoon and total data were analysed separately. There were significant differences in soil humidity between the different plots in all three categories (ANOVAs: morning: df = 4, F = 17.55, p << 0.001; afternoon: df = 4, F = 15.44, p << 0.001; total: df = 4, F = 28.70, p << 0.001, Fig. 18).
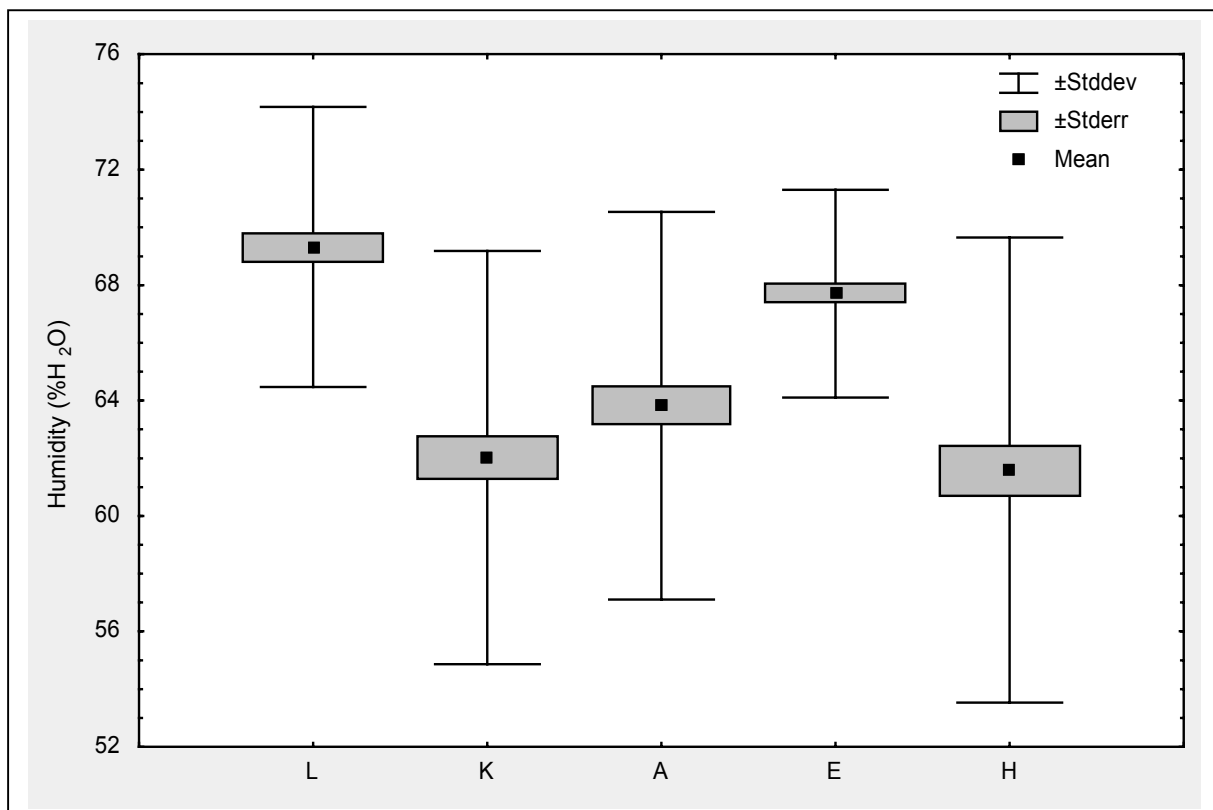
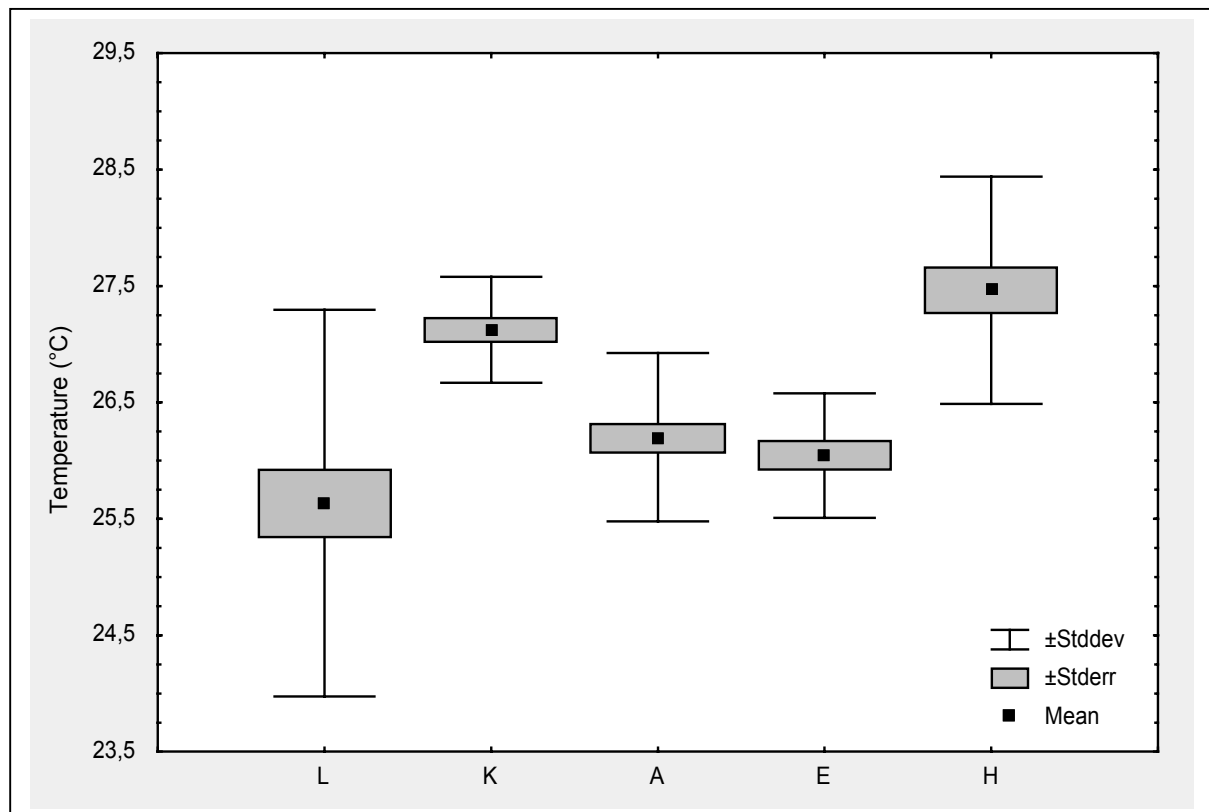**Fig. 18   Box-Whisker plot of the soil humidity in the five different forests: DVCA (L), SFR (K), DFR: good (A), regenerated (E), disturbed (H); (ANOVA: df = 4, F = 28.70, p << 0.001).**

A Scheffe post-hoc test revealed significant differences in soil humidity between L and H, L and K, L and A, K and E, H and E, and E and A (in all cases $p \ll 0.001$). The humidity measurements could be grouped in two classes: K, H and A had lower humidity levels compared to plots L and E. This is also obvious from the values in Tab. 6: the means of L and E (high humidity) and K, H and A (lower humidity) were very similar with a difference of about 5% H_2O between the two groups. The maximum in humidity was also higher in the two 'wet' plots. The lowest minimum humidity value was recorded in Sepilok Forest (K) followed by the disturbed forest H in Deramakot.

Tab. 6 Maximum, minimum and mean soil humidity (%H_2O) of the different plots.

Forests	Danum Valley primary	Sepilok Forest primary	Deramakot good	Deramakot regenerated	Deramakot disturbed
Plots	L	K	A	E	H
Maximum	76.9	72.2	73.6	74.0	71.4
Minimum	44.9	35.9	42.6	53.1	40.6
Mean	69.2	61.8	63.8	67.7	62.7

The results of the morning data set did not deviate from the total data set and are therefore not displayed here. As the measuring period was dominated by very wet weather, the afternoon data set is analysed separately because the influence of forest structure on the humidity might be reflected clearer by a higher contrast in the humidity values. After the significant differences in the ANOVA (see above) a Scheffe post-hoc test was performed: L was significantly different from H and K, K and H were different from A and E (Fig. 19; in all cases $p < 0.001$, except A with K: $p < 0.05$).
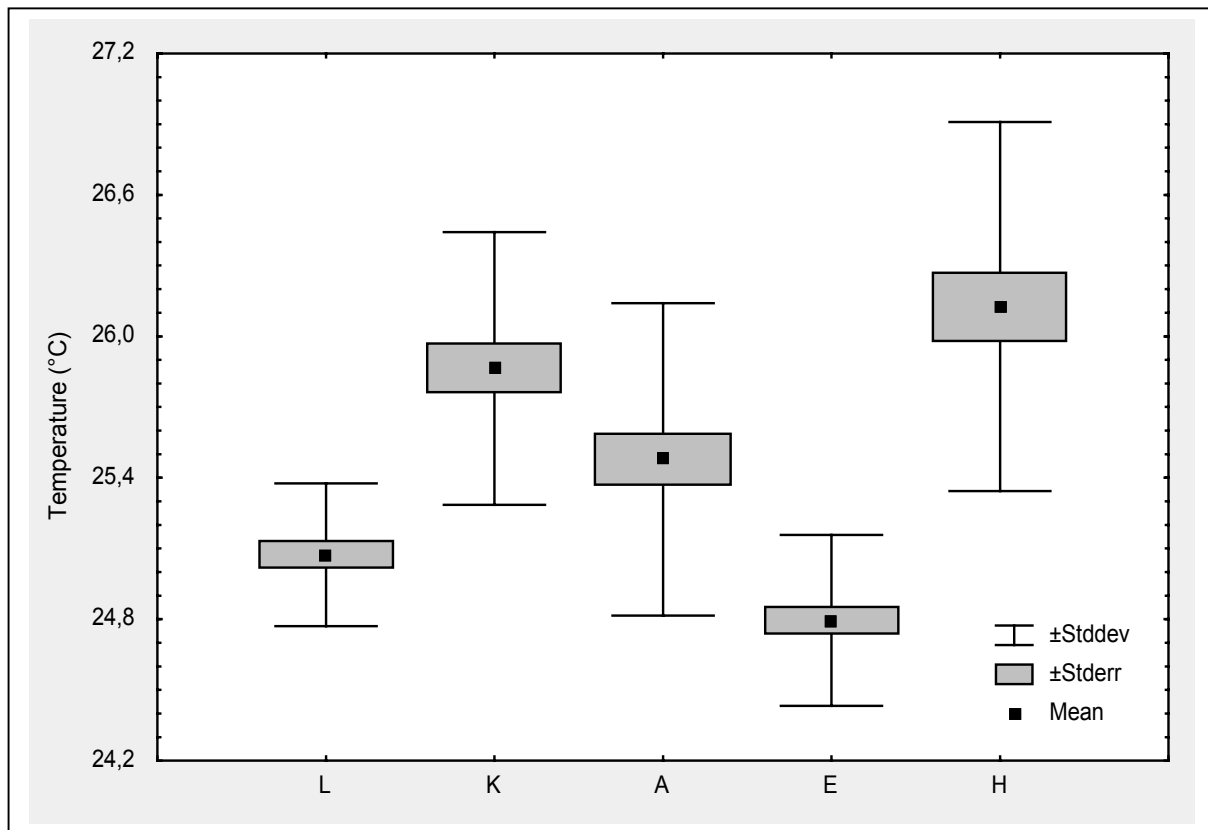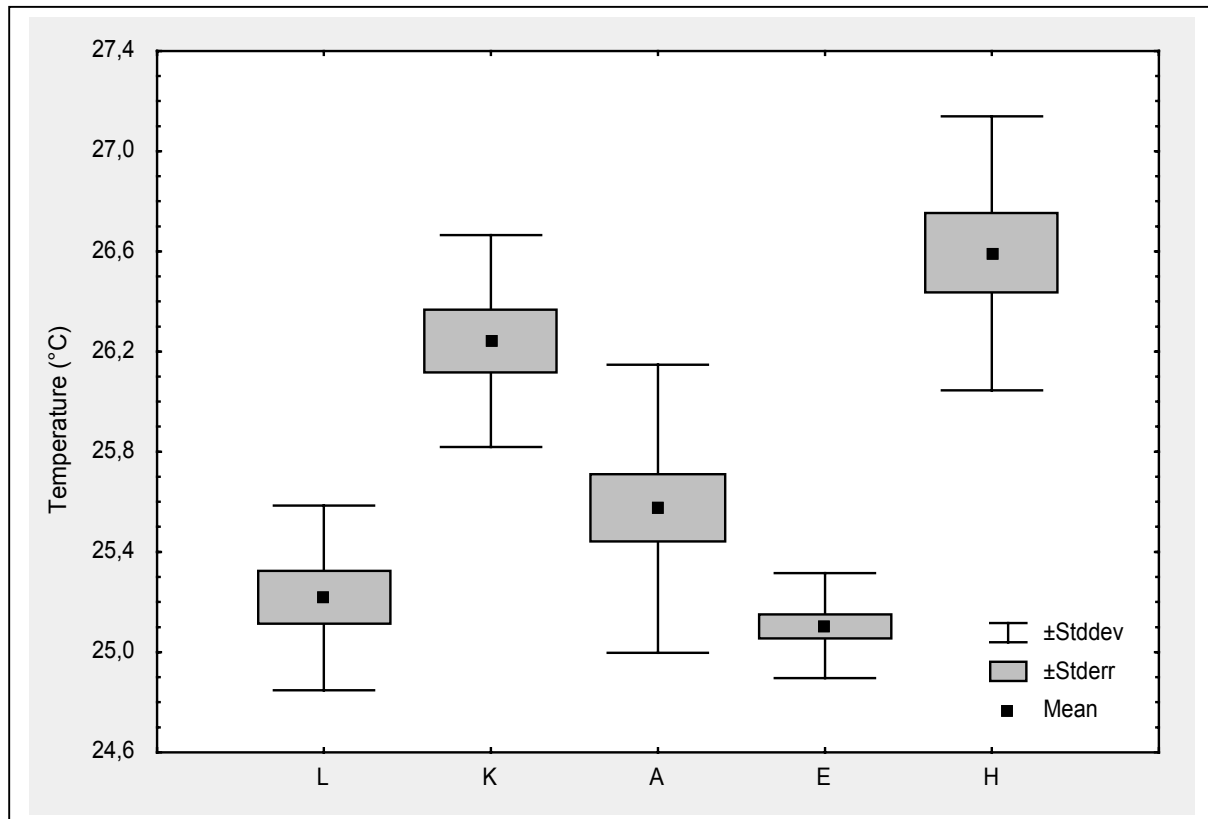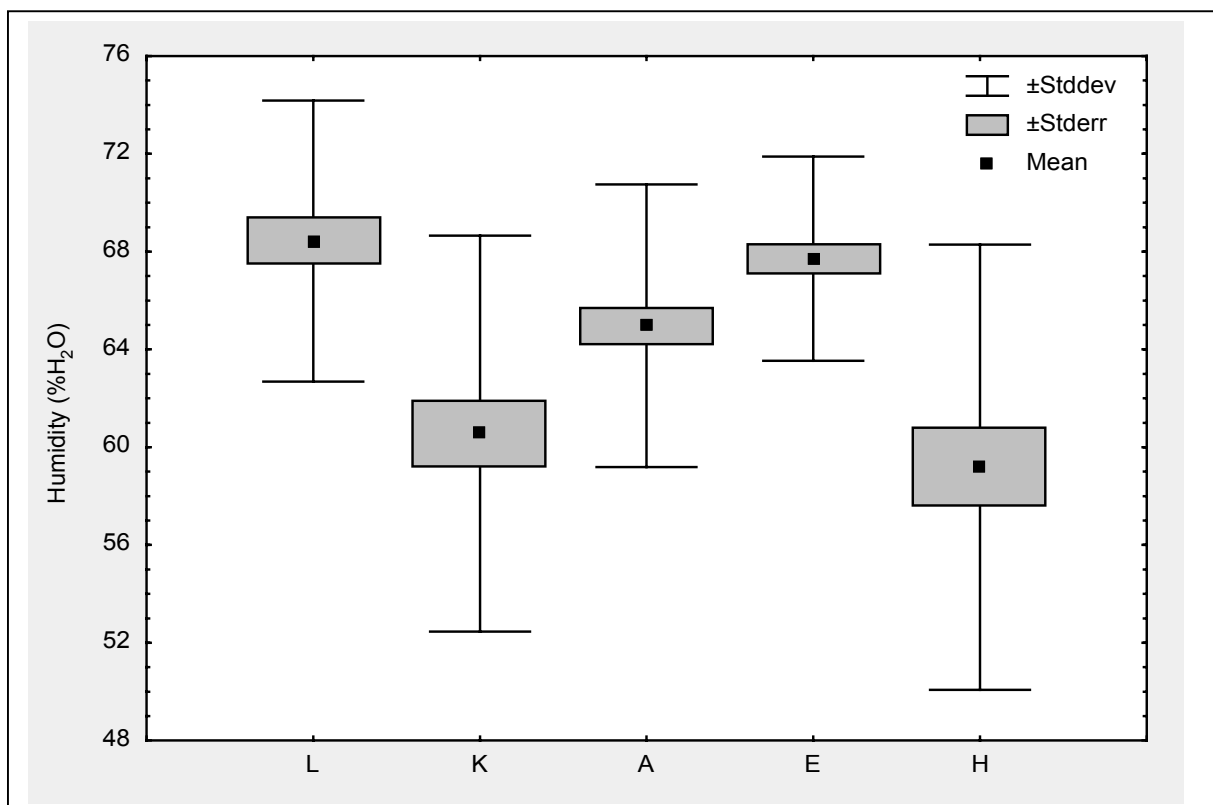

Fig. 19 Box-Whisker plot of the afternoon soil humidity in the five different forests: DVCA (L), SFR (K), DFR: good (A), regenerated (E), disturbed (H); (ANOVA: df = 4, F = 15.44, p << 0.001).

As obvious from Fig. 19, we obtained two groups of forests with different soil humidity: Danum Valley (L), Deramakot good (A) and regenerated (E) with higher afternoon humidity levels and Sepilok Forest (K) and the Deramakot disturbed forest (H) with lower values.

Tab. 7 Maximum, minimum and mean afternoon soil humidity (%H_2O) of the different plots

Forests Plots	Danum Valley primary L	Sepilok Forest primary K	Deramakot good A	Deramakot regenerated E	Deramakot disturbed H
Maximum	74.6	72.2	73.6	74.0	70.8
Minimum	44.9	35.9	44.7	53.1	40.6
Mean	68.4	60.6	64.9	67.7	59.2

The maximum, minimum and mean soil humidity values of the afternoon are displayed in Tab. 7: it shows a difference of more than 5% H_2O between the 'wet' and 'dry' forests. Sepilok Forest showed the lowest minimum humidity in the afternoon, and Danum Valley the highest maximum recorded. The difference between total values and afternoon values was obvious in the means, especially in plot H with a difference of more than 3% H_2O.

5.3.2 Leaf litter humidity

5.3.2.1 Methods

Parallel to the soil humidity (see above), leaf litter humidity was measured in the different forests of Deramakot (Plot A: good forest, Plot E: regenerated forest, Plot H: disturbed forest) in Sepilok Forest (Plot K) and Danum Valley (Plot L). Sampling was undertaken at these sites on the same day leading to a similar number of measurements. At each sampling site a leaf litter sample of about 0.5 m² was collected in the morning and afternoon. The samples were homogenised the same afternoon using a household mixer. Homogenising was necessary as there was too much air between the raw leaf debris which lead to inaccurate measurements with the Theta probe[©]. The leaf litter mixture was then filled into a plastic tube and humidity measurements were taken. Humidity values might be lower than in reality as some water was trapped in the plastic bag used for carrying the leaf litter sample and also in the mixer but this error will be similar for all samples in the different forests.

5.3.2.2 Results

The morning, afternoon and total data for leaf litter humidity were analysed separately. There were significant differences in leaf litter humidity between the different plots in all three categories (ANOVAs: morning: df = 4, F = 13.01, p << 0.001; afternoon: df = 4, F = 10.01, p << 0.001; total: df = 4, F = 21.74, p << 0.001). In Fig. 20 the means, standard errors and standard deviation of the leaf litter humidity are displayed for the complete data set (morning and afternoon measurements).
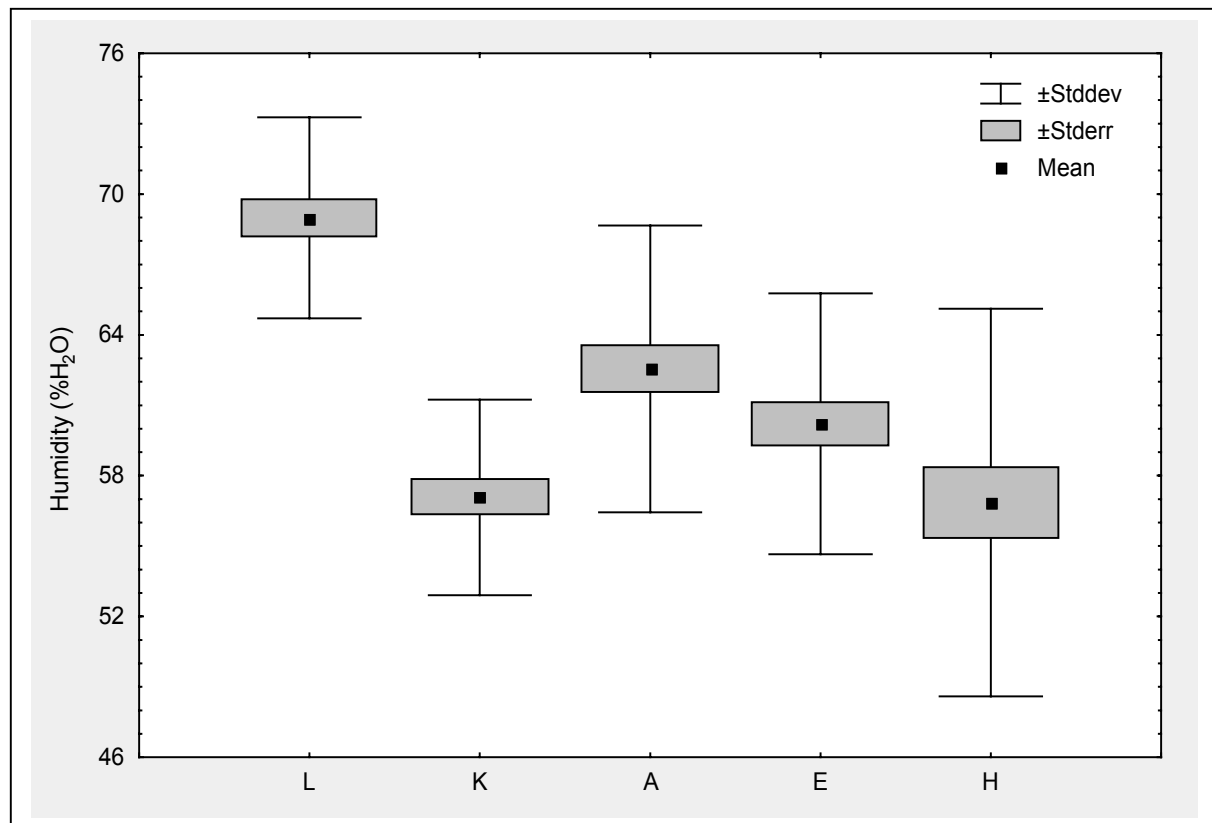
Fig. 20 Box-Whisker plot of the leaf litter humidity in the five different forests: DVCA (L), SFR (K), DFR: good (A), regenerated (E), disturbed (H); (ANOVA: df = 4, F = 21.74, p << 0.001).

A Scheffe post-hoc test displayed significant differences in the leaf litter humidity between L and all other forest plots, K and A, and A and H (in all cases p << 0.001). The humidity measurements can be grouped in two classes: K and H had lower humidity levels compared to the more humid plots L and A with E being intermediate between the two. This also becomes obvious from the values in Tab. 8: the mean of L is far above the other plot values followed by A (high humidity). The means of K and H are very close to each other (0.2 %H_2O). The mean humidity of E is intermediate between K/H and A. The maximum in humidity is clearly higher in L and A, the two 'wet' plots. The lowest minimum humidity value was recorded in the disturbed forest H in Deramakot.

Tab. 8 Maximum, minimum and mean leaf litter humidity (%H_2O) of the different plots.

Forests	Danum Valley	Sepilok Forest	Deramakot good	Deramakot regenerated	Deramakot disturbed
Plots	L	K	A	E	H
Maximum	74.8	65.0	72.4	70.6	71.9
Minimum	58.7	49.2	50.9	47.4	44.2
Mean	69.0	57.1	62.5	60.2	56.9

The results of the separate analysis of the morning and afternoon data set did not reveal any new insights and are therefore not displayed here.

5.4   Discussion

Temperature and humidity are combined in this discussion as both parameters are interrelated and describe essential habitat parameters for litter dwelling ants in tropical rain forests.

All temperatures measured displayed a very similar pattern: higher values were recorded in the primary forest of Sepilok (K) and in the disturbed forest (H) in Deramakot. The lowest mean temperatures were measured in the primary forest of Danum Valley (L), followed by the regenerated (E) and good (A) forests of Deramakot. The humidities displayed a reverse pattern with lowest values in Sepilok and Deramakot disturbed and highest in Danum Valley. Therefore we can assign the forests in two groups: The 'cool and wet' forests Danum Valley, Deramakot good and regenerated with buffered temperature curves and high humidity levels even in the afternoon, and the 'hot and dry' forests of Sepilok and Deramakot with higher daily fluctuations in temperature and humidity over the course of the day. The differences between the groups were about 0.9-1.9°C depending on the stratum where the measurement had taken place and the considered plots. The increase in temperature in the 'hot and dry' forests was not only measured in the air or in the leaf litter but also in the upper layer of soil (15 cm depth), a habitat very stable in its daily temperature behaviour (Vareschi, 1980; Walter & Breckle, 1991a; 1991b).

Muhamad and Kamaruzaman (1987) measured in 10 cm depth mean soil temperatures of 22.0°C in virgin forest and 25.0°C in logged over forest in peninsular Malaysia. They even detected a difference of 7.3°C to the primary forest in a log landing site. These data show an even more pronounced difference in soil temperature between primary and logged over forest than recorded in the Sabah forest types. Unfortunately no descriptions of the weather conditions were given as a dry and sunny season might have lead to the described results.

Higher temperatures during the day and especially the strong increase in the disturbed forest of Deramakot (H) at noon led to evaporation in the leaf litter and soil and therefore a drying of these strata. The effect of drying is even more pronounced in a comparison of the afternoon and morning soil humidity measurements; differences between the two forest groups reached 5-7% H_2O. The drying effect was most pronounced in the soil of plot H, the disturbed forest of Deramakot, with 3% H_2O loss in the afternoon. Compared to the soil, humidity was generally lower in the leaf litter which is directly exposed to evaporation and builds an isolating layer for the underlying soil. But temperature does not only affect humidity, this is also true vice versa. The soil in the 'cool and wet' forests had higher humidity levels. The pore spaces in these soils are filled with water which is a much better heat conductor than air that fills the pores of drier soils, therefore the soils stay cooler during the course of the day (Muhamad & Kamaruzaman, 1987).

What could explain the changes in the microclimate in the 'hot and dry forests'? One explanation for the climatic difference of Sepilok might be its proximity to the sea, which has an effect on climate although one should expect a cooling effect with lower temperatures and higher humidity levels as the sea buffers temperature. When we compare the two groups it is also obvious that altitude could be an important variable: all the cool forests are situated around 250 m a.s.l. compared to the hot forests at 60-85 m a.s.l. (see Study Sites). Altitude has an effect on climate, but more pronounced along an altitudinal transect on a mountain (Brühl, 1996; Kitayama, 1992; 1996). Studying the mean air temperature curves (Fig. 13) we see that temperature in the disturbed forest (H) in Deramakot, situated at 85 m a.s.l. reaches a

similar night value as plots on 250 m a.s.l. If altitude had a pronounced effect on temperature we would expect Deramakot H to show also at least 1°C hotter night temperatures, which is not the case. Therefore we have to seek another explanation for the climatic difference.

Considering the disturbed Deramakot forest (H) the most striking feature in its temperature behaviour is the strong increase displayed in the air temperature leading to mean values of up to 29.5°C. This increase in the morning and the steeper curve and longer cooling periods might be related to a drastically reduced canopy structure. There is only one canopy stratum left in most of the area in the disturbed forests compared to a multi layered canopy in primary forests. This difference in canopy structure can be derived from the forest stand structure measurements (see Forest Structure) with a clear shift towards smaller trees tending to have a smaller crown, and a high proportion of *Macaranga* trees which never reach above the lower canopy (see stratum map of Deramakot, Fig. 7). The open canopy in the disturbed sites allows direct sunlight to reach the ground, especially around noon with the sun at its zenith and the buffering function of a multi-layered canopy at loss. Sunlight reaching the forest floor has been measured at as little as 2% in closed-canopy tropical forests, selective logging raises this percentage manifold with canopy reduction rates being as high as 75% in Asian dipterocarp forests (Cannon *et al.*, 1994; Seidler & Bawa, 2001). Temperatures increase and humidity values in leaf litter and soil fall during the course of the day. The loss of humidity during the day reached the highest values in H compared to the other forests. But during the night, air temperature cooled down to a similar level as in the close-canopy forests of the 'cool and wet' group and humidity levels were restored due to afternoon rains or night fog. Therefore I suggest that the changes in canopy structure which is due to the severe impact of at least three logging operations in the disturbed forest type has a direct impact on the microclimate in the forest interior, leading to higher temperatures and lower humidity at ground level at day time.

In Sepilok Forest the increase in temperature and the decrease in humidity cannot be explained in this way because its multi-layer canopy is intact as can be inferred from the stand structure data. A possible explanation might be related to the isolation of Sepilok Forest, an increase in solar radiation at the forest edges (Saunders, Hobbs & Margules, 1991) and its oil palm plantation surroundings. Ground and air temperatures are getting very high in these plantations as an insulating canopy is almost totally lacking.

The conversion of large tracts of land into oil palm plantations started in the 1980s, the Sandakan area already having been deforested to a huge extent in the 1960s for the establishment of rubber tree plantations (Fox, 1969; 1973; R. Ong, FRC, pers. comm.). These large scale changes of landscape might have had a visible influence on temperature as Sandakan Airport records show an increase of 0.96°C in mean air temperature over 31 years since 1968. There were no significant increases over this time in absolute maxima or mean maxima but in lowest minima and mean lowest minima which then influenced mean air temperatures. If the increase in temperature would be due to global warming the maxima should have been affected as well and the measured increase rate at Sandakan would be unusually high. The important variables are the minima and their increase over time, which means that the Sandakan area is not cooling down to similar night temperatures as measured in the 1960s. This might be due to a gradual loss of cooling forests in the vicinity of the airport by the conversion into large scale plantations. Deforestation of tropical forests is known to locally cause a more extreme climate (Whitmore & Sayer, 1992). This local climate

change might be obvious even inside a forest fragment of the size of Sepilok, since forest fragments are more open to temperature exchange at their edges (Saunders *et al.*, 1991). Thus the increase in temperature of about 1°C over time might be one explanation for the shift of the mean air temperature curve inside Sepilok Forest of 1°C compared to the 'cool and wet' forest group, although the influences of altitude and location cannot be ruled completely.

I would like to point out that all measurements of the forest climate took place between March and April 1999. This period was comparably wet as can be seen from the rainfall measurements (see Study Sites), with 124% of normal rainfall and April being the wettest month recorded in Danum. Although skies were mostly cloudy, differences in the forest floor climate were detected even during this period and these are expected to be even more pronounced during droughts as the ENSO event at the beginning of our study in 1998. Short dry periods are frequently encountered in Borneo (MacKinnon *et al.*, 1996) with the occasional occurrence of severe dry ENSO events (Cao, 2000; Walsh, 1996). These droughts have a heavy impact on the ecosystem: in the 1982-83 ENSO the upper montane forest vegetation of Mount Kinabalu suffered severely, leading to changes in plant composition (Whitmore & Sayer, 1992), and fires raging in Sabah destroyed over 1 Mio ha of forest and plantations with an increased fire probability recognised in logged over forests (Cao, 2000; MacKinnon *et al.*, 1996).

Unfortunately I did not have the necessary equipment for climate measurements with me at the start of this study but some descriptions of the situation in the forests during that time might strengthen my point: air humidity levels of 30% were measured inside the forest of Danum Valley in May 1998 (D. Bebber, pers. comm.), the leaf litter in the forest interior was dry in all forests, major rivers, usually about 1-2 m deep dried out completely or were only present in form of small puddles. Whereas most of the little creeks disappeared in Deramakot they were still running in Danum Valley. We observed leaves drying at living trees in the understory of Sepilok Forest where huge litter layers accumulated due to leaf shedding of many dipterocarp trees. The measured difference in temperature and humidity levels is surely pronounced between primary and logged over forests over months during droughts and severe ENSO events and especially the maxima in temperature and the minima in humidity might be crucial for the existence of ants and other leaf litter arthropods.

5.5   Leaf litter

5.5.1   Introduction

Leaf litter is the main habitat for ground dwelling ants. Most ant species forage for food here and build their nests between twigs and rotten leaves. The leaf litter layer is also the stratum where decomposition takes place being one important process in nutrient cycling. In aseasonal tropical rain forests tree species and individuals differ in the pattern of their leaf fall with time which causes a heterogeneous mosaic of litter mass on the forest floor (Medway, 1972). This mosaic structure, contributing to niche diversification may be caused by differences between individual trees, tree species or families and, on a larger scale, between developmental phases of the forest canopy. Tree species possibly affect the heterogeneity of the forest floor by (1) leaf biomass or the quantity of leaf fall, (2) leaf phenology and the timing of leaf-shedding, (3) chemical characteristics of leaves, such as nutrients and secondary metabolites, and (4) physical characteristics of leaves, such as hairiness and leaf toughness (Burghouts, Campbell & Kolderman, 1994). I studied the first point mentioned, the patterns of leaf litter biomass on the forest floor in primary and logged over forests.

5.5.2   Methods

The amount of leaf litter was recorded along the transects at the six sampling sites in the five forests. The volume of leaf litter of each Winkler sample (1 m²) was measured after the extraction of arthropods using a household measuring cup. The litter was filled in the cup and shaken until it settled and formed a horizontal, flat surface. The volume was measured to the nearest measuring step of 50 cm³. As the leaf litter had already been sifted in the Winkler procedure (see General Methods) this fine leaf litter did not contain large leaves, twigs or branches. This point is important, because it is not possible to compare my data with absolute numbers obtained in other studies which concentrated on biomass production and flows in tropical forests. The amount of fine leaf litter in this study is a correlate of general leaf biomass on the ground. In Danum Valley and Sepilok Forest 180, in Kebun Cina 60 and in each of the different logged over forests of Deramakot 240 samples were collected.

5.5.3   Results

The total volume collected in the 60 m² in the different study plots are displayed in Tab. 9.

Tab. 9	Total volume of fine leaf litter (l) collected in the different plots on 60 m² in the plots of the forests under study.

Danum primary	L98	L99	M98	
	30.3	36	39.1	
Sepilok primary	K98	K99	K*99	
	17.7	19.5	14.1	
Kebun Cina primary	O00			
	31.2			
Deramakot good	A98	A99	B98	C98
	38.3	26.3	28.7	32.4
Deramakot regenerated	D98	E98	E99	F98
	17	14.6	15.1	16.1
Deramakot disturbed	G98	H98	H99	I98
	20.2	17.8	16.2	22.1

Highest total volumes were measured in all plots of Danum Valley, other values exceeding 30 l were measured in Kebun Cina and two plots in the good forests of Deramakot (A and C). Variation between years (1998 and 1999) was highest in plot A with 12 l difference followed by plot L of Danum Valley with 5.7 l. The difference between 1998 and 1999 in the other plots sampled to account for temporal variation was about 1-2 l.

The data of the different forests did not deviate from a normal distribution and all requirements for an ANOVA were met. The difference in the volume of leaf litter per sample in the different forests was significant (df = 5, F = 42.78, p < 0.001). A Scheffe post-hoc test revealed significant differences between Danum Valley and Sepilok, Deramakot regenerated and disturbed, between Sepilok and Kebun Cina and Deramakot good, between Kebun Cina and Deramakot regenerated and disturbed and between the good forest and the regenerated and disturbed forest of Deramakot (in all cases p << 0.001). The different volumes of leaf litter are visible in the Box-Whisker plot of Fig. 21.
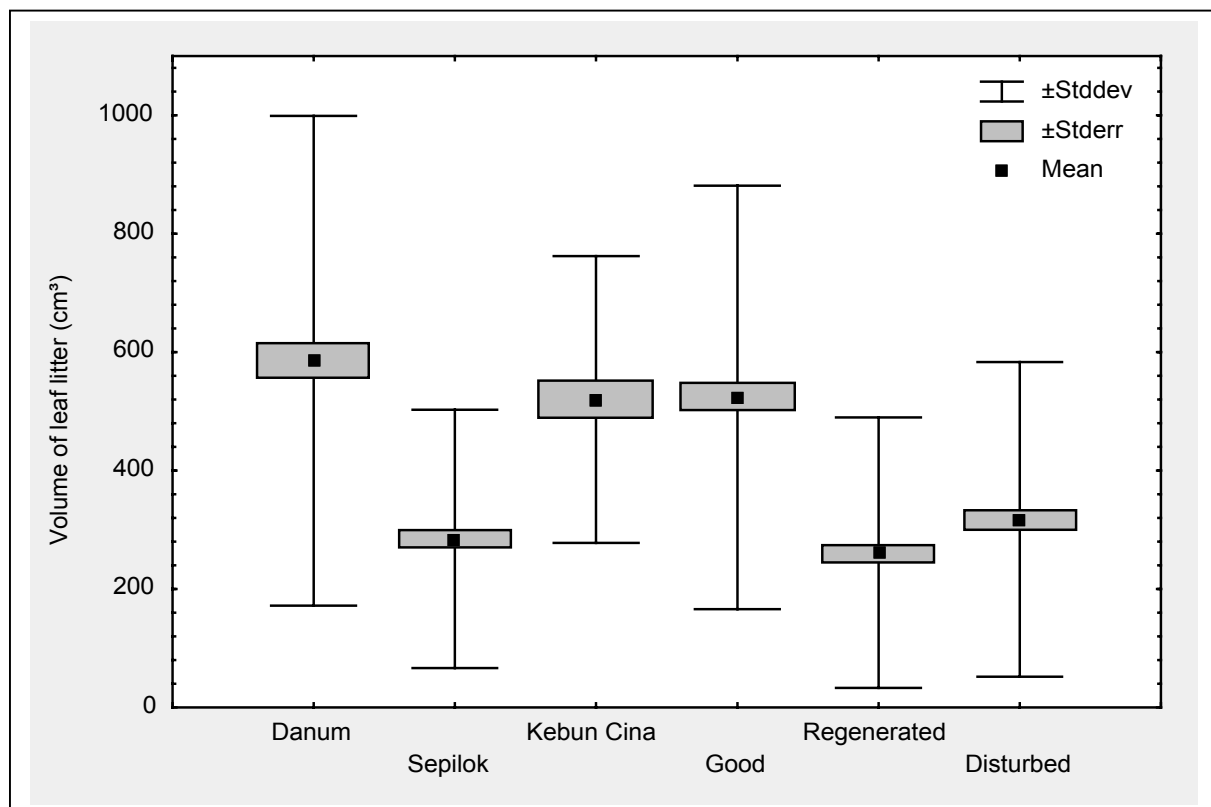
Fig. 21 Box-Whisker plot of the volume of leaf litter (cm³) per sample (1 m²) in the six forests: DVCA, SFR, KCFR, DFR: good, regenerated and disturbed (ANOVA: df = 5, F = 42.78, p << 0.001).

Tab. 10   Mean, range, minimum and maximum of the amount of fine leaf litter (cm³) collected in the different forests.

	Danum primary	Sepilok primary	Kebun Cina primary	good	Deramakot regenerated	disturbed
Mean	585.4	284.72	520	523.7	261.5	317.7
Range	2850	1950	1000	2150	1150	1350
Minimum	50	50	200	50	50	50
Maximum	2900	2000	1200	2100	1200	1400

The difference between the two groups in leaf litter volume distribution becomes even more obvious when we compare means, range and maxima with each other (Tab. 10): Danum Valley, Kebun Cina and the good forest of Deramakot have all higher mean volumes of leaf litter per Winkler sample (means: 520-585 cm³), whereas Sepilok Forest and the regenerated and disturbed forest of Deramakot show lower values (means: 260-318 cm³). The variation in leaf litter volume was remarkable in all forests reflecting the heterogeneity of the habitat on the forest floor. There were square meters with only 50 cm³ of fine leaf litter in all data sets even in the primary forest of Danum Valley as well as samples with high volumes of leaf litter in the disturbed forests of Deramakot (up to 1 400 cm³). The highest range of different leaf litter volumes was observed in Danum Valley with 2 850 cm³, although some square meters in Sepilok Forest yielded high volumes of leaf litter (up to 2 000 cm³) as well. The leaf litter in Kebun Cina seemed to be distributed more evenly with a lower range of leaf litter volumes recorded, but this might as well be related to the small sample size (60 m²).

5.5.4   Discussion

The highest volumes of fine leaf litter, in total and mean per square meter, were found in Danum Valley, Kebun Cina and the good forest of Deramakot. The minimum of leaf litter volume of 50 cm³ was recorded in most forest plots except for Kebun Cina, leading to highest ranges and therefore highest heterogeneity in the primary forest of Danum Valley and the good forest of Deramakot. The volume of litter was more evenly distributed in Kebun Cina resulting in a slightly lower range. Leaf litter volumes in Sepilok Forest and the regenerated and disturbed forest plots of Deramakot were falling below 55% of the Danum Valley values and mean sample volume was low. Although the leaf litter volume was generally reduced in the disturbed and regenerated forests leading to a lower heterogeneity, some patches revealed a leaf litter layer of up to 1 400 cm³, about 2.5 times more than the mean litter volume sample in the primary forest of Danum Valley.

In a comparison of leaf fall in primary and logged over forest sites in Danum Valley, Burghouts and co-workers (1994) also found a more pronounced litter patchiness in the primary forest compared to the logged forest. The higher leaf litter layer responsible for higher ranges in litter volume in Danum Valley, Kebun Cina, and the good forests of Deramakot might be explained by the multi-layered canopy which can be inferred from the data on stand structure (see Forest Structure, Fig. 7). This canopy has more leaves per forest floor area than the often single-layered canopy of the disturbed logged over forests.

Not only the canopy structure but also the species composition of the trees and the timing of leaf-shedding plays a role in the heterogeneity of leaf litter biomass on the forest floor. The single-layered canopy of the logged over forests is characterised by a high proportion of

Macaranga tree species and the input of e.g. *Macaranga hypoleuca* on total leaf fall was found to be continuously high throughout the year (Burghouts *et al.*, 1994). Therefore a reduction in tree species richness in logged over forests might also explain the low between year variation leading to a spatially and temporally very similar leaf litter layer. The primary forest of Danum Valley and the low impact logged good forest of Deramakot consists of many different tree species, including large dipterocarp trees. Dipterocarps such as *Shorea argentifolia* displayed alternating large peaks of leaf fall by different individuals and *S. johorensis*, and *pauciflora* showed synchronised peaks between individuals (Burghouts *et al.*, 1994) leading to a dramatic temporal and spatial variation of leaf litter biomass on the ground. As dipterocarp trees are targets for timber extraction in Sabah forests the pattern of leaf fall is expected to be different in heavily logged over forests leading to a reduction of the heterogeneity of leaf litter biomass on the forest floor.

Unfortunately the loss of a multi-layered canopy and many tree species cannot be used as an explanation for the reduced litter volume in Sepilok Forest with values as low as in the regenerated and disturbed forests of Deramakot because stand structure and species composition are very similar to the primary forest of Danum Valley. We can only notice the low litter volume as a robust pattern, because the data were identical in two successive, climatically very different years in two 500 m transects. Soil processes are hardly studied in tropical forests (Hagvar, 1998) and explanations for the occurring pattern are difficult to find. One could speculate that higher temperatures recorded might speed up litter decomposition, but this was not the case in Kebun Cina with a high volume of leaf litter and supposedly very similar temperatures as Sepilok. Decomposition rates in forest fragments in Brazil increased towards forest edges and were generally lower in smaller fragments (1-100 ha), but were not correlated with air temperature, evaporative drying rate or leaf litter invertebrate densities (Didham, 1998). Explanations for these alterations included different densities of litter feeding termites or basidiomycete fungal activity, but both parameters were not measured and are therefore highly speculative.

In Kebun Cina, the smallest forest fragment, I recorded high volumes of leaf litter, which agrees with the multi-layer canopy and tree species composition explanation. Another feature of the litter in Kebun Cina, not accounted for in this study quantitatively, was different from all other forests: small twigs and branches did not decompose and were accumulating on the forest floor. As decomposition processes are mediated by invertebrates, changes in the composition of the decomposer community in the forest fragments might affect the structure of the litter layer in the forest (Coleman, 2001; Eggleton *et al.*, 1996, 1997). The twig accumulation might be due to a reduction in density of wood feeding termites in this forest fragment.

It seems that the processes leading to lower litter volumes in forest fragments are difficult to understand and not easily explainable by canopy cover and/or tree species heterogeneity. For the comparison of leaf litter volume in the primary forests of different sizes we can just follow the conclusion of Didham (1998) that litter structure and nutrient cycling are inevitably altered by forest fragmentation.

In the logged over forests I measured a reduction of fine leaf litter volume but I also found effects of logging on litter heterogeneity. The consequences of changes in the tree species composition in logged over forests on leaf litter quality were studied in Danum Valley

(Burghouts *et al.*, 1994): in the logged forest *Macaranga hypoleuca* and *Euodia confusa*, two pioneer trees and 14 other species made up 34% of the leaf fall. In the primary forest the 16 most dominant species in the litter samples accounted only for 8% of the annual leaf fall, indicating that the litter is composed of leaves of more tree species. The higher species richness recognised in leaf fall therefore increases the chemical and physical heterogeneity of leaf litter and may lead to niche diversification for all kinds of soil organisms. Litter type for example altered the species composition of ectomycorrhiza in temperate forests (Conn & Dighton, 2000), similar studies in tropical forests are lacking until now.

6   Sampling Efficiency

6.1   Introduction

The problem of getting an approximate description of the biodiversity pattern of a taxon along a gradient (e.g. of forest disturbance) can be broken down into two parts (Colwell & Coddington, 1994; Longino, 1994; 2000): (a) measuring or estimating the species richness of species assemblages locally; (b) measuring or estimating the complementarity - the distinctness or dissimilarity - of these local inventories. A prerequisite for (b) is to sample the local communities (a) to a similar, preferably high level (Hammond, 1990; 1992; 1995; Lande, deVries & Walla, 2000; Longino, 2000; Mawdsley, 1996; Peterson & Slade, 1998; Soberon & Llorente, 1993). It is desirable to get into the section of the species accumulation curve that approaches the asymptote, which indicates that only few species would be added with additional sample units.

As tropical rain forests are patchy in their plant distributions and the variation in terrain is considerable (Basset *et al*., 1998; Burghouts, Campbell & Kolderman, 1994; Rosenzweig, 1997; Webb & Peart, 2000), it was expected that ant communities of the leaf litter would also show considerable heterogeneity. The sampling effort therefore has to be intense to cover the various microhabitats for leaf litter ants within a forest in a quantitative way. Two questions about the sampling design arose:

1.   How large is the minimal sample size required to obtain a high percentage of the leaf litter ant community of a tropical rain forest?
2.   How much is the species accumulation curve influenced by the sampling design?

6.2   Methods

This study was undertaken in the Danum Valley Conservation Area, because it was expected that ant diversity is highest in a contiguous primary rain forest. Therefore the estimated area and design for sampling should also be sufficient in the possibly less diverse habitat secondary forest, assuming a similar patchiness or heterogeneity. To answer the questions above, the following two sampling designs were established:

6.2.1   Area - Line comparison

The species accumulation curve might be different depending on whether we sample sites within a square or along a Line transect. Along a line, with greater distance covered, soil and litter conditions might be different enough to present new habitats for some ant species. Also, as ant species often exist in colonies with multiple nests it is probable that the communities of sampling sites are more similar, if the sites are situated next to each other. I sampled nine sites in two different ways (Fig. 22): in the Area design, sampling sites formed a square, in the Line design the neighbouring plots are arranged along a Line transect. Every sample site was 33.3 x 33.3 m, thus nine plots added up to one ha. From previous data on ant species richness (Agosti, Maryati & Chung, 1994; Brühl, 1996; Brühl, Gunsalam & Linsenmair, 1998; Brühl, Mohamed & Linsenmair, 1999; Delabie *et al*., 2000; Fisher, 1996; Rosciszewski, 1995; Ward, 2000) it was estimated that 90 m² should be a sample size large enough to obtain a high proportion of the litter ant community. The plots were situated along the West trail, from West 10 to West 14 (plot L, see Study Sites).

6.2.2   Short - Long comparison

A greater distance covered by a Line transect might include more habitats due to the heterogeneity of the forest on rugged and sloping terrain than a Line transect with neighbouring sites. It is likely that the ants collected in sites further apart from each other reflect the overall ant community of a forest type in a better way as more microhabitats are covered. The effect of transect length on sampling efficiency was tested along the Line transect of the previous set up in the following year. Transects of six sites (each 33.3 x 33.3 m) were established in two patterns: one with adjoining sites (Short: 200 m) and one with a gap of   100 m between the centers of the sampling sites (Long: 500 m, Fig. 22).This experiment was carried out in March 1998 along the West trail from West 10 to 15.
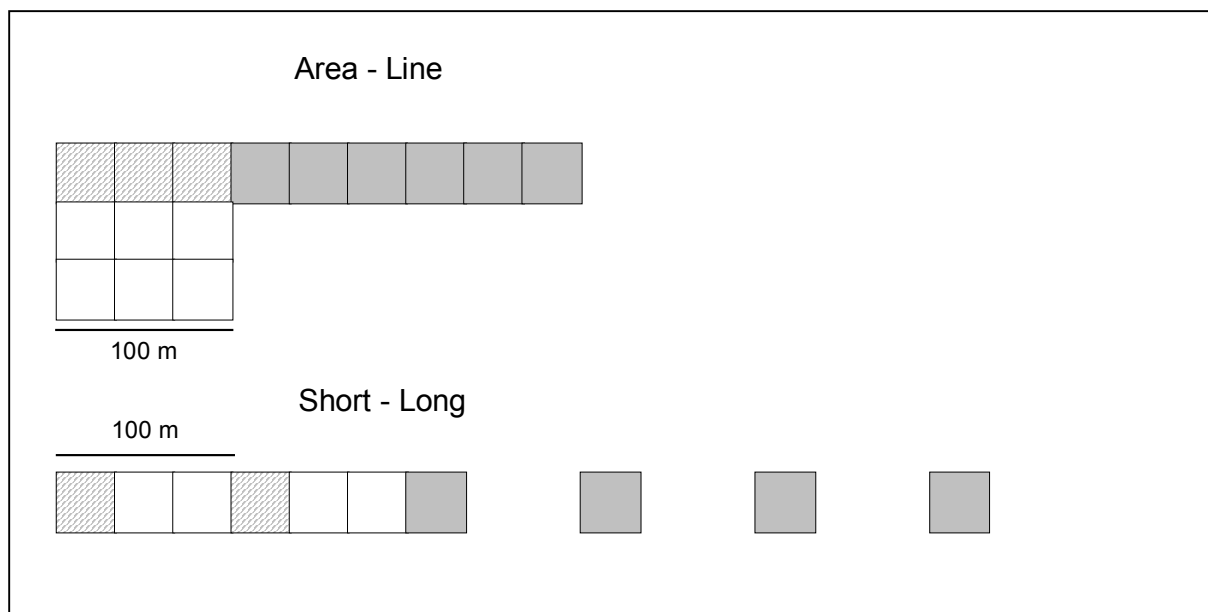
Fig. 22   Sketch of the different sampling designs tested: Area - Line design and Short - Long design. Sampling sites of Area and Short in white, of Line and Long in grey. The samples of hatched sampling sites were used in both designs of the two comparisons.

In all designs ten samples of leaf litter, each 1 m² were collected in one sampling event in one site. Samples within a site were separated by at least three metres. Sample selection and Winkler litter extraction followed the ant processing scheme as described in the General Methods section. Some species that are not effectively collected in a quantitative way by the Winkler litter sampling method were excluded.

6.3   Results

For the evaluation of the effect of design and number of samples on the completeness of the collected ant community 270 m² of leaf litter were sampled in total. After excluding ants not reliably collectable by the Winkler litter sifting method, and ants of other strata, the leaf litter ant community included 156 species in 44 genera and five subfamilies.

6.3.1   Area - Line comparison

This comparison was based on 150 m² samples of leaf litter with 138 ant species collected. In both, Area and Line design sampling amounted to 90 m² (with 30 identical samples used in both designs). The Area design yielded 113 species and the Line sampling 127 species. The smoothed species accumulation curve for the Line design continued to increase further after the Area design curve became already flatter.
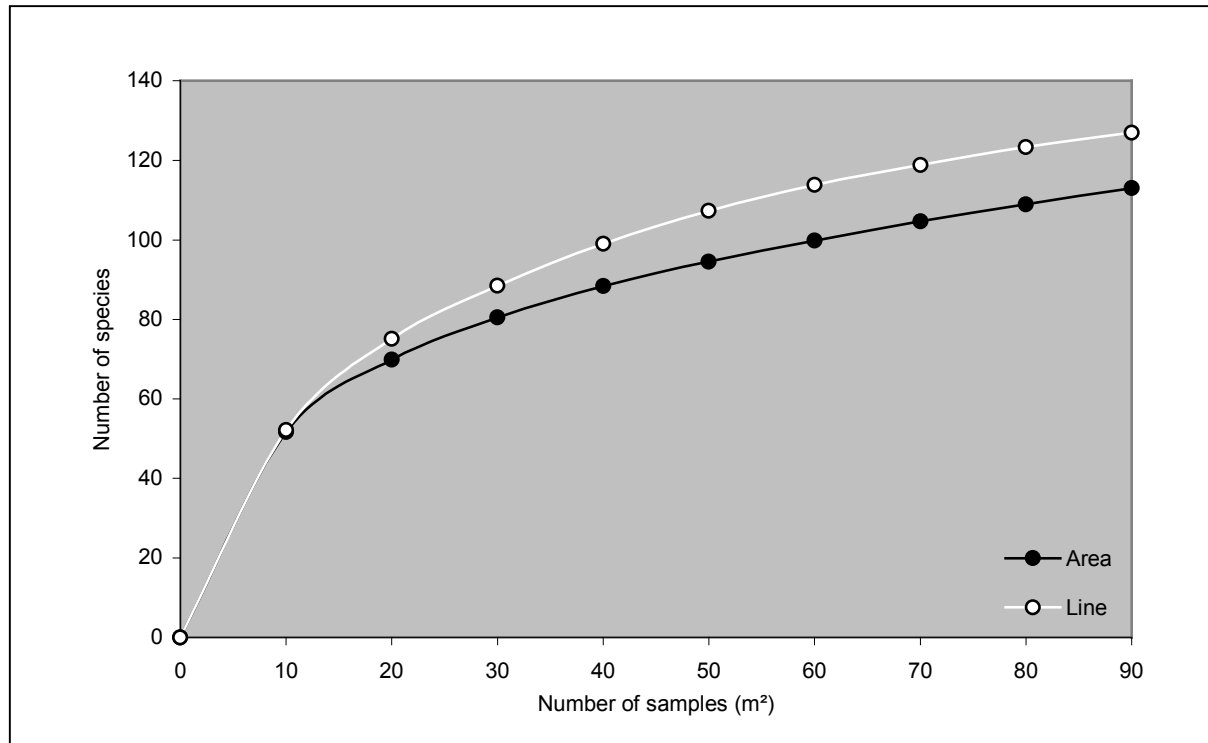
Fig. 23   Species accumulation curves of the Line and Area designs.

For a comparison of sampling efficiency of the two designs, the species richness estimator of the community of the total 150 m² samples collected at that time was calculated. Sampling efficiency (observed species divided by estimated species) was generally higher in the Line transect and reached at 60 m² a higher value than in 90 m² in the Area design. The same was true for the number of observed species: in the Line transect 114 species were collected at 60 m², while the Area sites yielded 113 species after sampling 90 m². In the Line transect the increase of species per ten square meters is less than five species after 60 m² which translates to less than 3% of the estimated species pool.

Tab. 11 Observed species and efficiency of estimators and means of estimators in relation to sample size. Efficiency is calculated as observed species divided by estimated species (%).

Estimator			ICE = Jack1		Chao2		Jack2		Bootstrap		MMMmeans		Mean of estimators	
Estimated species			172		179		190		153		150		169	
Sample size (m²)	Observed species		Efficiency (%)		Efficiency (%)		Efficiency (%)		Efficiency (%)		Efficiency (%)		Efficiency (%)	
	Area	**Line**	**Area**	**Line**	**Area**	**Line**	**Area**	**Line**	**Area**	**Line**	**Area**	**Line**	**Area**	**Line**
0	0	0	0.0	0.0	0.0	0.0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
10	52	52	30.0	30.3	28.8	29.1	27.2	27.4	33.7	34.1	34.4	34.8	30.6	30.8
20	70	75	40.6	43.7	39.0	42.0	36.8	39.5	45.6	49.1	46.6	50.1	41.3	44.5
30	80	88	46.8	51.4	44.9	49.4	42.3	46.5	52.6	57.8	53.6	58.9	47.6	52.3
40	88	99	51.4	57.5	49.4	55.3	46.5	52.1	57.8	64.7	58.9	66.0	52.3	58.6
50	95	107	55.0	62.4	52.8	60.0	49.8	56.5	61.8	70.2	63.0	71.6	55.9	63.5
60	**100**	**114**	**58.0**	**66.2**	**55.8**	**63.6**	**52.5**	**59.9**	**65.3**	**74.4**	**66.6**	**75.9**	**59.1**	**67.3**
70	105	119	60.8	69.1	58.5	66.4	55.1	62.5	68.4	77.7	69.8	79.2	61.9	70.3
80	109	123	63.3	71.7	60.8	68.9	57.3	64.9	71.2	80.6	72.6	82.2	64.4	73.0
90	113	127	65.7	73.8	63.1	70.9	59.5	66.8	73.9	83.0	75.3	84.7	66.9	75.1

The Shannon-Wiener index H', Simpson index D and Eveness J were calculated for the different designs (Tab. 12). The randomisation tests showed that diversities of the Line design were significantly higher in all indices.

Tab. 12 Measures of species diversity (Species number, Simpson index D, Shannon-Wiener index H', Eveness J) for the ant communities of the two sampling designs with p values of comparisons (randomisation tests, 10 000 runs, one-sided).

Design	Species number	D	H'	J
Area	113	88.66	4.45	0.90
Line	127	101.35	4.58	0.93
p		0.01	0.05	0.05

6.3.2 Short - Long comparison

One hundred and twenty-three species were collected in the 100 m² samples for this comparison (each line consisted of 60 m², but two sites with 10 m² were identical in the comparison). The 200 m transect with neighbouring sites (Short) yielded 107 species and the 500 m transect with sites 100 m apart from each other (Long) 105 species (Fig. 24). The species accumulation curves of the two different designs were very similar, almost overlapping over the range of the sample size.
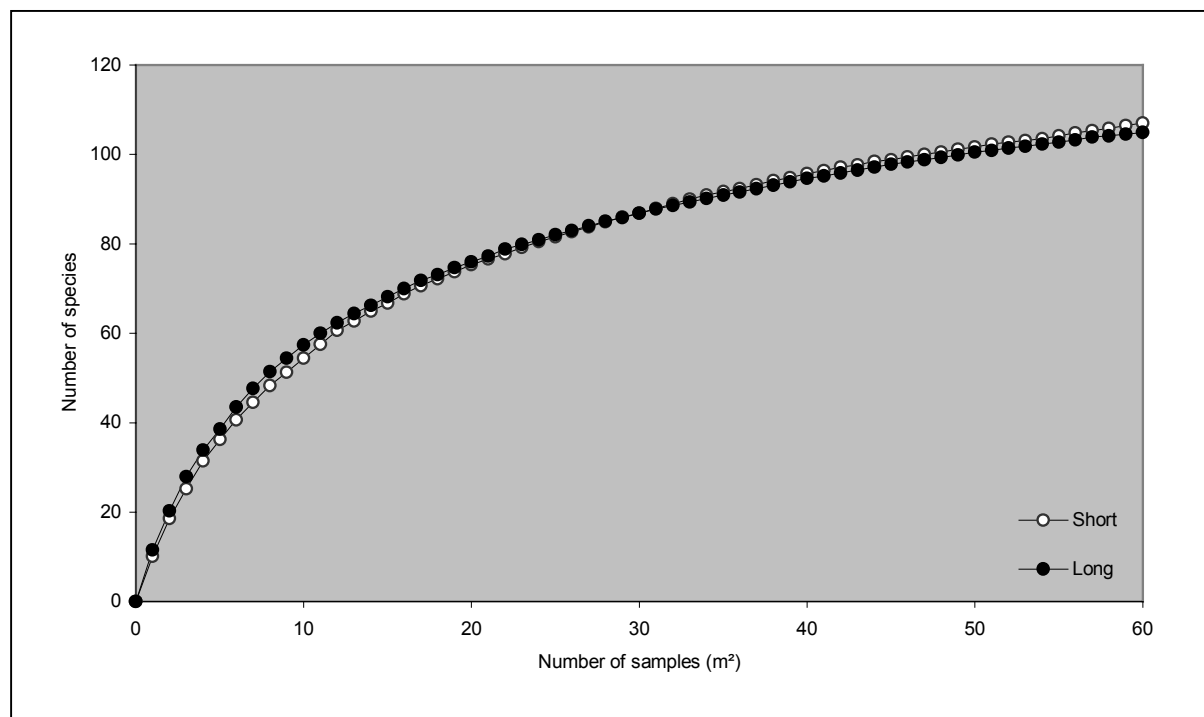
Fig. 24   Species accumulation curves of the Short (neighbouring plots) and Long (plots at 100 m distance) design along a line.

The sampling efficiency of the two designs was calculated by comparing the estimated species of the total leaf litter ant community in the set-up (of 120 m²) with the observed species in each design (Tab. 13).

Tab. 13   Sampling efficiency (in %) of the Short (neighbouring plots) and Long (plots at 100 m distance) design along a line.

Design	Species number	ICE (151)	Chao2 (160)	Jack1 (157)	Jack2 (172)	Bootstrap (141)	MMMean (135)	Mean (153)
Short	107	70.9	66.8	68.1	62.2	75.9	79.3	69.9
Long	105	69.6	65.6	66.9	61.0	74.4	77.8	68.6

The α-diversities for the two sampling designs were very similar (Tab. 14, randomisation test: in all cases n.s.)

Tab. 14   Measures of species diversity (Species number, Fisher's α, Simpson index D, Shannon-Wiener index H', Eveness J) for the ant communities of the two sampling designs.

Design	Species number	α	D	H'	J
Short	107	37.01	57.66	4.21	0.88
Long	105	34.92	57.43	4.28	0.87

6.4   Discussion

Area - Line comparison:
When comparing the Area with the Line design, it was obvious from the steeper slope at the starting point of the accumulation curves that species accumulated in a faster way along the Line transect. Additionally more species were recorded in the Line design with 127 species compared to 113 species in the Area design. The higher sampling efficiency of the Line design was indicated by higher values for all six estimators compared to the Area design. All α−diversity measures showed significantly higher values for the Line design. Therefore the Line design recorded a more diverse leaf litter ant community sampled at a higher level of completeness.

Number of samples:
After 60 m², 67.3% (mean of six estimators) of the species of the estimated community were sampled in the Line design (Tab. 11). Additional sampling only yielded less than 3% of the estimated species - or five species - every 10 m². To compromise between sampling effort and completeness of the survey the preferred design was to sample 60 m² along a line. The 60 m² sampled in the Short and Long designs the following year produced a similar mean sampling efficiency close to 70% (Tab. 13).

Short - Long comparison:
The difference between distance and neighbouring plots in the second comparison is not prominent regarding the number of collected species, performance of the species accumulation curves, sampling efficiency or α−diversity values. Therefore it did not make much of a difference to sample along a transect which covered 200 m or 500 m in a primary rain forest. Rates of species accumulation were also not improved by taking samples 10 or 15 m apart, compared with samples taken 5 m apart in a study in a primary forest in Madagascar (Fisher, 1999). Nevertheless, I decided to use the 500 m transect approach with 100 m distance between sampling sites as for my questions on changes of the ant communities along a disturbance gradient sampling was also necessary in logged over forests.
Due to the selective logging system, where clumps of valuable timber trees are targeted, the heterogeneity of the forest structure is more variable than within a primary forest, with large sized gaps or areas where the canopy is at least damaged and thinned and patches of near primary forest structure that escaped logging interspersed within highly disturbed habitat (Cannon, Peart & Leighton, 1998; Cannon *et al*., 1994; MacKinnon *et al*., 1996; Pinard, Barker & Tay, 2000). Therefore in logged over forests only a greater distance covered by a transect is likely to reveal the habitat heterogeneity for leaf litter ants and was therefore chosen.

The Line design was preferred over the Area design, a sample size of 60 m² (six times 10 m²) was estimated as sufficient sampling effort for community comparisons with a distance of 100 m between sampling sites. I want to emphasise that less heterogeneous habitats with a lower species pool than tropical rain forests probably require less samples over a smaller scale to reach a similar completeness of the sampled community. Fisher found in Madagascar that

relative ranking of between-site patterns of species richness and complementarity stabilised before 25 samples (1 m²) and was not predicted to change with the addition of 50 more stations to each transect (Fisher, 1999). Transects were running at higher altitudes and the respective fauna is less species rich than the one found in lowland rain forests. The lowlands of Madagascar are then dominated by tropical dry forests inhabited by a litter ant species pool that also has lower species number than found within the lowland rain forest in Sabah. A smaller local species pool together with a highly homogenous habitat do not need sample sizes of 60 m² to collect the present ant community at a high level of completeness. A sample size of 20 m² was recommended for Winkler sampling for areas comparable to a 1 ha 20 year old cocoa plantation where this sample size proved to be ideal (Delabie *et al*., 2000). Again this habitat is relatively homogenous compared to a tropical rain forest and sampling for a comparison of litter ants of different types of large forests need surely a higher sample size. The sample size of 60 m² is very similar to the 50 m² suggested by Agosti and Alonso (2000) for a first determination of the actual sample size needed to collect a desired percentage of the ant species of a habitat.

A trained person is able to sample and process 30 m² of leaf litter in the 100 m distance design in one day (three sites a 10 m², distance covered 300 m). Adding extraction time, it takes at least five days to finish the sampling of 60 m². But as sampling should only be carried out in drier conditions, one week is a more reasonable time and this does not include the establishment of the transect. The majority of total working time however is spent on sorting the ants of the samples gathered, mounting and identifying them. One has to compromise between sampling effort and completeness of the inventory, as it is also valuable and necessary to sample replicates in space and time of the same forest community to assess its variability. This accumulates very quickly in hundreds of square meters sampled.

Compared with other collection methods as hand collecting, fogging, Berlese funnels or light traps used for other insect taxa in community comparisons in tropical rain forests (e.g. Beck, 1998; Floren & Linsenmair, 1997; Hammond, 1990; Schulze, 2000; Wolda, 1983) the Winkler method and the proposed sampling design for leaf litter ants yields a very high proportion of the locally expected species which allows the comparison of communities of different habitats.

7   Leaf Litter Ant Communities along a Gradient of Forest Disturbance

7.1   Introduction

The world is clearly heading towards an extreme reduction of tropical forests which will be accompanied by a massive extinction of species (Wilson, 1992) and there is widespread concern about the effects of tropical forest disturbance on biodiversity (Linsenmair, 1997; Myers, 1988; Rice, Gullison & Reid, 1997; Whitmore & Sayer, 1992). Despite all considerations the rate of deforestation in the tropics continues to increase (Bawa & Seidler, 1998).

At least 70% of the resident vertebrate species are commonly reported to be dependent upon closed tropical forest (Johns, 1992a). Unfortunately relatively little information on the effect of logging practices on rain forest organisms exist (Eggleton *et al.*, 1996; Holloway, Kirk-Springs & Chey, 1992; Johns, 1992a; Jullien & Thiollay, 1996; Laidlaw, 1996; Olson & Andriamiadana, 1996). Most present studies have been concentrating on large, conspicuous taxa as birds or mammals and a majority follows a disturbance gradient from recovering clear cut forest to primary forest, and did not include logged over forests of different forest structure.

In Malaysia only trees of commercial value are harvested during logging operations therefore called selective (Awang, 1996), leaving a forest with a canopy disturbance of up to 75% behind (Cannon *et al.*, 1994). In the state of Sabah the first timber concession was issued in 1879 and since then annual log production has been constantly increasing reaching its peak in 1978 with a volume of timber exceeding 13 million m³. These heavy logging activities led to dwindling forest resources. It is estimated that under present management practices the timber supply level will drop seriously and make it difficult to meet even the domestic demand (Kleine & Heuveldop, 1993). 40% of the state area is designated commercial forest reserve, utilised primarily for timber production (Marsh *et al.*, 1996; Uebelhör & von der Heyde, 1993). 3.5% of the production forests are selectively logged annually.

Although the impact on the dipterocarp forests in Sabah and all over Southeast Asia is very high, only a few studies concentrated on the reaction of invertebrates to forest disturbance (Chung *et al.*, 2000; Beck & Schulze, 2000; Schulze, 2000; Willott *et al.*, 2000). As pointed out lately (Lawton *et al.*, 1998), attempts to assess the impact of tropical forest modification on a given taxa, based on the response of another or a limited number of so called indicator taxa, may be misleading.

Because ants are highly important in tropical ecosystems (Fittkau & Klinge, 1973) and successfully used in other habitats to evaluate biotic responses to ecosystem change (Alonso, 2000; Majer, 1996; Roth & Perfecto, 1994) I studied their community composition in different primary and logged over forests in Sabah. The impact of forest disturbance on leaf litter ants in Southeast Asia has so far not been studied along a natural disturbance gradient which is now present in a similar appearance all over the region.

7.2   Methods

Sampling was undertaken in the different forests in the established plots in Danum Valley and Deramakot Forest Reserve (see Study Sites) between 1998 and 2000 using the Winkler litter

sifting method. Detailed information on sampling design and processing, data entry and various statistical methods are given in the General Methods chapter.

7.3 Results

7.3.1 Taxonomic structure of the total community

186 leaf litter ant species in 48 genera and five subfamilies were recorded in the 900 m² of this analysis (Tab. 15). Most species and genera were found in the subfamily Myrmicinae, followed by Ponerinae and Formicinae. Cerapachyinae and Dolichoderinae included only one genus in the leaf litter ant communities under study.

Tab. 15 Genera and species number (and proportions in %) in the different subfamilies of the total leaf litter ant community.

Subfamily	Number of genera	Number of species
Myrmicinae	25 (52.1)	118 (63.4)
Ponerinae	14 (29.1)	38 (20.4)
Formicinae	7 (4.6)	17 (9.2)
Cerapachyinae	1 (2.1)	7 (3.8)
Dolichoderinae	1 (2.1)	6 (3.2)
Total	48	186

When the genera were ranked (Tab. 16) only four included more than 5% of the total species pool (*Pheidole:* 30 spec., *Strumigenys:* 20 spec., *Pyramica* and *Tetramorium:* 10 spec.). 23 of the 48 genera included only one species.

Tab. 16 Ant genera ranked after number of species. The proportion of the species number of the genus to the total species pool (186 spec.) is given in %.

Genus	Number of species	(%)	Genus	Number of species	(%)	Genus	Number of species	(%)
Pheidole	30	16.1	*Recurvidris*	4	2.2	*Cryptopone*	1	0.5
Strumigenys	20	10.8	*Anochetus*	3	1.6	*Dacetinops*	1	0.5
Pyramica	10	5.4	*Pheidologeton*	3	1.6	*Emeryopone*	1	0.5
Tetramorium	10	5.4	*Acanthomyrmex*	2	1.1	*Mayriella*	1	0.5
Paratrechina	9	4.8	*Discothyrea*	2	1.1	*Myrmicaria*	1	0.5
Pachycondyla	8	4.3	*Eurhopalotrix*	2	1.1	*Mystrium*	1	0.5
Cerapachys	7	3.8	*Myrmoteras*	2	1.1	*Myopias*	1	0.5
Hypoponera	7	3.8	*Pseudolasius*	2	1.1	*Prenolepis*	1	0.5
Gnamptogenys	6	3.2	*Lophomyrmex*	2	1.1	*Pristomyrmex*	1	0.5
Oligomyrmex	6	3.2	*Acropyga*	1	0.5	*Proatta*	1	0.5
Technomyrmex	6	3.2	*Amblypone*	1	0.5	*Probolomyrmex*	1	0.5
Crematogaster	5	2.7	*Brachymyrmex*	1	0.5	*Proceratium*	1	0.5
Vollenhovia	5	2.7	*Cardiocondyla*	1	0.5	*Prionopelta*	1	0.5
Monomorium	4	2.7	*Carebara*	1	0.5	*Rhoptromyrmex*	1	0.5
Myrmecina	4	2.2	*Calyptomyrmex*	1	0.5	*Solenopsis*	1	0.5
Ponera	4	2.2	*Cladomyrma*	1	0.5	*Lordomyrma*	1	0.5

7.3.2 Sampling efficiency

In the following comparisons I use the ant communities collected in the plots of the different forest types (see General Methods). Sampling was undertaken in Deramakot in three plots in

1998 and in one plot in 1999 in each forest type (3 x 60 m² + 60 m² = 240 m²). In Danum Valley the same sampling scheme was applied in two plots in 1998 and in one plot in 1999 (2 x 60 m² + 60 m² = 180 m²).

7.3.2.1 Species richness estimators

Highest species numbers per plot (60 m²) were reached in Danum Valley (97, 100 and 105 spec.) and the lowest was found in D98 (63 spec.), in the regenerated forest in Deramakot (Tab. 17). Plot species numbers were very similar in the different forests of Deramakot. Sampling efficiency calculated as a percentage of observed versus expected species, did not vary greatly between plots and estimators (six different estimators, see General Methods and Appendix for calculations); with the exception of the Chao2 estimator which yielded the most extreme values. Sampling efficiency was lowest for plot F98 in the regenerated forest of Deramakot in all estimators, varying from 33.8-81.9%.

Tab. 17 Species numbers (rounded) of the different species estimators for the litter ant communities in the plots. Percentages of estimated species to observed species are given in brackets *(italic)*. Lowest and highest estimates of sampling efficiency are given in bold.

Forests	Plots – year	Species number	ICE	Chao2	Jack1	Jack2	Bootstrap	MMMean
Danum Valley primary	L98	105	126 *(83.1)*	133 *(78.9)*	132 *(79.8)*	145 *(72.3)*	117 *(89.7)*	118 *(88.9)*
	L99	97	116 *(83.8)*	112 *(86.8)*	120 *(81.1)*	125 *(77.8)*	108 *(89.5)*	114 *(85.4)*
	M98	100	133 *(74.9)*	141 *(70.5)*	132 *(75.5)*	152 *(65.8)*	114 *(87.4)*	114 *(87.4)*
Deramakot good	A98	88	103 *(85.2)*	**97 *(90.6)***	108 *(81.7)*	106 *(82.9)*	99 *(89.2)*	104 *(84.9)*
	A99	69	84 *(82.0)*	83 *(83.3)*	88 *(78.7)*	94 *(73.6)*	78 *(88.3)*	83 *(82.7)*
	B98	70	88 *(79.3)*	90 *(77.5)*	93 *(75.6)*	103 *(68.3)*	81 *(86.9)*	91 *(76.7)*
	C98	74	90 *(82.1)*	96 *(77.0)*	95 *(78.2)*	105 *(70.2)*	84 *(88.5)*	90 *(82.2)*
Deramakot regenerated	D98	63	91 *(68.2)*	90 *(68.6)*	87 *(71.6)*	100 *(61.8)*	73 *(84.9)*	83 *(74.5)*
	E98	68	94 *(72.1)*	94 *(72.3)*	93 *(73.4)*	105 *(64.5)*	79 *(85.8)*	88 *(77.2)*
	E99	72	86 *(84.0)*	80 *(90.4)*	89 *(81.2)*	87 *(82.7)*	81 *(88.6)*	90 *(80.0)*
	F98	75	150 *(50.1)*	**222 *(33.8)***	116 *(64.5)*	151 *(49.6)*	92 *(81.9)*	101 *(73.9)*
Deramakot disturbed	G98	66	91 *(72.1)*	85 *(77.7)*	89 *(74.5)*	98 *(67.7)*	77 *(86.2)*	81 *(81.6)*
	H98	71	94 *(75.7)*	93 *(76.3)*	94 *(75.8)*	104 *(68.0)*	81 *(87.3)*	82 *(86.3)*
	H99	67	113 *(59.1)*	97 *(69.0)*	95 *(70.9)*	109 *(61.3)*	79 *(84.5)*	85 *(78.9)*
	I98	79	113 *(69.9)*	129 *(61.2)*	109 *(72.8)*	129 *(61.3)*	92 *(86.2)*	97 *(81.5)*

For an easier assessment of sampling efficiency, the mean of the six estimators was calculated and compared with the observed species (Fig. 25). The lowest value of mean sampling efficiency was found in Plot F98, effected by the high value in the Chao2 estimator. 70.9-85.6% of the estimated species were sampled in the other plots.
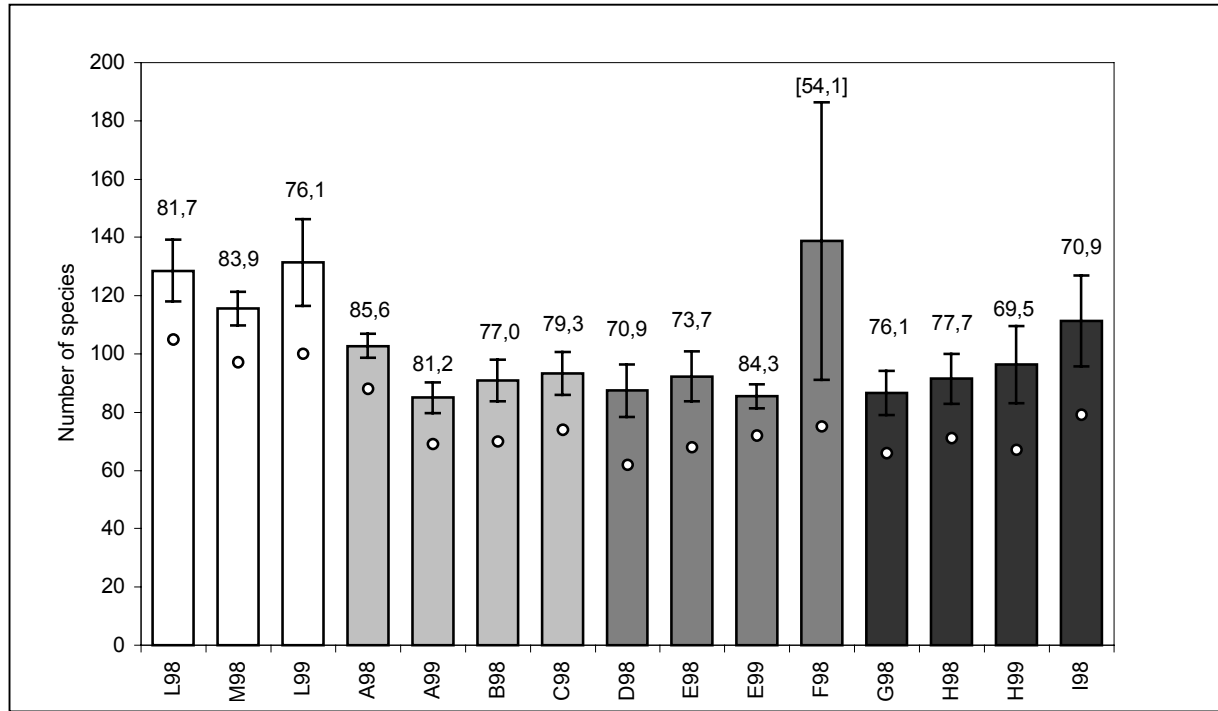
Fig. 25   Mean of all estimators (columns) and observed species (open circles) in the different plots. Sampling efficiency (observed/estimated species) given above the columns in %.

7.3.2.2 Species accumulation curves

The calculated species accumulation curves of the primary forest plots of Danum Valley lay above the curves of the logged over forest plots of Deramakot (Fig. 26).
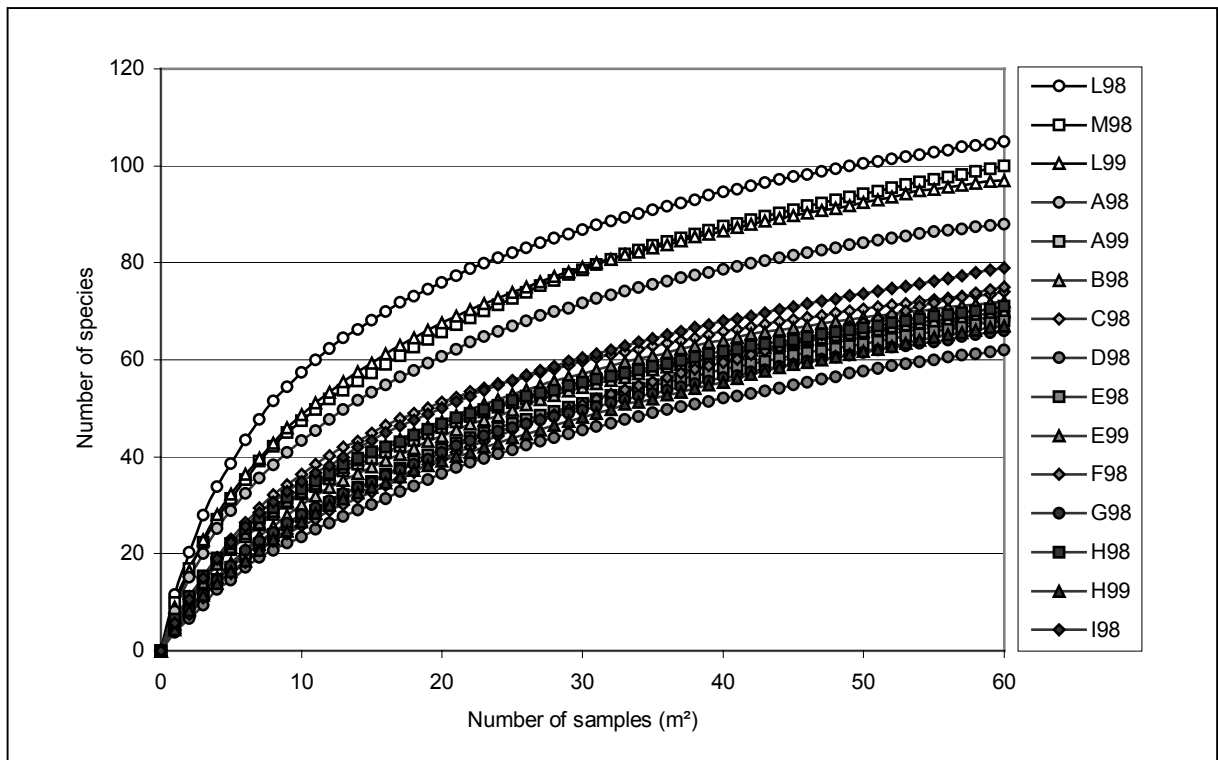
Fig. 26   Randomized species saturation curves (100 runs) of the different plots.

Most of the curves of the Deramakot plots formed a densely packed group, although the plots were situated in forests of different degrees of disturbance. An exception is A98: the community seemed to be sampled to a higher degree because the slope is comparably flatter and showed an intermediate species number between the Danum Valley and the rest of the Deramakot forest plots. Generally the slopes of the species accumulation curves of the different plots were very similar.

The species accumulation curves for the different forests types were also calculated. Only the independent spatial replicates of 1998 were used for this comparison including two plots in Danum Valley and three in each of the three forest types of Deramakot. The pattern I obtained for the plots (Fig. 26) became even clearer (Fig. 27):
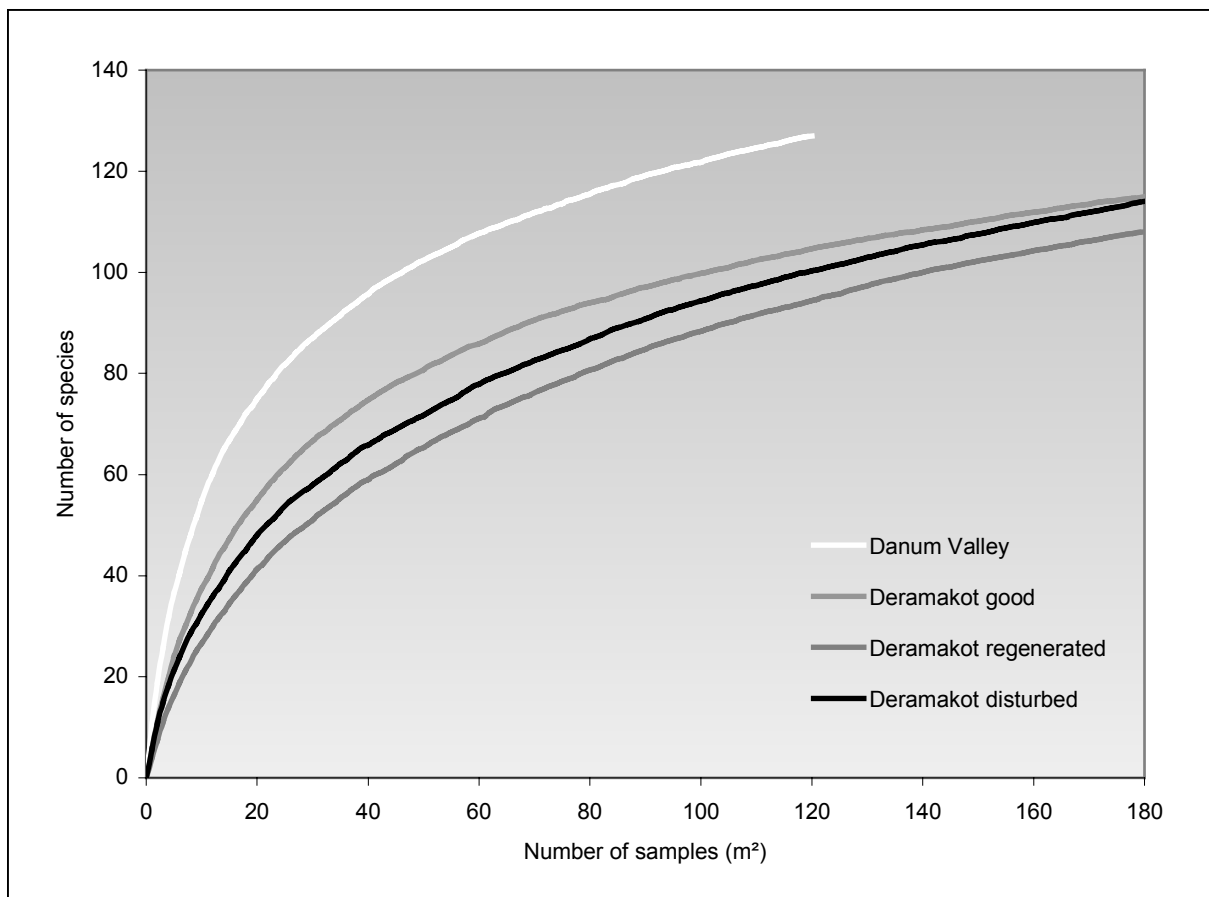
Fig. 27   Randomized species accumulation curves (100 runs) of the different forests; DVCA: two plots (120 m²), all DFR forests: three plots (180 m²).

The Danum Valley accumulation curve shows the steepest increase in species at the beginning of the curve. The Deramakot forests perform very similar in steepness, Deramakot good increasing most, followed by the regenerated forest nearly meeting the curve of the good forest with a similarly high number of species in the end of sampling. The last ten samples in all forests yielded one to two new species, which leads to a similar slope at the end of sampling. Although there is a difference of 60 samples between the Deramakot forests and Danum Valley, the primary forest yielded more species (Danum Valley: 127 spec., Deramakot good: 115 spec., regenerated: 108 spec., disturbed: 114 spec.).

7.3.3   Rare and common species – abundance distributions of the forest types

A common way to display abundance distribution is the rank order of species (Fig. 28). The species on first ranks have the highest abundances (common species) and the tail of the curve consists of species which were encountered only in a few samples (rare species, encountered in < 5 samples). In this study, abundance of a species means occurrence in a sample and not the number of workers (pseudo abundance, see General Methods): the maximum abundance per plot was 60 samples.
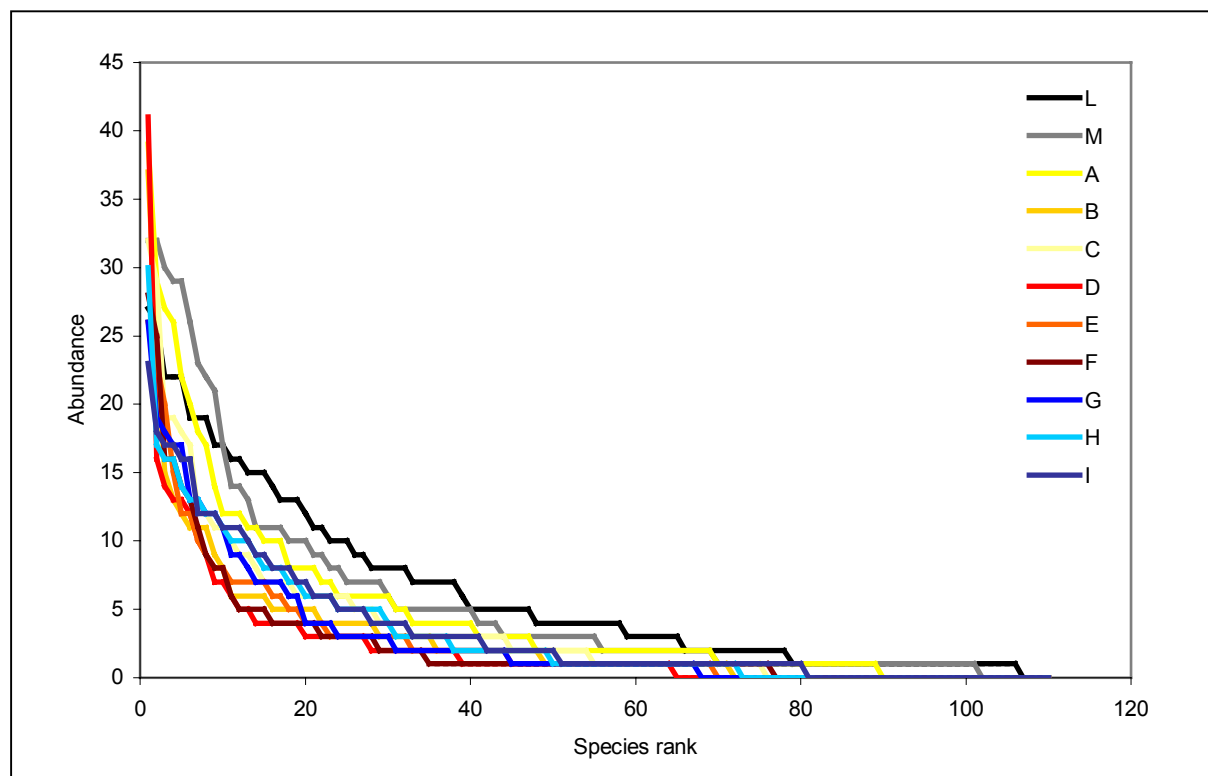
Fig. 28   Rank abundance distribution of the ant communities of the plots sampled in 1998; DVCA: L, M, DFR good: A, B, C, regenerated: D, E, F, disturbed: G, H, I. Species abundance is plotted against rank order for each sample (60 m² per plot).

The rank abundance curves for the Danum Valley plots lay above the others including most species and therefore displaying the longest tail. They are followed by plot A of the Deramakot good forest type. The other Deramakot plots show similar distribution patterns. The highest abundances are reached by the first ranked species, the most common, in plot D (regenerated) with 41, followed by the good forest plots A: 39, B: 37, C: 32 and plot M of Danum Valley with 32. All other first ranks reach abundances between 23 and 30. The number of species recorded in only one sample are between 20 and 32 species with an exceptional high number in plot F (regenerated) with 42 species.

The rank abundance pattern gets more transparent for the forest communities. The Danum Valley community, including two instead of three plots, was corrected for the lower sampling size by multiplying with 1.5 (Fig. 29). The species on first rank have highest abundances in Deramakot good, followed by Danum Valley and the disturbed forest sites. Abundances are generally lowest for the regenerated forest, although this might be effected largely by plot F. From rank 20 onwards Danum shows highest abundances, followed by the Deramakot good,

disturbed and regenerated forests. The number of uniques (species only collected in one sample) was 27 in Danum and increased with disturbance in Deramakot (good: 26, regenerated: 32, disturbed: 36). Species sampled below five times (rare) were encountered in Danum 59 times, and the Deramakot forests 59, 68 and 69 times along the disturbance gradient.
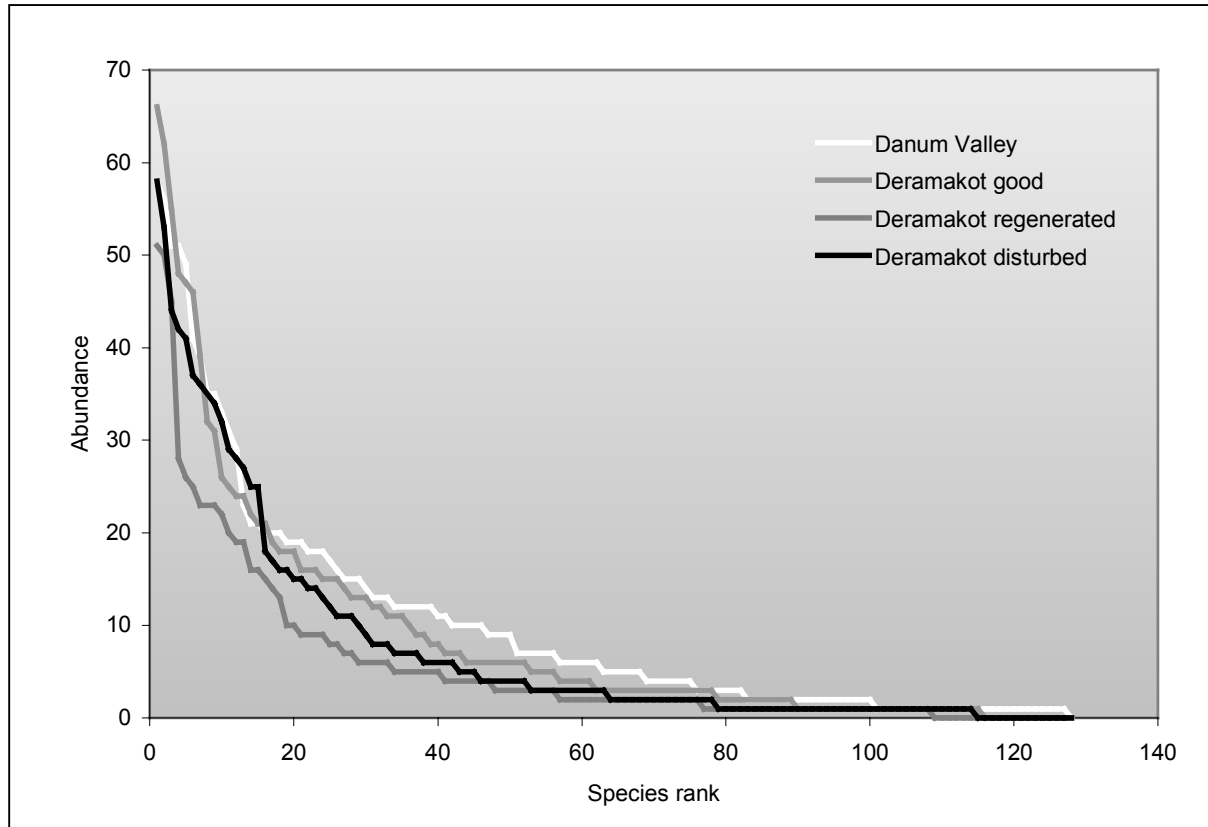
Fig. 29 Rank abundance distribution in the different forests. Species abundance is plotted against rank order for each sample (DVCA: N = 120 corrected by x 1.5, DFR: good, regenerated and disturbed forests N = 180).

7.3.4 Alpha-diversity indices

The abundance distributions of the plot communities were tested for their fit to the log series model. All distributions except for H99 fitted the model (Tab. 18) which is a prerequisite for the calculation of Fisher's α–diversity index (see below and General Methods).

Tab. 18   Alpha-diversity values (Fisher's α) and significance values (p) for the species abundance distribution fitted to the log series model in the different plots.

Forests	Plots	α	Chi	dfr	p	fit
Danum Valley	L98	34.99	5.17	4	0.26	yes
	L99	33.17	2.21	4	0.69	yes
	M98	34.07	2.53	4	0.63	yes
Deramakot good	A98	31.30	0.56	5	0.98	yes
	A99	26.35	1.14	4	0.88	yes
	B98	30.51	1.65	4	0.79	yes
	C98	28.15	4.28	4	0.36	yes
Deramakot regenerated	D98	30.21	3.92	3	0.26	yes
	E98	29.34	0.40	4	0.98	yes
	E99	36.53	2.69	4	0.61	yes
	F98	26.98	1.25	4	0.86	yes
Deramakot disturbed	G98	26.89	2.07	4	0.72	yes
	H98	27.92	8.32	4	0.08	yes
	H99	27.95	11.02	4	0.02	no
	I98	31.31	1.13	4	0.88	yes

Three standard indices were used to express the diversity of the forest types: Fisher's α, which is derived from the log normal distribution (see above), and two indices which are free from any abundance model assumption: the Shannon-Wiener index H' and the Simpson index D (see Appendix for details of the calculations). Tab. 19 summarises the diversity values obtained for the different forest plots.

Tab. 19   Measures of species diversity (Species number, Fisher's α, Shannon-Wiener index H', Simpson index D and Eveness J) for the ant communities of the plots of the four different forest types.

Forests	Plots	Number of species	α	H'	D	J
Danum Valley	L98	105	34.99	4.22	57.44	0,81
	L99	97	33.17	4.07	45.23	0,78
	M98	100	34.07	4.02	41.57	0,77
Deramakot good	A98	88	31.30	3.96	38.34	0,76
	A99	69	26.35	3.79	35.74	0,73
	B98	70	30.51	3.85	38.19	0,74
	C98	74	28.15	3.87	38.14	0,74
Deramakot regenerated	D98	63	30.21	3.72	34.11	0,71
	E98	68	29.34	3.76	33.89	0,72
	E99	72	36.53	3.85	37.37	0,74
	F98	75	26.98	3.74	29.11	0,72
Deramakot disturbed	G98	66	26.89	3.71	33.62	0,71
	H98	71	27.92	3.86	42.10	0,74
	H99	69	-	3.66	30.68	0,70
	I98	79	31.31	3.91	41.32	0,75

The highest diversity values were found in the primary forests of Danum Valley, the lowest in the disturbed forest of Deramakot, although there was some variation between indices and plots in the different forest groups: A99 had the lowest species number and diversity in the good forest type of Deramakot. E99 and F98 showed higher values than the other two plots in

the regenerated forest type and I98 of the disturbed forest type displayed similar values as found in the good forests of Deramakot. The eveness value J describes the heterogeneity of the species distribution (see General Methods). The highest eveness values were found in Danum Valley with M98 being only slightly higher than the values in the Deramakot plots. The eveness in Deramakot was very similar, independent of forest type and the underlying degree of disturbance.

I also calculated the α−diversity and eveness values for the forest types using the spatial replicates (plots sampled in 1998) (Tab. 20). All abundance distributions fitted the log series model and Fisher's α could be calculated.

Tab. 20 Measures of species diversity (Species number, Fisher's α, Shannon-Wiener index H', Simpson index D and Eveness J) for the ant communities of the four different forest types (DVCA two plots, DFR forests three plots).

Forests	Number of species	α	H'	D	J
Danum Valley primary	127	35.05	4.26	52.69	0.83
Deramakot good	115	32.07	4.10	42.78	0.80
Deramakot regenerated	108	35.09	4.01	37.09	0.78
Deramakot disturbed	114	33.49	4.01	39.28	0.78

Fisher's α was similar in all forests, whereas the Shannon-Wiener H' as well as Eveness J followed the disturbance gradient. The Simpson index D showed a reversal in the regenerated and disturbed forests. A randomisation test (10 000 runs) was calculated for the comparison of different diversity values (Tab. 21): the differences in Fisher's α were not significant in any comparison. The higher diversity of Danum Valley compared with the Deramakot good forest was highly significant in all other indices and the Simpson D index value was also significantly higher in the good Deramakot forest compared with the regenerated forest.

Tab. 21 P values of the randomisation tests (10 000 runs, one-sided) of the pair-wise comparisons of the different diversity indices.

1	2	α	H'	D	J
Danum Valley primary	Deramakot good	n.s.	0.001	0.001	0.001
Deramakot good	Deramakot regenerated	n.s.	n.s	0.05	n.s.
Deramakot regenerated	Deramakot disturbed	n.s.	n.s.	n.s.	n.s.

7.3.5   Diversity ordering: the Renyi family

To compare the community diversities, the Renyi index was used (see General Methods). Fig. 30 displays the diversity profile of the different plots of the four forests.
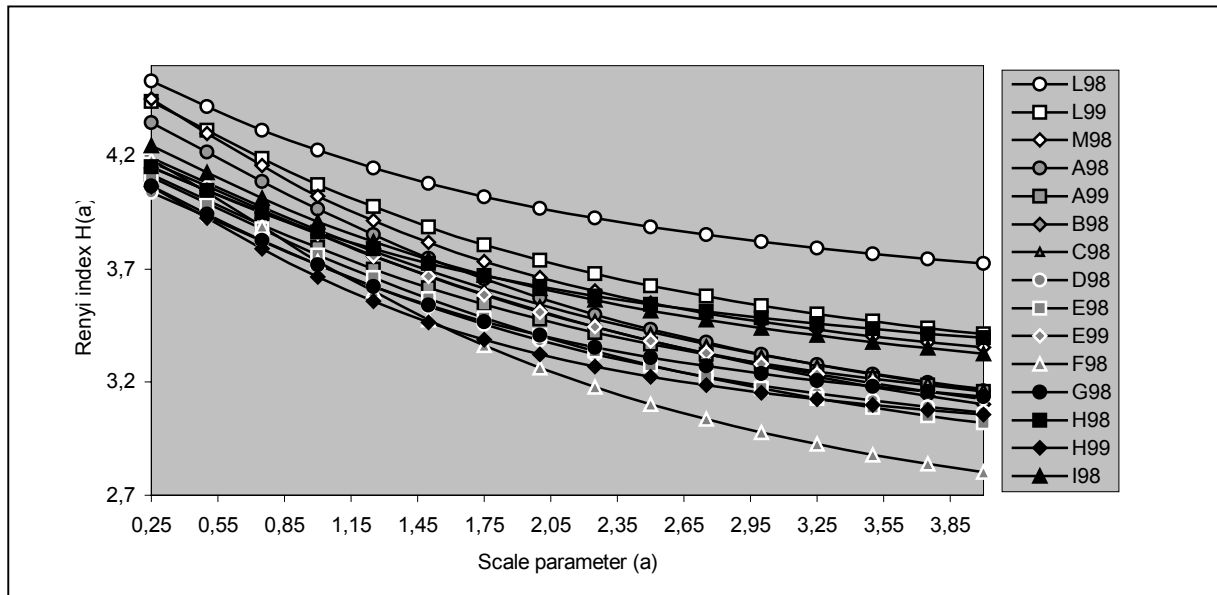
Fig. 30 The Renyi family: Renyi index H(a) of the leaf litter ant communities of the different plots with varying scale parameter (a).

The Renyi curves of the Danum Valley communities L98 and L99 lay above all other communities over the complete range of the scale parameter (a). M98 of Danum Valley is crossed by the H98 plot and therefore non comparable. Within the Deramakot forest types it is visible that a few curves intersect and are as well not comparable. Diversities are too similar to distinguish between the plots.

The Renyi distribution became clearer when the spatial replicates are added up in the four different forest types (Fig. 31).
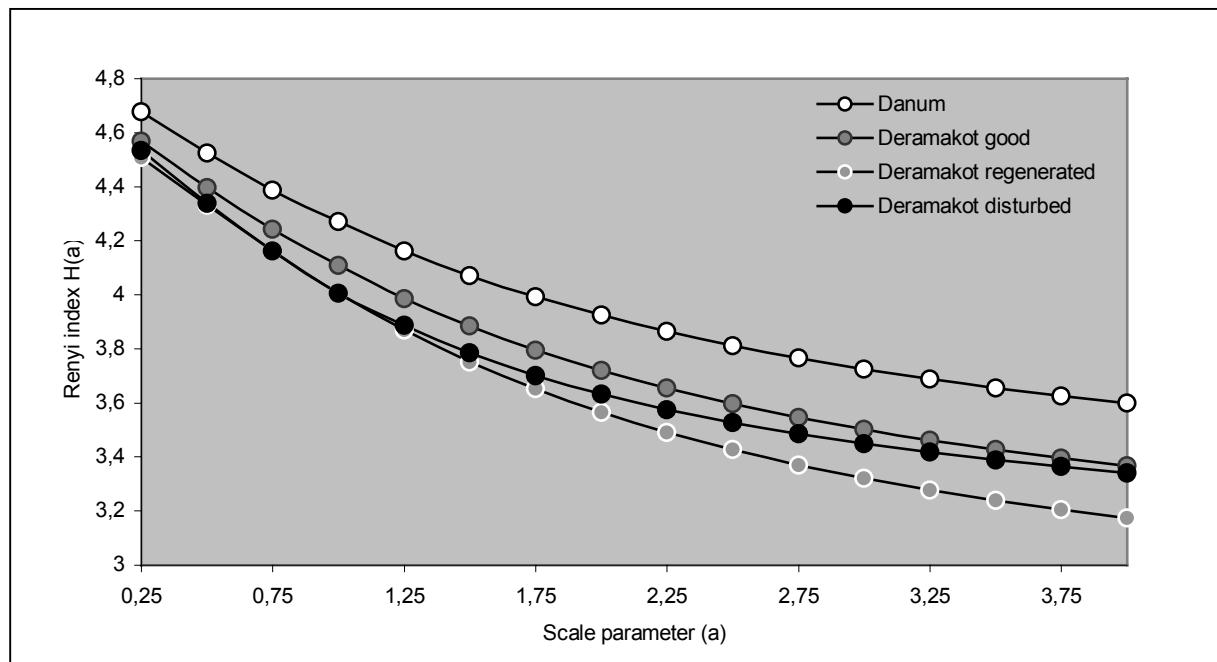
Fig. 31 The Renyi family: Renyi index H(a) of the ant communities of the different forests (DVCA two plots, DFR forests three plots each) with varying scale parameter (a).

The Danum Valley forest community curve runs above all other curves. In Deramakot there is a difference in diversity detectable between the good and the other two forest types. The Deramakot good forest displays over all scale parameters a higher diversity. The regenerated and disturbed forest curves cross and could therefore not be ordered according to their diversity.

7.3.6   Species number per sampling site

For a comparison of the different forests the number of species found at a sampling site was analysed (12 sampling sites for Danum Valley and 18 in every forest type of Deramakot). An ANOVA revealed a significant difference for species number per sampling site (df = 3, F = 12.35, p << 0.001). The means and standard deviations are displayed in Fig. 32. A Scheffe post-hoc test yielded significant differences between Danum Valley and Deramakot (Danum-Deramakot good: p < 0.01, Danum-Deramakot regenerated: p << 0.001, Danum-Deramakot disturbed: p < 0.001). Species numbers per site were not significantly different between the forests of Deramakot.
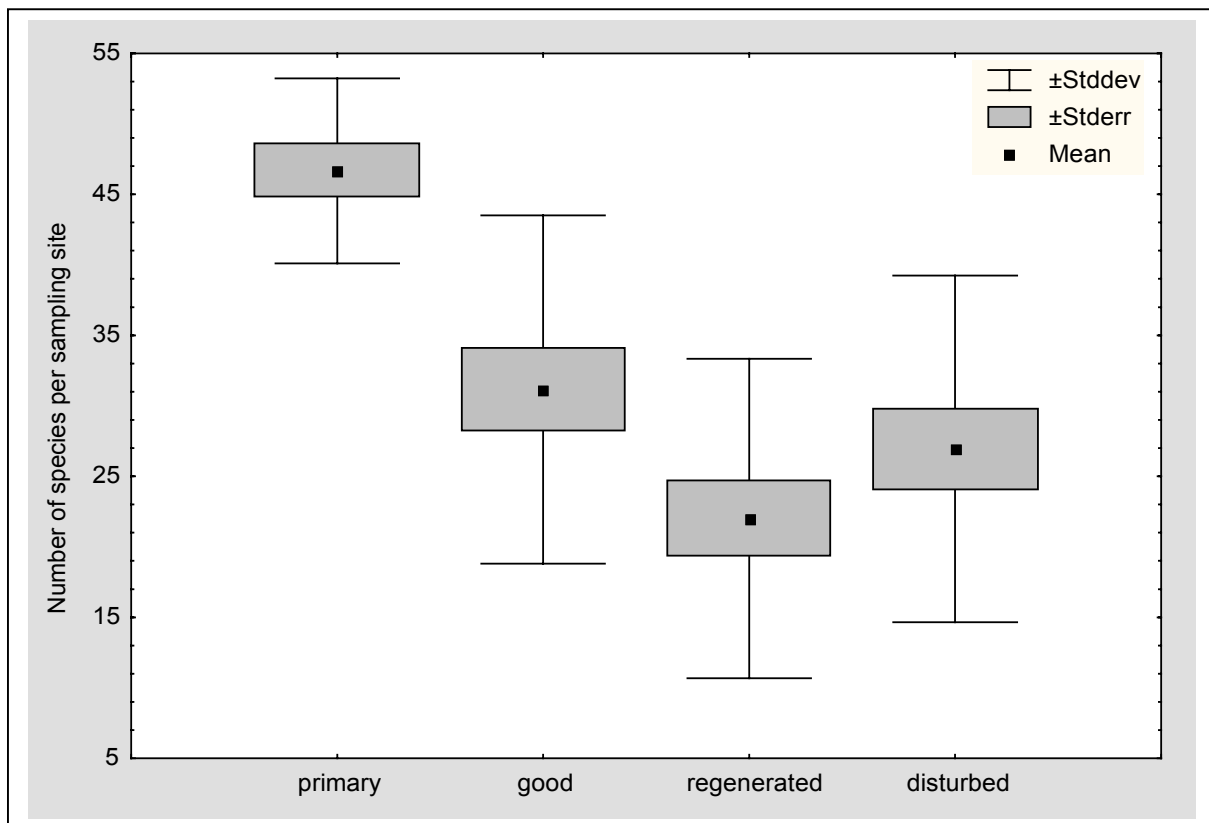
Fig. 32   Box-Whisker plot of the species number per site in the four different forest types (DVCA: primary, DFR: good, regenerated, disturbed).

7.3.7   Species density in the forest types

Another measure for the diversity of an ecosystem – although rarely analysed – is the species density distribution (Vasconcelos, 1999). As each of the Deramakot forests included three plots I corrected the Danum Valley density distribution (two plots) by multiplying the numbers with 1.5. All occurrences of the same number of species found in a sample (1 m²) are summed up from zero to a maximum of 29 leaf litter ant species (Fig. 33). The shape of the

distribution curves of the forest types is different: whereas the distribution of Danum Valley is bell-shaped, the curves of the Deramakot forests are skewed to the left. In Danum Valley around 10 species are present in an average square meter. This value decreases to 4-6 species in the Deramakot forests with lower values in the more disturbed sites. Another feature displaying the difference in the species density distribution is the starting point of the curve: in the primary forest of Danum Valley ants were present in every square meter of forest floor. This was not the case in the Deramakot good and disturbed forests (nine and eight samples without ants). Absence peaked in the regenerated forest with 25 m² out of 180 lacking ants.
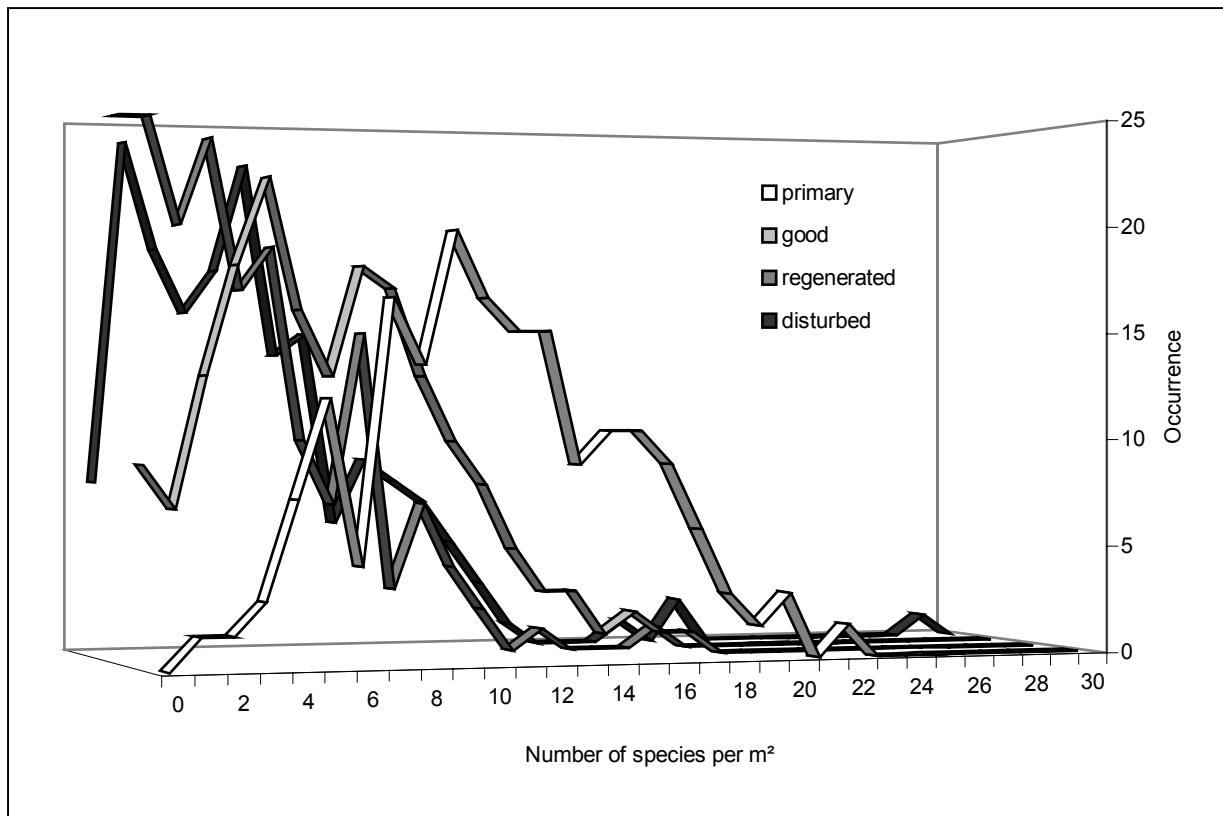
Fig. 33 Species density distribution per square meter. The number of ant species occurring in the 1-m²-unit samples in the different forests. DVCA: primary (corr. x 1.5), DFR: good, regenerated, disturbed).

7.3.8   MDS

For an analysis of the community structure in the different forests the plots sampled in 1998 were included. As a measure of similarity I used the standardised Steinhaus index (see General Methods and Appendix for calculations). The four different forest types form four distinct groups in the MDS plot based on the similarities of their communities (Fig. 34). The Danum Valley plots are positioned on the left, the Deramakot forests grouped on the right. The two-dimensional MDS explains 94.6% of the variation, dimension 1 accounts for 74.5% and dimension 2 for 19.1% of the entire raw stress. An ANOVA of the dimension 1 values shows significant differences between the forests (df = 7, F = 15.64 p < 0.01; dimension 2 n.s.). A Scheffe post-hoc test reveals significant differences between Danum Valley and the

forests of Deramakot (good and disturbed: $p < 0.05$, regenerated $p < 0.001$), but not between the different logged over forests.
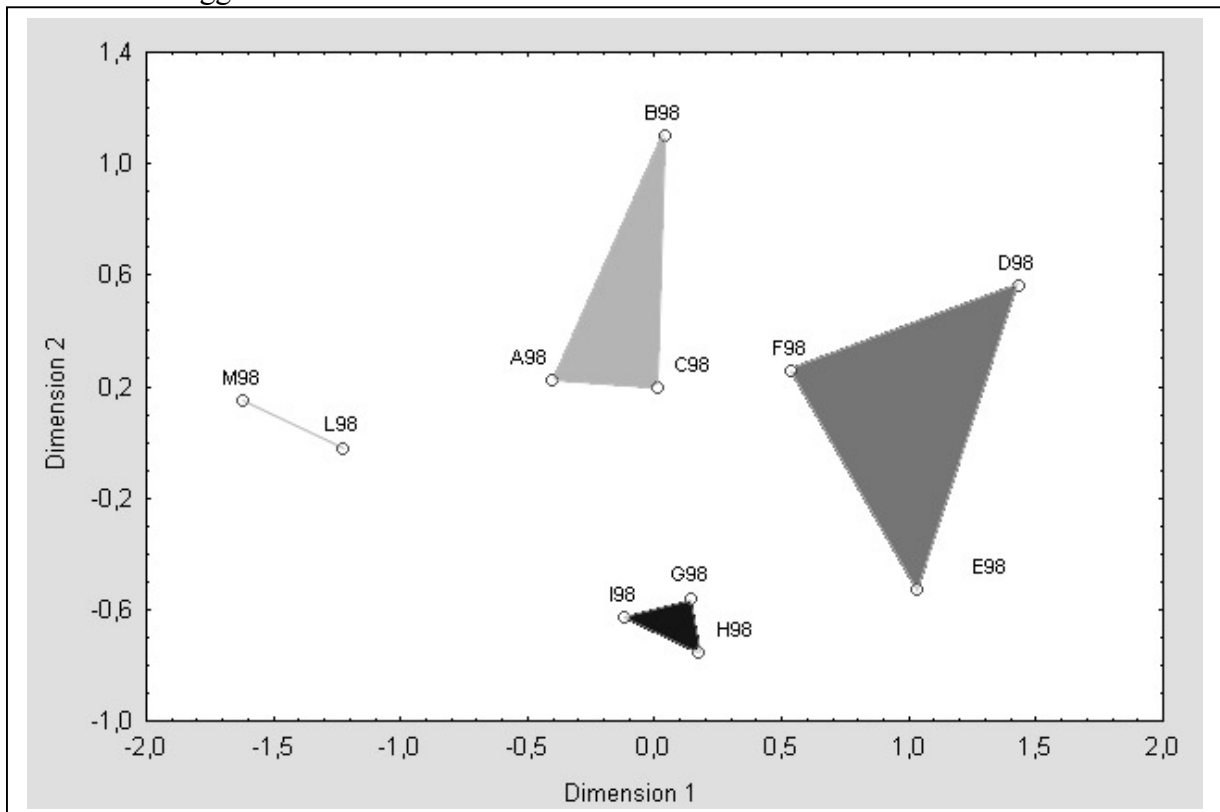
Fig. 34   MDS ordination (based on the Steinhaus index) of the ant communities of the different plots (two dimensions, stress: 0.064). The positions of plots of the same forest type are connected with a line. The primary forests are separated from the different Deramakot forests along dimension 1 (ANOVA, p << 0.001).

7.3.9   Cluster analysis

The dissimilarity values (1 - Steinhaus index) were calculated and a cluster analysis was performed.
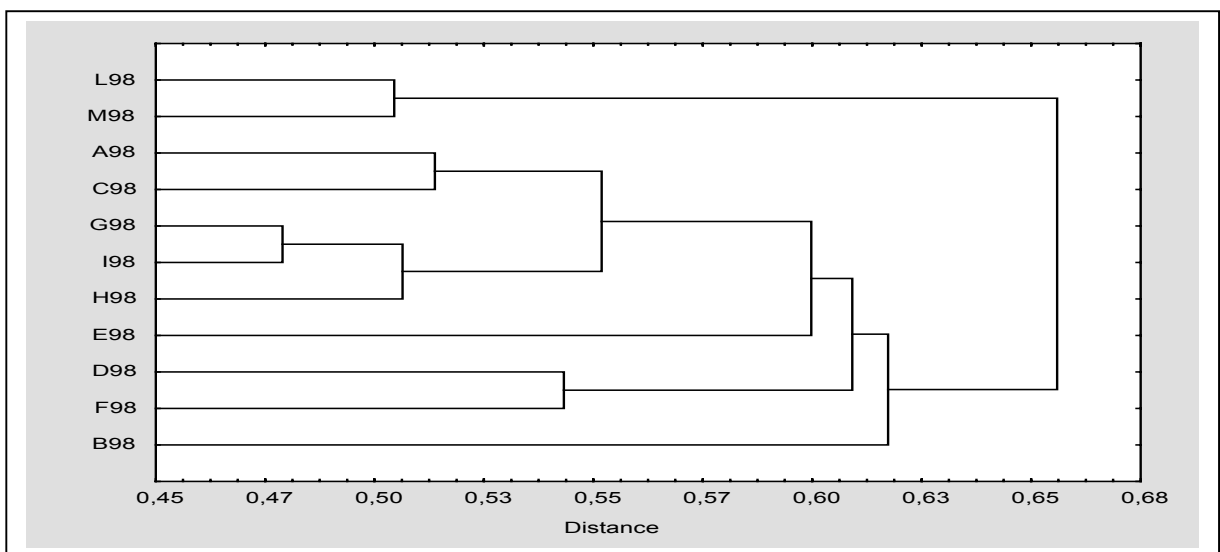
Fig. 35   UPGMA dendrogram using 1 - Steinhaus as distance measure.

UPGMA and Single Linkage were used as cluster algorithms (see General Methods).The basic clusters of the Danum Valley and the Deramakot good and disturbed forest plots are detectable in the UPGMA dendrogram (Fig. 35). L98 and M98 formed a distinct cluster at the first splitting point. G98, H98 and I98 are linked to the good forest plots A98 and C98 but grouped as in the MDS. The other forest plots in Deramakot showed no obvious pattern. In the Single Linkage dendrogram (Fig. 36) the Danum Valley forest plots still form a distinct cluster as well as the disturbed forest plots (G98, H98, I98) and the two plots of the good forest in Deramakot (A98 and C98). The pattern is very similar to the UPGMA dendrogram but distances are different as expected for this algorithm (Krebs, 1989).
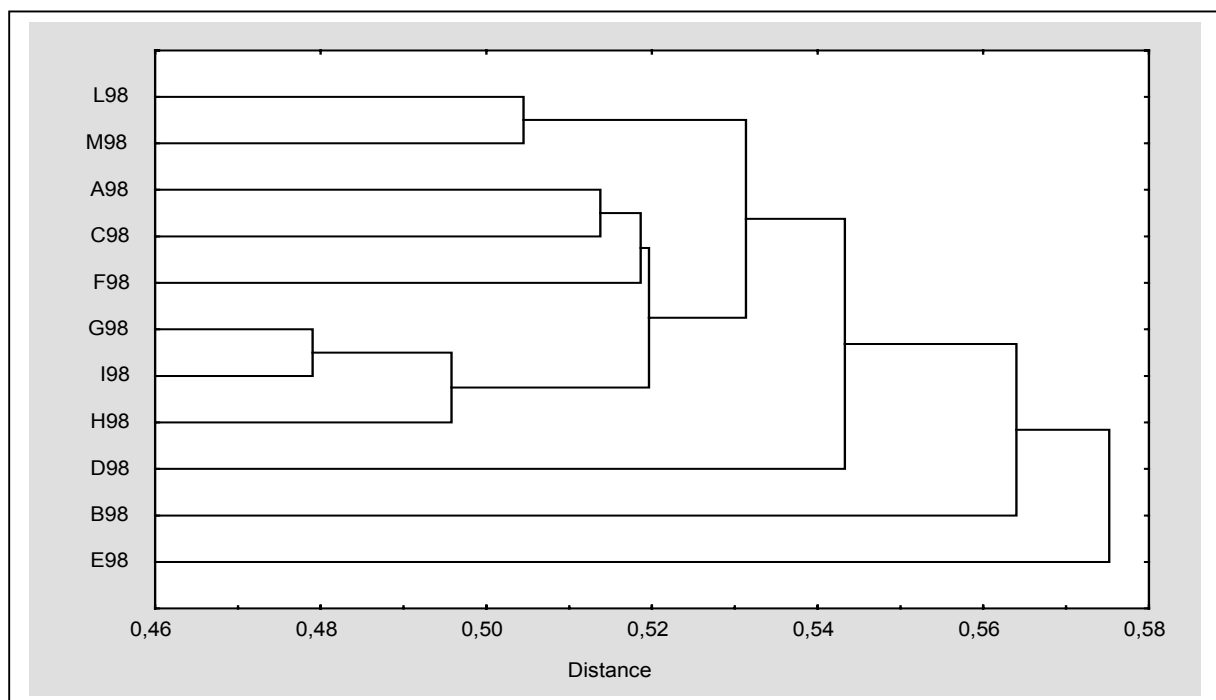
Fig. 36   Single Linkage dendrogram using 1 - Steinhaus as distance measure.

7.3.10 Widely distributed and restricted species

For an assessment of common and rare species of the different forest types I analysed the abundance distributions in all plots sampled in 1998. Typical common species had to occur in at least two plots per forest type among the ten most abundant species (rank 1-10 in the rank abundance distribution). Tab. 22 shows the presence and absence for each of these common species in the different forest types.

Five of the common species were present in the primary forest plots of Danum Valley and in various logged over forests of Deramakot. These species seem to be typical for the forest leaf litter ant community as they occurred in highest abundances. If we consider the species presented below the generalists we follow a gradient from primary to more disturbed forests: *Ponera e* was found among rank 1-10 only in the Danum Valley plots (L98: 27; M98: 29) but was still present in the logged over forests in lower abundances (A98: 13; B98: 5; C98: 9; D98: 4; E98: 5; F98: 10, G98: 11; H98: 10; I98: 11). The same is true for *Hypoponera f. Pheidole clypeocornis* occurred mainly in primary forests or the good forest type of Deramakot.

Tab. 22 Distribution of species found among the ten most abundant species in at least two plots in each forest type.

Species	Danum Valley primary	Deramakot good	Deramakot regenerated	Deramakot disturbed	Type
Paratrechina h	x	x	x	x	Generalists
Tetramorium a	x	x	x	x	
Hypoponera e	x	x	x		
Strumigenys juliae	x	x		x	
Pachycondyla b	x		x	x	
Ponera e	x				primary
Hypoponera f	x				
Pheidole clypeocornis	x	x			
Pseudolasius a		x	x		
Lophomyrmex bedoti		x	x	x	
Crematogaster a		x		x	
Pheidole annexus				x	
Oligomyrmex c				x	
Lophomyrmex longicornis				x	disturbed

Pseudolasius a and *Lophomyrmex bedoti* were common only in more disturbed forests. *Lophomyrmex bedoti* was among rank 1-10 of the most abundant species in the logged over forests and was only a medium abundant species in primary forest plots. It is recognised a common ground dweller and surface scavenger in logged over forests (Rigato, 1994). *Pheidole annexus, Oligomyrmex c* and *Lophomyrmex longicornis* were only in the most disturbed sites among the common species. Again, all species were present in each of the four forest types, only the difference in abundance lead to the classification above.

Another aspect of the community was species present in one forest type and completely absent in others. 22 species were restricted to Danum Valley, 11 to the Deramakot good forest, six to Deramakot regenerated and three to Deramakot disturbed. All these species occurred in low pseudo abundances (collected in 1-5 m²) and were clearly belonging to the rare species in the different forests. An exception was *Prionopelta a* which was collected only in Danum Valley in 12 out of 120 samples (10%). Six species were typical for the logged over forests of Deramakot in general. 68 of the 186 species (36.5%) were found in all forests, although in variable abundances. 24 of these were even collected in each of the eleven plots.

7.3.11 Seasonality

To account for seasonal changes in the leaf litter ant community, one plot in each forest type was sampled again in 1999. In 1998 sampling took place during the onset of an ENSO event in Sabah: due to the absence of significant rainfall, the leaf litter was very dry from March to May 1998 (see Study Sites). 1999 was a very wet year and it was interesting to see, if the leaf litter ant community would show any response to seasonality. The resampled plots did not change drastically in the estimator and species number values (Tab. 17) compared to the values of the same plots sampled the previous year or the other plots in the forest types, although there was some variation. The number of species collected in 1999 in L, A and H was lower than in the previous year. The opposite was the case for plot E. The resampling of A yielded an interesting result which becomes most obvious when comparing the species accumulation curves (Fig. 26): whereas the number of species collected in A98 were closer to

the Danum Valley community, A99 showed a behaviour typical of the other forest plots sampled in this type in 1998. In the other forest types no difference in the species accumulation curves of the different years was detectable. All resampled plots fitted the log series except for H99 (Tab. 18). The α-diversity values of the 1999 plots were also very similar to the 1998 plots (Tab. 19).

For a comparison of the communities of 1998 and 1999, I calculated the Steinhaus matrix for MDS (Fig. 37). The two dimensions explained 84.6% of the variation in the data matrix, dimension 1 accounted for 72.2%, dimension 2 for 12.4%. The forest types were still clearly distinct, although the Deramakot good and regenerated forests showed some overlap due to plot E99, including more shared species with the good forest type than in 1998. The Danum Valley plots still formed a significantly different group along dimension 1 in the MDS (ANOVA: df = 3, F = 19.2, p << 0.001; dimension 2 n.s.; Scheffe post-hoc test: differences between Danum and Deramakot forests in all cases p < 0.01).
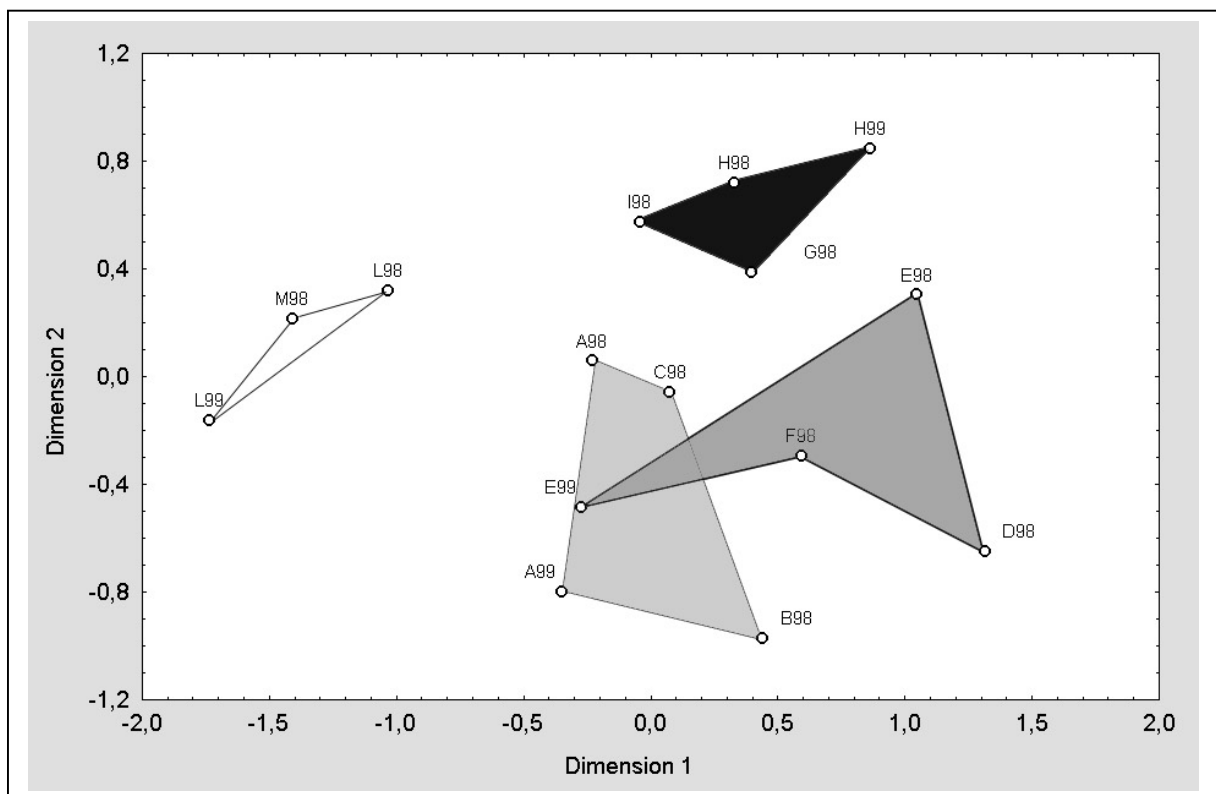
Fig. 37 MDS ordination (based on the Steinhaus index) of the ant communities including the plots resampled in 1999 (two dimensions, stress: 0.154). The positions of plots of the same forest type are connected with a line. The primary forests are separated from the different Deramakot forests along dimension 1 (ANOVA, p << 0.001).

For a confirmation of the results I performed a cluster analysis. Only the UPGMA dendrogram is displayed here as the Single Linkage did not provide any additional information (Fig. 38). The resampled communities were clustering together with the previous year communities in Danum Valley and the good and disturbed forests of Deramakot. Only the resampled plot E99 of the regenerated forest is not similar to the plot communities collected the previous year and was clustering closer to the disturbed forest plots.
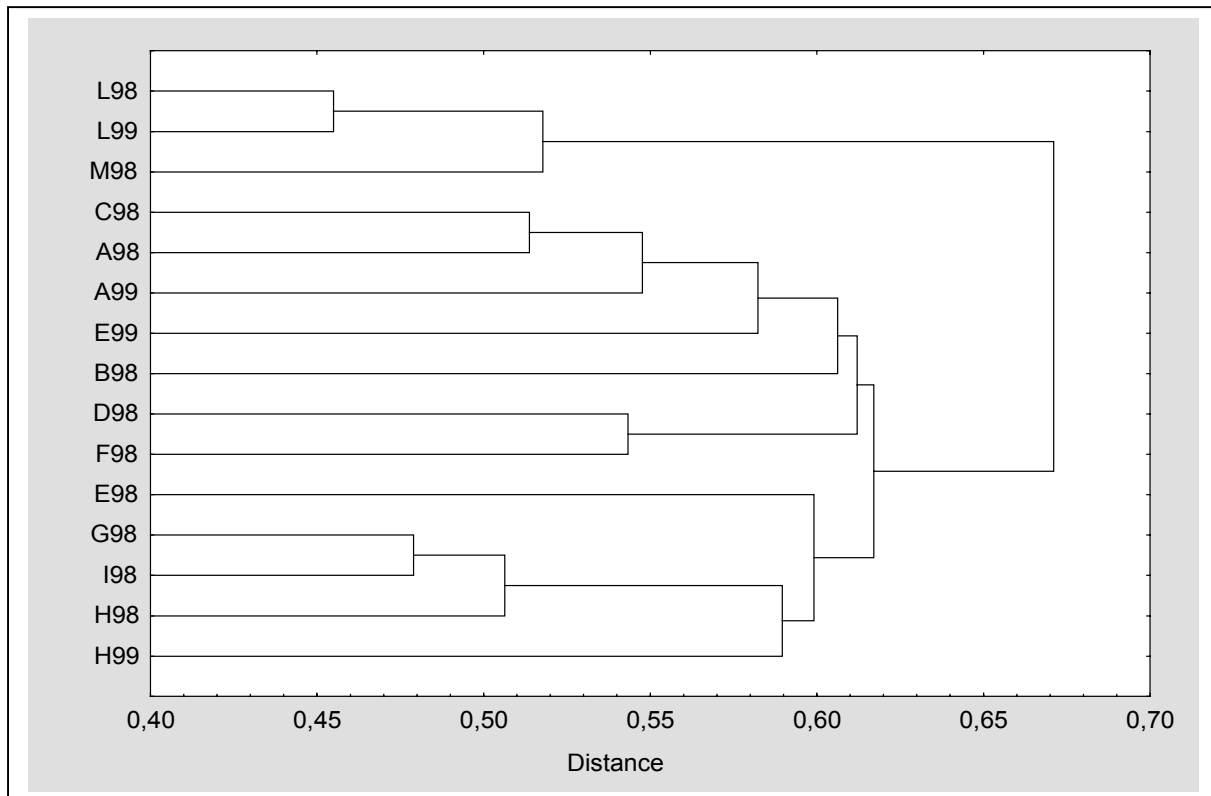
Fig. 38 **UPGMA dendrogram using 1 - Steinhaus as distance measure. The communities of the resampled plots of 1999 are clustering close to the 1998 communities, except for plot E.**

7.4 Discussion

7.4.1 Taxonomic structure of the total community

The taxonomic structure of the total ant community sampled in this study is comparable to others obtained in the leaf litter of Southeast Asia in respect to the subfamilies and the number of genera sampled (Brühl, 1996; Brühl, Gunsalam & Linsenmair, 1998; Brühl, Mohamed & Linsenmair, 1999; Rosciszewski, 1995; Ward, 2000). In a study in Poring Hot Springs, Sabah, 43 genera and 189 species were sampled in the leaf litter (Brühl, Gunsalam & Linsenmair 1998) compared to 48 and 186 in this study. The number of species was higher than described for Lambir Hills National Park (23 genera and 51 spec.) (Yamane, Itino & Nona, 1996; Yamane & Nona, 1994), Poring Hot Springs (51 genera and 125 spec.) (Maryati, Azizah & Arbain, 1996) and Pasoh Forest Reserve (51 genera and 148 spec.) (Bolton, 1996), due to larger sample size and the high efficiency of the Winkler litter extraction method compared to honey baiting or hand collecting. The number of genera is likely to be lower now as the revision of the Dacetine ants combined many genera in *Pyramica* (Bolton, 1999). Some genera were also excluded from the total community in this study as they were not quantitatively collected with the method chosen (e.g. *Diacamma*, *Odontomachus*, *Odontoponera*,...; see General Methods), but they are included in others. The proportion of number of species in the subfamilies was similar to world wide patterns especially in the proportion of Myrmicinae and Ponerinae of around 55% to 25% (Brühl, 1996; Ward, 2000).

Compared with an inventory in Pasoh Forest Reserve where the same collection method was used (Bolton, 1996), similar proportions of species per subfamilies were found with slightly higher values for Myrmicinae and lower for Ponerinae (Tab. 23). The differences were higher compared with the proportions found in a general Indo-Australian leaf litter sample (Ward, 2000), possibly due to a lower sample size over a larger geographical area.

Tab. 23   Number and proportions of species in the different subfamilies found in this study, in Pasoh Forest Reserve (Bolton, 1996) and general Indo-Australian leaf litter samples (Ward, 2000). Winkler litter extraction was used in all studies.

Subfamily	This study	Bolton, 1996	Ward, 2000
Myrmicinae	118 (63.4%)	87 (59.2%)	52.0%
Ponerinae	38 (20.4%)	35 (23.8%)	34.3%
Formicinae	17 (9.2%)	17 (12%)	11.2%
Dolichoderinae	6 (3.2%)	4 (2.5%)	1.8%
Cerapachinae	7 (3.8%)	4 (2.5%)	0.7%
Total number of species	186	147	-

Most of the genera included a similar number of species as described for the so far known fauna of Borneo in general (Yamane, 1997). Differences occurred in the number of *Hypoponera* and *Ponera* species which was lower than described for Borneo by Yamane (1997). This might be due to differences in the collection method, higher γ-diversity in these genera or differences in morphospecies designation. I did not split morphospecies in the two genera as there was no major taxonomic revision after Taylors work on *Ponera* (Taylor, 1967) and even the separation of the two genera remains questionable (B. Bolton, pers. comm.).

7.4.2   Sampling efficiency

To get an idea about the efficiency of sampling and an estimation of the total species richness, one has to obtain many samples to reach a high degree of species saturation, because the different estimators available are highly dependent on sample size and at least half of the total fauna should have been recorded (Colwell & Coddington, 1994; Longino, 1994; 2000). This was most certainly the case in this study since the total fauna collected was comparable to those observed in other investigations in Southeast Asia.

7.4.2.1   Species richness estimators

Sampling efficiency was highest for all estimators in the Danum Valley plots. The Bootstrap and MMMeans estimators showed very similar performances, yielding efficiency values of over 80% in most of the plots. Generally, the Chao2 index followed the pattern, but the range of difference in efficiency was highest in this index, with a lowest value of 33.8% and the highest being 90.6%. This is due to the characteristics of the estimator which rates uniques and duplicates, species occurring in only one or two samples, high. It is especially obvious in the case of plot F98 with the highest estimate of 222 species, translating in a sampling efficiency of only 33.8%. In this plot, the number of uniques was highest with 48 species (rank abundance distribution, Fig. 28) out of 75 species collected (64%), thus producing a high estimate of species richness in the Chao2 index. The ICE and Jack1 estimators showed a

similar range but lower values than Bootstrap or MMMeans, Jack2 values were even lower. The difference in performance is due to the calculations of the estimators (see Appedix I).

So far there is no agreement on preferences of estimators (Coddington, Young & Coyle, 1996): some authors favour or recommend Chao2 (Butler & Chazdon, 1998) others MMMeans (Beck & Schulze, 2000). Since there are good reasons for the different mathematics behind each of the estimators, I calculated several here. The similarity between the plots became obvious comparing the means of all estimators with the efficiency values located between 70.9% and 85.6% except for F98. Highest species richness values were reached in all estimators for plot F98, especially pronounced in the Chao2, leading to the lowest mean value of sampling efficiency (54.1%). In general, around 80% of the total estimated leaf litter ant fauna was sampled in each plot with the applied design and method.

7.4.2.2   Species accumulation curves

The species accumulation curves display a similar pattern as seen in the species richness estimators, with the plots of Danum Valley and A98 displaying the highest values and steepest increases in species at the start of the curve. All other plots in Deramakot are very similar in their behaviour, showing considerable overlap in many cases. The high sampling effort became especially obvious in the comparison of the accumulation curves of the forests, showing a low increase of species at the end (one to two species in the last ten m²). This high species saturation of the community is apparent in contrast to accumulation curves obtained in canopy fogging in other insect groups (Floren & Linsenmair, 1994) or light trapping of moths (Schulze, 2000), where the increase of species with additional samples is very high even after considerable sampling effort, leading to steeply increasing lines instead of accumulation curves reaching an asymptote.

From the analysis of species richness estimators and accumulation curves the conclusion can be drawn, that the applied sampling method and design yielded a similarly high number of the estimated species of plots and forest type. Therefore differences between communities are real and not due to differences in sample size. Consequently no rarefaction method to account for differences in species accumulation is necessary.

7.4.3   Rank abundance distribution

Generally the rank abundance distributions were very similar and followed the log series distribution except for H99. The number of species occurring in only one sample (uniques) was similar in most plots, except for F98 with the consequences for the species richness estimations mentioned above. All distributions show a long tail, indicating a high number of species with low occurrences typical for tropical communities (Connell, 1978; Fedorov, 1966; Gaston & Hudson, 1994; Magurran, 1988; May, 1995).

There is a discussion if the form of rank abundance distributions changes in logged over or secondary forests allowing the fit of different models to the data (Hill *et al*., 1995; Nummelin, 1998). In this study of forest leaf litter ant communities the behaviour of the rank abundance distributions was similar in all forests from primary to heavily disturbed logged over forests and no distinction could be made in their fit to the log series model (see below). This was also recognised in a study on fruit feeding nymphalid butterflies in the same research sites (Jalil, 2000). Nevertheless, the rank abundance curves of the primary forest of Danum Valley were

situated above the distributions of the logged over forests for most ranks. Only the first ranks, the common species, reached similar values in the logged over as in the primary forest. The number of uniques and rare species increased with disturbance on the forest level. Together with a reduction of species along the disturbance gradient this leads to the proportional increase of rare and unique species (rare species on forest level: Danum Valley 46.5%, Deramakot good 51.3%, regenerated 62.9%, disturbed: 60.5%). The curves of the logged over forests were characterised by a lower total number of species and similar abundances in the common species (rank 1-10) as found in the primary forest of Danum Valley, leading to a more compressed shape. The abundances of the common species increased in the logged over forests. The resulting rank abundance distributions are therefore descending steeper at the beginning and are in total shorter. These differences are directly affecting the eveness values.

7.4.4   Species number, density and α-diversity

One absolute measure of diversity is the number of species occurring in one place. In the primary forests of Danum I found 101 species in 60 m² on average in the different plots, in the Deramakot forest plots species number decreased to a total mean of around 72 species (means of forest types: good: 75, regenerated: 70, disturbed: 71). This pattern in species number persisted when plots were pooled and forests were compared. The similarity of species diversity was obvious in all forest types and the different plots of Deramakot, regardless of the index used. The values of Danum Valley forest and plots were higher in all indices than the Deramakot logged over forests. For the comparison of Danum Valley and Deramakot good this difference was highly significant for H', D and J, but not for Fisher's α.

Fisher's α is influenced by species number and does not take divergences of the log series due to common and rare species into account (Magurran, 1988). As there are changes in the abundances of the most common species in the logged over forests (see above) and the differences in species number is not too pronounced on the forest level, I do not expect the index to be very sensitive for this comparison.

The Eveness J followed the disturbance gradient and showed a significantly higher value in Danum Valley, indicating more balanced abundances there. As discussed in the section on rank abundance curves, there is an increase in the common species in the different logged over forests, producing lower eveness values. Combined, the diversity indices reveal the highest diversity in Danum Valley followed by Deramakot good and no significant differences could be found between the other logged over forests.

This pattern was again confirmed by the diversity ordering of the Renyi series, where the Danum Valley forests and plots were separated from the Deramakot sites, which overlapped or were very close to each other.

The number of species per sampling site (10 m²) also showed a significant decrease from an average of 46 species in Danum Valley to 22 to 31 in the different forests of Deramakot, where no significant difference was detectable.

The smallest scale of species richness analysis is reached in the number of species per square meter or species density, resulting in a distribution when all samples are taken in consideration. The density distribution showed a bell-shaped form for Danum Valley and skewed curves for the Deramakot forests, the latter with a substantial number of square meters without ants. This reduction in density was also obvious from the mean numbers of species

per square meter. The changes in the density distribution show a thinning of the ant community in the logged over forests: fewer ant colonies exist on a square meter and some samples are even lacking ants, which never occurred in the primary forest. This thinning translates at higher spatial scales in a reduction of species per forest. The most common species in the logged over forest showed similar abundances as found in the primary forest. In the primary forest common species were present in most samples with many other species (mean species number per m²: 10 spec.), in the logged over forests these are present with only a few other species (mean: 4-6 spec.).

7.4.5 Community composition

After species number and diversity were analysed, the dissimilarity of the plot communities was examined in MDS and cluster analysis. The plots of the four forest types formed distinct groups in MDS and showed significant differences in composition between primary and logged over forests. This difference was also pronounced in cluster analysis. The disturbed forest plots G, H and I formed a robust cluster as well as A and C of the good forest type. The other plots were not arranged in distinct clusters, confirming the picture of similarities between the logged over forest types which could not be separated in MDS based on significant differences along dimensions 1 or 2. The similarity of these communities can be explained by studying the distribution of common and rare species.

7.4.6 Widely distributed and restricted species

Common species, widely distributed and therefore shared between forests and plots, produce strong ties and result in clusters of more similar plots. In contrast, common species not shared between forests separate the communities. Among the first ten ranks in species abundance (common species) I found five generalistic species in high abundances in most of the plots. These species neither separate nor tie the forest communities, although there are some differences between the logged forest types. A strong tie results from *Lophomyrmex bedoti*, the most characteristic species of logged over forest, commonly present in all the Deramakot forest plots. This presence also separates all the Deramakot forests from the Danum Valley community. The common species found in only one forest such as *Ponera e* and *Hypoponera f* for Danum Valley and *Pheidole annexus, Oligomyrmex c* and *Lophomyrmex longicornis* for the disturbed forest in Deramakot are separating these communities from each other. It is quite obvious that among the ten most common species there were no species only confined to Deramakot good or regenerated. This lack leads to a high similarity between the Deramakot forest types which is especially influenced by species present in two forests as *Pseudolasius a* and *Crematogaster a*.

Species with lower abundance are also important for the similarity of communities and accounted for in the Steinhaus index (Legendre & Legendre, 1998). A high proportion of the recorded species was found in various abundances in all forests (39.5%) and even all plots (13.9%), six species producing a tie between the Deramakot forests. Nevertheless, the differences in abundance still lead to dissimilarities of the communities. A clear separation of forests is produced by usually rare species restricted to one type: 22 species were only collected in Danum Valley, clearly separating its community from the Deramakot forests. In Deramakot good this value decreased to 11 and further to six and three in the regenerated and disturbed forests. Although the number of unique species was similar between the forests, the

characteristics of these species are different: rare species in Danum Valley mostly occurred only there (22 of 59 spec.: 37.2%), but only a few of the rare species in the Deramakot forests were confined to one forest type (good: 11 of 59 spec.: 18.6%; regenerated: 6 of 68 spec.: 8.8%; disturbed: 3 of 69 spec.: 4.3%). Most of them were collected in other forests as well.

From this species level analysis it becomes quite obvious, that rare species are an important community aspect in Danum Valley as they are restricted to the primary forest. The impact of the high percentage of rare species might even surpass the importance of the few common species found in Danum Valley in separating the primary and logged over forest communities. In Deramakot the rare species are seldomly restricted to one forest type and therefore their low effect on community distinction is exceeded by the common species found in all or two forests. Consequently ties between the logged over forests prevail and the dissimilarity of communities is not significant.

I would therefore like to question the approach suggested for community analysis to exclude rare species from the analysis (Longino, 2000). Although this might produce excellent results in vegetation analysis in temperate regions it doesn't seem to work in tropical communities characterised by a unique set of rare species. One should, however, only include rare species in an analysis, if the local community was sampled to a fairly high degree and one can be confident that the resulting pattern is not only an outcome of undersampling.

The thinning of the logged over forest communities especially affected the rare species of the primary forest ant community, as most of them only occurred there. These rare species might be in first line microclimate or food specialists.

7.4.7   Seasonality

Species numbers and community compositions did not alter their general appearance when the resampled communities of 1999 were included in the various analyses: species numbers were slightly lower in L, A and H and higher in E. But diversity and species numbers of Danum were still higher than in Deramakot and generally fitted around the values collected in 1998 in the same plots, producing a similar pattern in the respective α−diversities and Renyi curves. The pattern of community composition in MDS or cluster analysis did not change when the plots sampled in 1999 were included. In MDS distances between temporal replicates were often higher than between spatial replicates indicating seasonal variability in the community, although the pattern of community similarity and significances did not change. This was also found in cluster analysis with stable clusters for Danum, with L98 and L99 clustering next to each other, a high similarity of A98 and A99, as well as H98 and H99. Only E99 differed more from the community sampled in 1998 and showed a high similarity to the good forest plots of Deramakot in both, MDS and cluster analysis.

These differences in community composition might be among the most pronounced as sampling took place in a very dry habitat due to the ENSO event in 1998, and in very wet circumstances in 1999. As these years were among the most extreme in respect of temperature and rain fall, the differences in community composition should reach their maximum here. Although I found variations, the general pattern between the communities of the different forest types did hold and the sampling design produced similar results over the years.

So far we found the primary forest of Danum Valley to be more species rich and diverse on all ranges of scale from forest types to square meter. Community composition differed between primary and logged over forests due to more restricted rare species and two common species only present in Danum Valley. The thinned leaf litter ant communities of DFR were characterised by a lower density and lower number of species and high abundance in a few common species. Among those common species are many that are shared between the different forests, leading to strong ties between the logged over forest communities.

On the plot level only 70% of the species of Danum Valley were found in Deramakot. One could argue that this is not a true species loss due to disturbance, but a result of a different local species pool. I cannot exclude an influence of a different, reduced, local species pool in Deramakot as the two forests are not situated next to each other. Nevertheless, a few points indicate the probability of an identical local species pool: (1) The distances between Danum Valley and Deramakot and between the different Deramakot plots are very similar: the distance between Danum and Deramakot regenerated is 70 km, between Deramakot disturbed and regenerated almost 30 km. If distance had an effect on the community, it should become apparent in the MDS plot, but the MDS distances between the Deramakot sites and Danum and Deramakot were very similar. (2) There is still a connection consisting of logged over forests between the two forests; soils and forest type are similar as well as altitude and terrain (see Study Sites), resulting in a link of similar habitat. (3) In an analysis of nymphalid butterfly communities in Sabah, the communities of Danum and Deramakot were closely related to each other (Jalil *et al*., in prep.), indicating a similar local species pool. The same was found for ants of the lower vegetation showing low β-diversity values between Danum and Deramakot, but large differences in comparison with the Kinabalu Park fauna (Gossner, 1999). (4) A similarity in the local species pool of the two forests might also be deduced from the fact that only 22 species or 11.8% of the total leaf litter ant fauna in this study were restricted to Danum Valley. (5) In moths it was found that the species pool of Danum is not especially species rich in comparison with other primary forests in Sabah (Chey, Holloway & Speight, 1997).

If these arguments for a similarity of the local species pools of Danum Valley and Deramakot are accepted, the reduction in species richness in the logged over forests would be due to disturbance. The logging activities in the area would then have effectively reduced species numbers to 70% of the primary forest status, changed the density of ants on the forest floor and affected community composition. This impact was not only present in the severely disturbed forests, but also in the regenerated forest, logged more than 25 years ago. Even this time span has not been long enough for a recovery of the community to primary forest status. This is in so far not inexplicable as the forest structure in the logged over forests is still different from primary forest and has influences on the microclimate (see chapters on Forest Structure and Microclimate).

Community changes to various degrees along disturbance gradients were also found in other studies on ants in tropical forests in species richness, diversity and composition. In Amazonia the ant community in experimental logging treatments in 4 ha plots showed similar species richness, mean abundances and eveness compared to a primary forest control, although these results might have been influenced by the small scale approach of the study (Vasconcelos, Vilhena & Caliri, 2000). Nevertheless the density of ants on the forest floor changed as a

result of logging and persisted for at least ten years after timber extraction. A clear separation of primary and logged over forest communities could be demonstrated in MDS ordination, possibly due to a few very abundant species restricted to logged forest, as found in this study. No evidence for significant differences in species composition or richness was found in Ghana, in a comparison between primary forests, logged over forests and old cacao plantations (Belshaw & Bolton, 1993; 1994), although cumulative species number was reduced in the logged over forest sites. A recent reanalysis of the data set could reveal significant differences in species diversity and community composition (P. Eggleton, pers. comm.) although this effect might be related to forest size and not disturbance (see Forest Size).

No effect of logging on the species richness and diversity of the ground ant community was detected in a study in a dry forest in Madagascar (Burkhardt *et al*., 1996; Olson & Andriamiadana, 1996), but effects of selective logging might have been overruled by site distances to the river. However the logged forest showed a pronounced edge effect with reduced numbers of individuals and lower biomass. In neotropical granivorous ants changes in community composition were detected in a comparison of open and closed forest, although species number was similar (Kaspari, 1993). Under greater levels of disturbance including clear cutting or use of fire and conversion of mature forest to plantations of various crops and pastures, ant species richness decreased between 50% to one third of is original level and eveness and abundance were also dramatically altered (Chung & Maryati, 1996; Greenslade & Greenslade, 1977; Roth & Perfecto, 1994; Vasconcelos, 1999; Verhaag, 1991). Interestingly, in one study ant abundances increased contrary to species numbers in these severely disturbed habitats (Vasconcelos, 1999).

All studies on ground living ants in tropical habitats demonstrated influences of disturbance on community composition and in severe cases always a reduction of species richness and diversity. The forest disturbance gradient in this study is not as extreme as in the other studies: selective logging has a much lower impact on the ecosystem as clear cutting or burning the rain forest. Nevertheless the influence of disturbance on the ant community could be clearly demonstrated in the comparison of logged over versus primary forest.

Lately, studies on the effects of disturbance on tropical forest animal communities have increased and also included different insect taxa. In termites, communities were reduced in species richness only in severely disturbed forests, but a shift in feeding guilds occurred even in the regenerating forests leading to differences in composition (Eggleton & Bignell, 1995; Eggleton *et al*., 1995; 1996; 1997). Dung beetles decreased from virgin forest to plantations in Uganda, but this effect was not significant (Nummelin & Hanski, 1989). Higher abundances due to a few abundant species were detected in arboreal beetle communities in logged over forests compared to a primary forest, but more species were found in the latter (Wagner, 2000). No influence of logging was found in the distribution of carabid beetles in a dry forest of Madagascar (Butterweck, 1992). A detailed study in Sabah, where beetles of the forest floor, lower vegetation and the lower canopy were studied, showed a decline in species richness, abundance and community composition changes along a gradient from primary forest to plantation, which was especially pronounced in the ground living beetles (Chung, 1997; Chung *et al*., 2000).

In moths a loss of diversity was observed in disturbed habitats (Holloway *et al*., 1992), and in an elaborate study in Sabah, different moth taxa followed a disturbance gradient with reduction in species richness and changes in community composition (Schulze, 2000). In geometrid moths logged over forest communities showed a different composition than primary forest communities with slightly higher species richness in one case (Chey *et al*., 1997; Chey, Speight & Holloway, 1992) and a reversal in others (Beck, 1998; Intachat & al., 1997). Butterflies generally revealed reduced species richness in logged over forests compared to primary forests (Beck & Schulze, 2000; Hamer & Hill, 2000; Hill *et al*., 1995) and/or changes in community composition (Spitzer, 1997; Willott *et al*., 2000), although the difference between various logged over forest types did not necessarily translate in different species numbers (Beck & Schulze, 2000).

Soil nematodes were studied in Cameroon and produced a significant decrease in species numbers to 40% after slash and burn practices and complete mechanical clearance, and general lower species numbers after disturbance (Bloemers *et al*., 1997). Birds are often used as a group for studies on the effect of disturbance and always indicated changes in community composition and often thinning (Johns, 1992a; Jullien & Thiollay, 1996; Mason, 1996), a loss of rare species (Lambert, 1992) and sometimes an increase of open habitat birds in the logged over forests, leading to even higher numbers than found for primary rain forest (Johns, 1996). In primates few consistent trends have been found for their reaction towards forest disturbance (Johns, 1992b, Laidlaw, 1996), but generally breeding rates seem to get depressed (Johns, 1992b).

For an inventory of diversity along a disturbance gradient in the tropics it is desirable to compare community composition in a few taxa to confirm the resulting patterns. The most comprehensive study was conducted by Lawton and co-workers (1998), who investigated nine taxa, including canopy ants and ground dwelling ants, in a semi-deciduous forest in southern Cameroon. Positive correlations in their reaction towards disturbance were found for canopy ants with ground dwelling ants, canopy beetles and butterflies, although sample size for the groups under study was fairly low and only a small part of the fauna was recorded.

During my project, two Diploma students worked with ants of the lower vegetation (Gossner, 1999) and fruit feeding nymphalid butterflies (Jalil, 2000) in the same study plots. The ants of the lower vegetation were sampled with different baits and by hand collecting in plots A, D and I in the three different logged over forests of Deramakot and plot L in Danum Valley in 1998 with a sampling efficiency of around 70%. Species richness was significantly higher in the primary forest of Danum Valley. The communities of vegetation ants could not be distinguished on a significant level in their species richness between the three logged over forests, although community composition was different. The fruit feeding nymphalid butterflies were studied in Plots A and C of the good and plot I of the disturbed forest in Deramakot as well as plot L in Danum Valley in 1999 with a sampling efficiency near 80%. Species richness decreased along the disturbance gradient (L: 22 spec., A: 19 spec., C: 16 spec., I: 14 spec.) and was significantly different between the primary and logged over forest, but not within the forests of Deramakot. Species diversity, eveness and density of most species decreased with disturbance and community composition in all plots was different. During his Ph. D. study on stingless bees conducted in the same forests at the same time, T. Eltz recorded a low variation in nest density along the disturbance gradient. Bee abundance

was dependent on floral resources and subject to huge temporal fluctuations between years. However the extremely low nest densities in the most recently logged areas in Deramakot (G, H, I) may still indicate a direct logging impact.

Ants of the lower vegetation and nymphalid butterflies show a similar pattern in all community variables as found in the ants of the leaf litter: in all three taxa there are significant differences in species richness and diversity between the primary and logged over forest as a whole, but although differences exist between the logged over forests they are not significant. This is in so far remarkable as the logged over forests are very different in their stand structure due to their logging history (see Forest Structure). Extraction rates were lower in the good forest of Deramakot than in the regenerated forest that were logged 25 years ago and the disturbed forest that was logged illegally at least three times in the 1980s.

A similarity of the species richness and diversity in the different logged over forests of Deramakot might be explained by the structure of the Forest Reserve. On a small scale patches of primary forest are even found in the disturbed forest due to steep slopes or rivers which did not allow logging. These small patches represent islands of favourable habitat with an extraordinary species richness: in plot H one square meter yielded the highest number of ant species collected in the whole study: 29 litter ant species and additional 12 species that were excluded from the analysis as they were not typical ants of the leaf litter (see General Methods), resulting in a total of 41. In these patches most of the rarer litter ant species are found, also present in the good forest of Deramakot. On a larger scale one has to recognise the blocks of different forest quality in Deramakot (Fig. 7): in the north of DFR the forest was heavily logged but the centre presents a core area of relatively good forest which had been logged with low extraction rates.

This matrix of forest structure on a larger scale produces a patchwork of sources and sinks that smooth the differences between the communities of leaf litter ants and presumably as well those of other taxa. The good forest is a source from where ant queens fly out to neighbouring, damaged forests. There they might successfully establish colonies for some time but might also vanish, e.g. during a severe drought. The heavily disturbed forests would therefore act as sinks over time. As all the area is covered by forest, movement between these forest patches is possible. If sensitive species encounter on a smaller scale suitable sites in a highly disturbed forest by chance, they might persist there for a long time. This mechanisms might lead to similar species numbers and diversities in different logged over forest types. Still they are different from primary forests as there is no large primary forest that could operate as a source around Deramakot. All the neighbouring forest reserves are harvested or transformed in tree or oil palm plantations. Distance is a crucial factor for the recolonisation of so called primary forest species in disturbed forests (Roth & Perfecto, 1994; Vasconcelos, 1999; Willott *et al.*, 2000) and the large distance to a primary forest pool might explain the reduced species number, diversity and difference in community composition which is obvious in Deramakot even 25 years after logging.

The communities of leaf litter ants, ants of the lower vegetation and nymphalid butterflies did not recover from the logging impact, if recovery means a near 100% similarity of community descriptors as species richness and diversity to a primary forest level. Species numbers of leaf litter ants in the different plots in Deramakot Forest Reserve reached 70% of those found in the primary forest. Vasconcelos (1999) came to the conclusion that recovery of the ground-

dwelling ant community is rapid – usually less than 25 years – if intensity and scale of disturbance are low, although species richness and community composition were still different. The term recovery was not defined, but surely could not mean a near 100% similarity to a primary forest community. In a more recent study, the ground ant community did not 'recover' after ten years in a small scale experiment (Vasconcelos *et al*., 2000). The possibility of a recovery time of 20 years from logging disturbance to an equilibrium stage, which is again not defined in detail, is discussed for various insect groups in a study in Uganda, although tree regeneration in logged over forests has still been poor (Nummelin, 1998).

For dipterocarp lowland rain forests estimates of regeneration time of secondary to primary forest vary between 150 to 500 years because of the longevity of trees in these forests (MacKinnon *et al*., 1996). Model simulations confirmed the poor regenerative powers of Southeast Asian tropical rain forests, which show drastic differences in stand structure and species composition even 110 years after logging (Bossel & Krieger, 1994). The evidence from the study on leaf litter ants and the other taxa surveyed in the same forests in Sabah does not suggest a recovery of these insect communities to primary forest status, even 25 years after logging.

8   Leaf Litter Ant Communities in Primary Forests along a Gradient of Forest Size

8.1   Introduction

As described in the previous chapter the logging impact had a tremendous effect on the leaf litter ant community in Sabah. Not only is the tropical rain forest affected by disturbance due to timber harvesting, but it also becomes more and more fragmented because of a conversion of the landscape into agricultural plantations. This process often starts with selective logging within a matrix of natural forest and extends over time through the development of progressively more intensive agricultural landscapes (agroscapes). These agroscapes eventually become the matrix themselves, finally leaving only isolated islands of residual forest (Seidler & Bawa, 2001). A key study discovered that by 1988 the area of forest in Brazilian Amazonia which was fragmented or prone to edge effects was over 1.5 times larger than the area actually deforested (Laurance, 1998a).

In the last decades tropical rain forest in Sabah was not only subjected to selective logging at various degrees, but has been also cleared completely for the establishment of large scale plantations of oil palm, a major cash crop in the area. The remaining primary forests only persist in the form of small forest isolates within a matrix of highly disturbed habitat. Most of these isolates are protected Virgin Jungle Reserves (VJR) covering a total of 90 386 ha in Sabah. The average size of VJRs in Sabah is 1 802 ha compared to 244 ha in Peninsula Malaysia (Laidlaw, 1996). The condition of the rain forest in the reserves is in most cases unclear and the Forest Research Center has just started an ITTO (International Timber Trade Organisation) funded inventory programme of the VJRs. In 2000, a VJR of 100 ha was logged illegally within a few weeks and others were affected by the 1997-98 forest fires due to the ENSO event (H. Petol, pers. comm.).

Following the theory of island biogeography (Mac Arthur & Wilson, 1967) species richness in habitat fragments is expected to be a function of island size and degree of isolation. Effects of fragmentation on tropical rain forest fauna are so far mostly based on observational studies on butterflies (e.g. Shahabuddin & Terborgh, 1999; Thomas, 2000), birds (e.g. Anciaes & Marini, 2000; Arango-Velez & Kattan, 1997; Cooper & Francis, 1998; Jullien & Thiollay, 1996; Stouffer & Bierregaard, 1995) and mammals (e.g. Chiarello, 2000; Laidlaw, 1996; Laidlaw, 2000). The only experimentally fragmented landscape studying tropical rain forests was created in Brazil in the Biological Dynamics Forest Fragments Project (BDFFP) in 1980 (Debinski & Holt, 2000). Despite its limitations in replicates, size of fragments and matrix composition (Bierregaard *et al.*, 1992; Laurance & Bierregaard, 1996), this experiment so far provided us with most insights on the reaction of tropical rain forests towards fragmentation. Due to the differences in the ecosystem characteristics between tropical forests, the results from Brazil are not easily transferable to Southeast Asian rain forests (Linsenmair, 1997).

Studies on forest fragmentation and its effects on fauna or flora are scarce in Malaysia (Laidlaw, 1996; Laidlaw, 2000) and do not exist in Sabah for any taxa, despite the described large scale landscape alterations. This chapter presents the results from an analysis of the leaf litter ant fauna of the primary rain forest fragments of Sepilok Forest Reserve and Kebun Cina Forest Reserve in comparison with Danum Valley, a contiguous rain forest (see Study Sites).

8.2   Methods

The sampling of the ant communities in the three forests was conducted in the established sampling plots (see Study Sites) using the Winkler litter sifting protocol. Details on sampling design, sample and data processing, morphospecies identification, and various statistical methods are described in the chapter on General Methods.

8.3   Results

8.3.1   Taxonomic structure of the total community

187 species in 48 genera and five subfamilies were recorded in the 420 m² sampled in this comparison of primary forest leaf litter ant communities (Tab. 24). The most species and genera were found in the subfamily Myrmicinae, followed by Ponerinae and Formicinae. The Cerapachyinae and Dolichoderinae included only one genus.

Tab. 24   Species and genera number (and proportions in %) in the different subfamilies of the total leaf litter ant community.

Subfamilies	Genera	Species
Myrmicinae	25 (52.1)	115 (61.5)
Ponerinae	14 (29.1)	38 (20.3)
Formicinae	7 (4.6)	20 (10.7)
Cerapachyinae	1 (2.1)	8 (4.3)
Dolichoderinae	1 (2.1)	6 (3.2)
Total	**48**	**187**

After ranking (Tab. 25) three genera included more than five percent of all species (*Pheidole:* 26 spec., *Strumigenys:* 19 spec. and *Pyramica:* 12 spec.). 19 of the 48 genera comprised only one species.

Tab. 25   The ant genera ranked after number of species. The proportion of species number of the genus to total species number (187 spec.) is given in %.

Genus	Number of species	%	Genus	Number of species	%	Genus	Number of species	%
Pheidole	26	13.9	*Pseudolasius*	4	2.1	*Carebara*	1	0.5
Strumigenys	19	10.2	*Recurvidris*	4	2.1	*Cladomyrma*	1	0.5
Pyramica	12	6.5	*Anochetus*	3	1.6	*Cryptopone*	1	0.5
Pachycondyla	9	4.8	*Eurhopalotrix*	3	1.6	*Dacetinops*	1	0.5
Cerapachys	8	4.3	*Myrmoteras*	3	1.6	*Emeryopone*	1	0.5
Tetramorium	8	4.3	*Acanthomyrmex*	2	1.1	*Mayriella*	1	0.5
Hypoponera	7	3.8	*Acropyga*	2	1.1	*Meranoplus*	1	0.5
Paratrechina	7	3.8	*Cardiocondyla*	2	1.1	*Myrmicaria*	1	0.5
Oligomyrmex	6	3.2	*Dsicothyrea*	2	1.1	*Mystrium*	1	0.5
Technomyrmex	6	3.2	*Euprenolepis*	2	1.1	*Myopias*	1	0.5
Crematogaster	5	2.8	*Lophomyrmex*	2	1.1	*Prionopelta*	1	0.5
Gnamptogenys	5	2.8	*Lordomyrma*	2	1.1	*Pristomyrmex*	1	0.5
Vollenhovia	5	2.8	*Pheidologeton*	2	1.1	*Proatta*	1	0.5
Monomorium	4	2.1	*Amblypone*	1	0.5	*Probolomyrmex*	1	0.5
Myrmecina	4	2.1	*Brachymyrmex*	1	0.5	*Proceratium*	1	0.5
Ponera	4	2.1	*Calyptomyrmex*	1	0.5	*Solenopsis*	1	0.5

8.3.2   Sampling efficiency

8.3.2.1   Species number and species richness estimators

The entities for the following analysis were the ant communities found in the different plots, collected in 60 m² of leaf litter with the identical sampling scheme (see General Methods). Sampling was conducted in two plots in 1998 and in one plot in 1999 in Danum Valley and in one plot in 1998 and in two plots in 1999 in Sepilok Forest. Kebun Cina Forest was sampled once in 2000 (see Study Sites). Highest species numbers in 60 m² sampling were reached in Danum Valley (97, 100 and 105 spec.) and the lowest species number in a plot was recorded in Sepilok Forest (plot K*99: 39 spec.) (Tab. 26). Estimated sampling efficiency (observed/estimated species) did not vary greatly between plots of Sepilok and Kebun Cina.

Tab. 26 Species numbers (rounded) of the different estimators for the litter ant communities in the plots. Percentages of estimated to observed species are given in brackets *(italic)*. Lowest and highest estimates of sampling efficiency are given in bold.

Forests	Plots – year	Species number	ICE	Chao2	Jack1	Jack2	Bootstrap	MMMean
Danum Valley	L98	105	126 *(83.1)*	133 *(78.9)*	132 *(79.8)*	145 *(72.3)*	117 *(89.7)*	118 *(88.9)*
	L99	97	116 *(83.8)*	112 *(86.8)*	120 *(81.1)*	125 *(77.8)*	108 *(89.5)*	114 *(85.4)*
	M98	100	133 *(74.9)*	141 *(70.5)*	132 *(75.5)*	152 *(65.8)*	114 *(87.4)*	114 *(87.4)*
Sepilok Forest	K98	49	77 *(63.6)*	**97 *(50.5)***	70 *(69.0)*	87 *(56.3)*	58 *(84.4)*	68 *(72.0)*
	K99	61	98 *(62.2)*	105 *(58.0)*	89 *(68.5)*	107 *(57.0)*	73 *(83.5)*	76 *(80.2)*
	K*99	39	49 *(79.5)*	46 *(84.7)*	50 *(78.0)*	52 *(75.0)*	44 *(88.6)*	48 *(81.3)*
Kebun Cina Forest	O00	45	65 *(69.2)*	71 *(63.3)*	61 *(73.7)*	71 *(63.3)*	52 *(86.5)*	**49 *(91.8)***

For an easier assessment of sampling efficiency, the mean of six estimators was calculated and compared with the observed species (Fig. 39). The lowest value of mean sampling efficiency was found in the Sepilok Forest Plot K98. The values of completeness of sampling in the other plots varied between 66.8% and 83.9%.
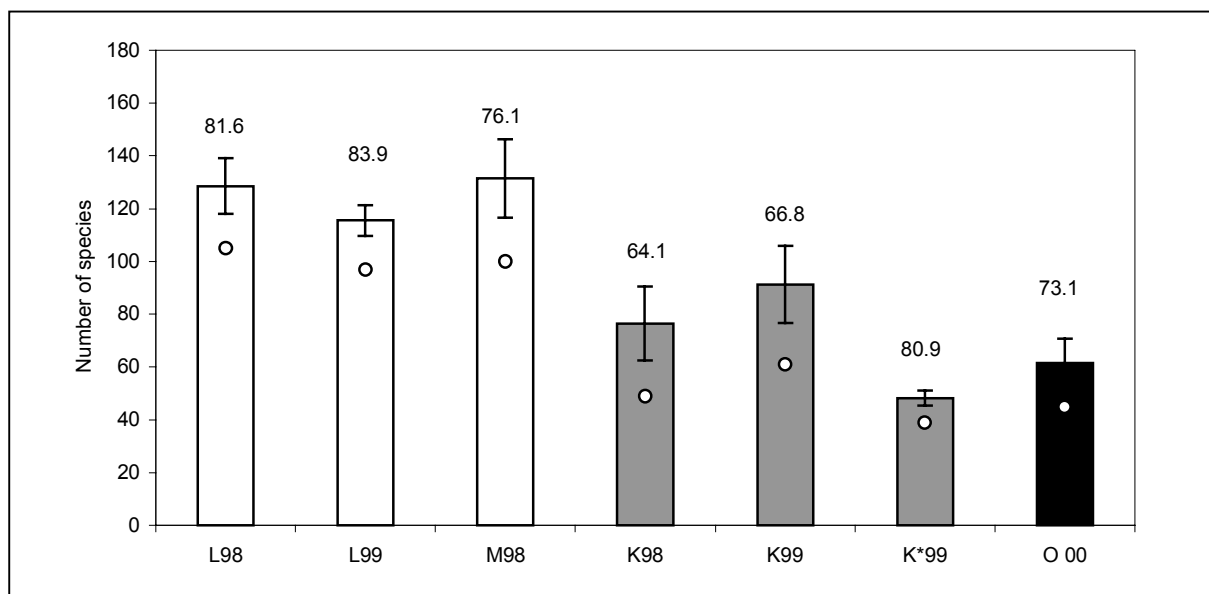
Fig. 39   Mean of all estimators (columns) and observed species (open circles) in the different plots. Sampling efficiency (observed/estimated species) is given above the columns (%).

8.3.2.2 Species accumulation curves

The slope of the species accumulation curves of the different plots were very similar (Fig. 40). All curves are getting flatter with higher sample size and reach an asymptote. This similarity in slope and the high values in estimated species versus observed species (Tab. 26 and Fig. 39) indicates a similarly high degree of completeness of sampling in the different plots with the methodology chosen.
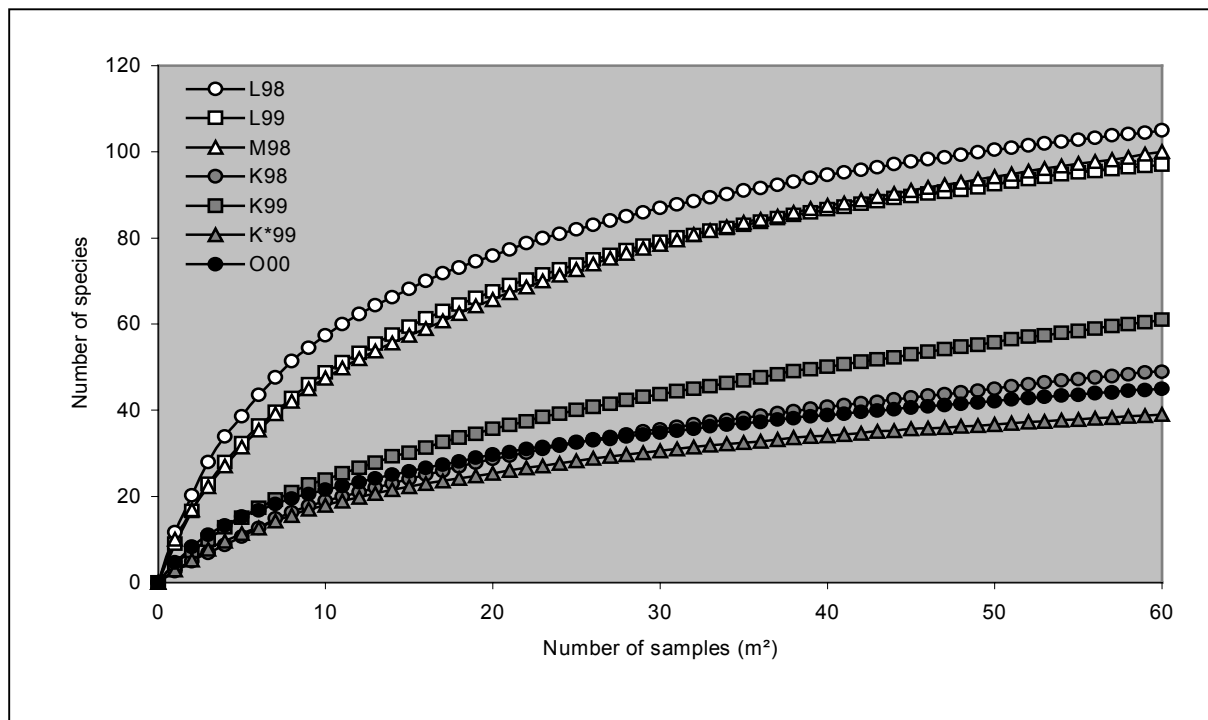
Fig. 40 Randomised species saturation curves (100 runs) of the different plots.

The species accumulation curves of plots of the large primary forest of Danum Valley are increasing faster in the first ten samples and are all situated above the curves of the smaller forests of Sepilok and Kebun Cina. The curve of the Kebun Cina Forest plot (O00) is interspersed between the curves of the less species rich plots of Sepilok Forest. It has to be noted that the slope of the Kebun Cina Forest plot is flatter than the Sepilok Forest plot curves. The high degree of completeness of Kebun Cina is also obvious from the higher percentage values indicated in the plot species richness estimation (see Tab. 26 and Fig. 39).

The species saturation curves for the three forests were also calculated, using the independent spatial samples (Danum Valley: M98, L98; Sepilok Forest: K98, K*99). The accumulation curve of Danum Valley lays far above the other curves (Fig. 41) and the increase in species number at the beginning of sampling is highest in Kebun Cina. The slope at the end of sampling is very similar, although sample size was different, and produces an increase of two to three individuals in the last 10 square meters.
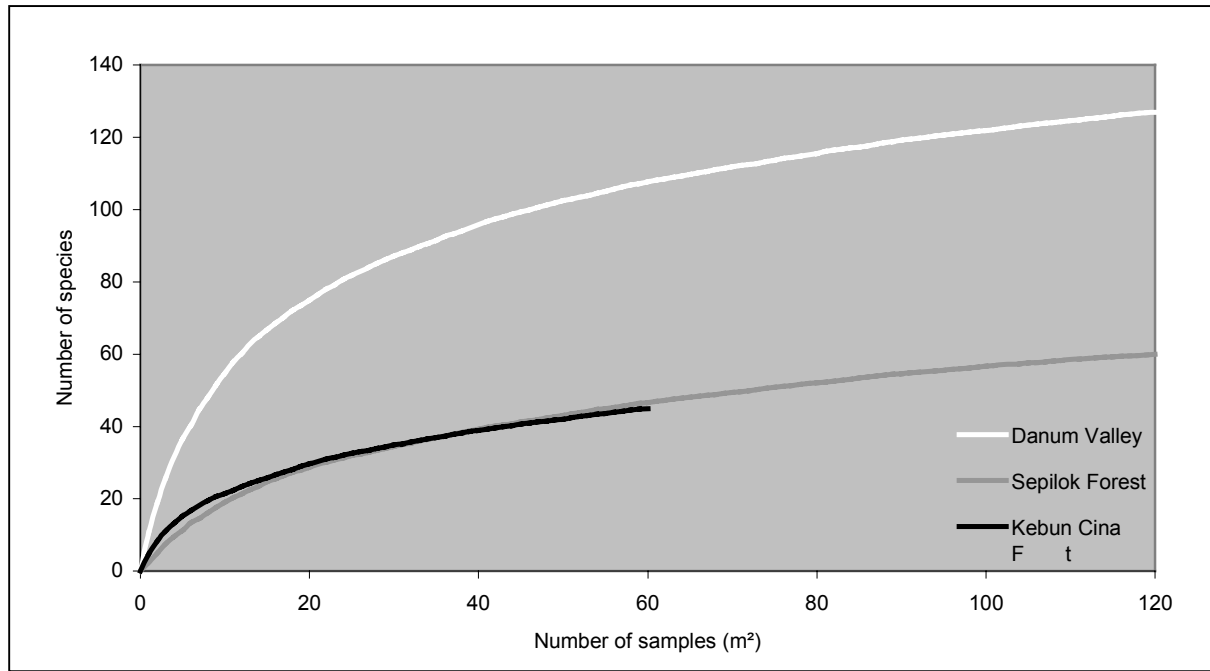
Fig. 41   Randomised species accumulation curves (100 runs) of the three forests; DVCA and SFR two plots (120 m²) and KCFR one plot (60 m²).

8.3.3   Rare and common species – abundance distributions of the forest types

In Fig. 42 species abundance was plotted against rank order for each sample (rank abundance curve). The species on first ranks were collected in most samples (common species). The species forming the tail of the curve were only encountered in a few samples (rare species).
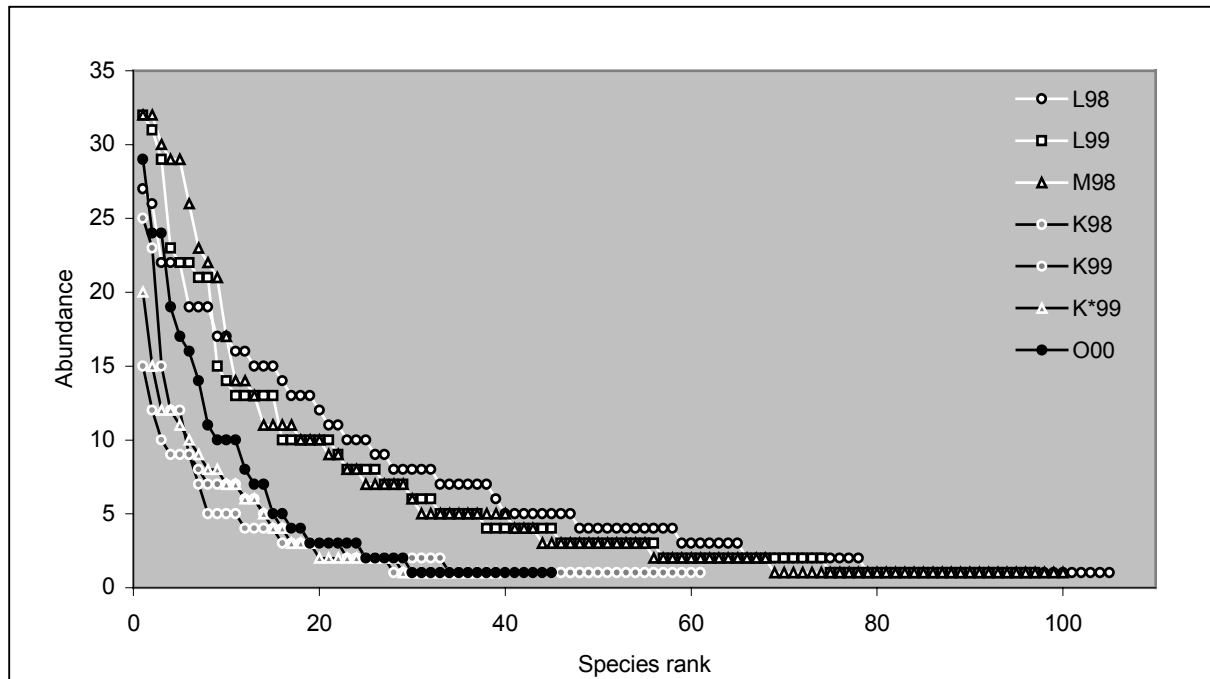
Fig. 42   Rank abundance distribution of the ant communities of the plots; DVCA: L98, L99, M99, SFR: K98, K99, K*99, KCFR: O00. Species abundance is plotted against rank order for each sample (60 m² per plot).

The rank abundance curves for the Danum Valley plots (L98, L99, M98) are situated above the others, displaying the longest tail related to more species in the communities. The resolution between the Sepilok plots and Kebun Cina distributions is not very clear. Highest abundances for the most common species are reached in Danum Valley (M98: 32 samples.) but are closely followed by the plot in Kebun Cina (O00: 29 samples). In Sepilok most common species show mean abundances of 20 samples (K98: 15, K99: 25, K*99: 20) compared to Danum Valley with 28 samples (L98: 27, L99: 26, M98: 32). The number of uniques (species collected in only one sample) is slightly higher in the Danum Valley plots (L98: 27 spec., L99: 23 spec., M98: 32 spec.) than in Sepilok or Kebun Cina (K98: 22 spec., K99: 28 spec., K*99: 11 spec., O00: 16 spec.). The high number of uniques is remarkable in K98 compared to the other plots in Sepilok forest. The plots of the different forests are even more clearly separated when the number of species collected below five samples (rare species) is regarded: the Danum Valley plots show similar high numbers of rare species (L98: 58 spec., L99: 60 spec., M98: 60 spec.), whereas the numbers were lower in Sepilok and Kebun Cina (K98: 38 spec., K99: 46 spec., K*99: 25 spec., O00: 29 spec.).

8.3.4   Abundance distributions and their fit to the log series

The abundance distributions of the different forest types were tested for their fit to the log series model. All distributions fitted the model (Tab. 27), a prerequisite for Fisher's α−diversity index (see General Methods).

Tab. 27 Abundance distributions fitted to the log series model.

Forests	Plots	α	Chi	dfr	p	fit
Danum Valley	L98	34.99	5.178	4	0.269	yes
	L99	33.18	2.216	4	0.696	yes
	M98	34.07	2.535	4	0.638	yes
Sepilok Forest	K98	24.09	3.960	3	0.265	yes
	K99	27.12	0.738	4	0.946	yes
	K*99	15.23	2.096	4	0.718	yes
Kebun Cina	O00	15.47	2.249	4	0.690	yes

8.3.5   Alpha-diversity indices

Three standard methods were used to calculate the diversity of the forest types: Fisher's α which is derived from the log distribution (see above), and three indices which are free from any abundance model assumption, the Shannon-Wiener index H', the Simpson index D and Eveness J (see General Methods and Appendix). Tab. 28 summarises the diversity values obtained for the different plots in the three primary forests.

Tab. 28 Measures of species diversity (Species number, Fisher's α, Shannon-Wiener H', Simpson D, and eveness J) for the ant communities of the plots.

Forests	Plots	Species No.	α	H'	D	J
Danum Valley	L98	105	34.99	4.22	57.45	0.83
	L99	97	33.18	4.08	45.24	0.80
	M98	100	34.07	4.03	41.57	0.79
Sepilok Forest	K98	49	24.09	3.51	29.24	0.68
	K99	61	27.12	3.57	25.49	0.70
	K*99	39	15.23	3.27	22.53	0.64
Kebun Cina	O00	45	15.47	3.24	19.98	0.64

The highest diversity values were found in plot L98 of Danum Valley, and the lowest were recorded for most of the indices in Kebun Cina. Similarity was high within the forest types, clearly decreasing from Danum Valley to the smaller forests. Randomisation tests were performed for the different diversity indices (Tab. 29). The one-sided test gives an estimated probability that the diversity of sample 1 $\leq$ sample 2 (see General Methods).

Tab. 29   P values of the randomisation test (10 000 runs, one-sided) of the pair-wise comparisons of the different diversity indices.

Forests	Sample 1	Sample 2	α	H'	D	J
Danum	L99	L98	n.s	0.05	0.01	0.01
Valley	M98	L99	n.s	n.s	n.s	n.s
Sepilok	K98	M98	0.01	0.01	0.05	0.01
Forest	K99	K98	n.s	n.s	n.s	n.s
	K*99	K99	0.001	n.s	n.s	0.05
Kebun Cina	O00	K*99	n.s	n.s	n.s	n.s
	O00	K99	0.05	0.001	0.05	0.05

In all diversity indices a significant difference was obvious between the most diverse plot in Sepilok (K98) and the least diverse plot in Danum Valley (M98). Fisher's α as well as Eveness J were significantly different when comparing plots K*99 with K99. The Kebun Cina forest plot was not significantly different to the least diverse plot in Sepilok (K*99), but to K99 in all indices. The difference in diversity between L99 and L98 in Danum Valley became significant in H', D and J, but not in Fisher's α.

8.3.6   Diversity ordering: the Renyi family

The Renyi index was also calculated to compare the diversities of the ant communities (see General Methods). Fig. 43 displays the diversity profile of the seven plot communities.
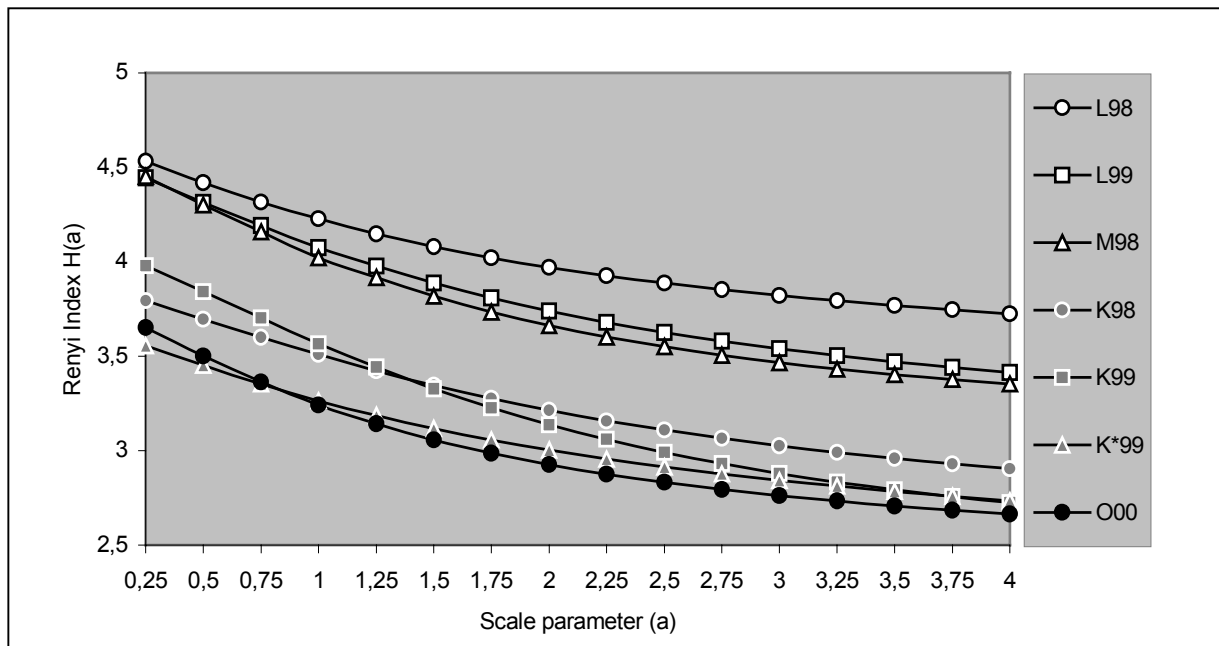
Fig. 43   The Renyi family: Renyi index H(a) of the leaf litter ant communities of the different plots with varying scale parameter (a).

The curves of the Danum Valley communities are positioned above those of the smaller forests for all scale parameters, with L98 being the most diverse community over the complete range of the scale parameter. The communities L99 and M98 of Danum Valley and K98 and K99 of Sepilok could not be ordered because the curves cross each other. The communities of Sepilok Forest plot K*99 and the Kebun Cina plot O00 were also non-comparable. The diversities of the Kebun Cina community are over all scale parameters lower than in the Sepilok Forest plots K98 and K99.

8.3.7   Species number per sampling site

For a comparison of the three forests at a lower spatial scale, the number of leaf litter ant species collected at a sampling site (10 square meters) were compared. The independent spatial samples (plots M98, L98, K98, K*99) yielded 12 sampling sites for Danum Valley and Sepilok Forest and six for Kebun Cina. An ANOVA revealed a significant difference for the species number per site between the three forests (df = 2, F = 101.67, p << 0.001; Fig. 44). A Scheffe post-hoc test exposed highly significant values for the comparisons between Danum Valley and the two other forests (p << 0.001). There was no significant difference in the species numbers per site between Kebun Cina and Sepilok.
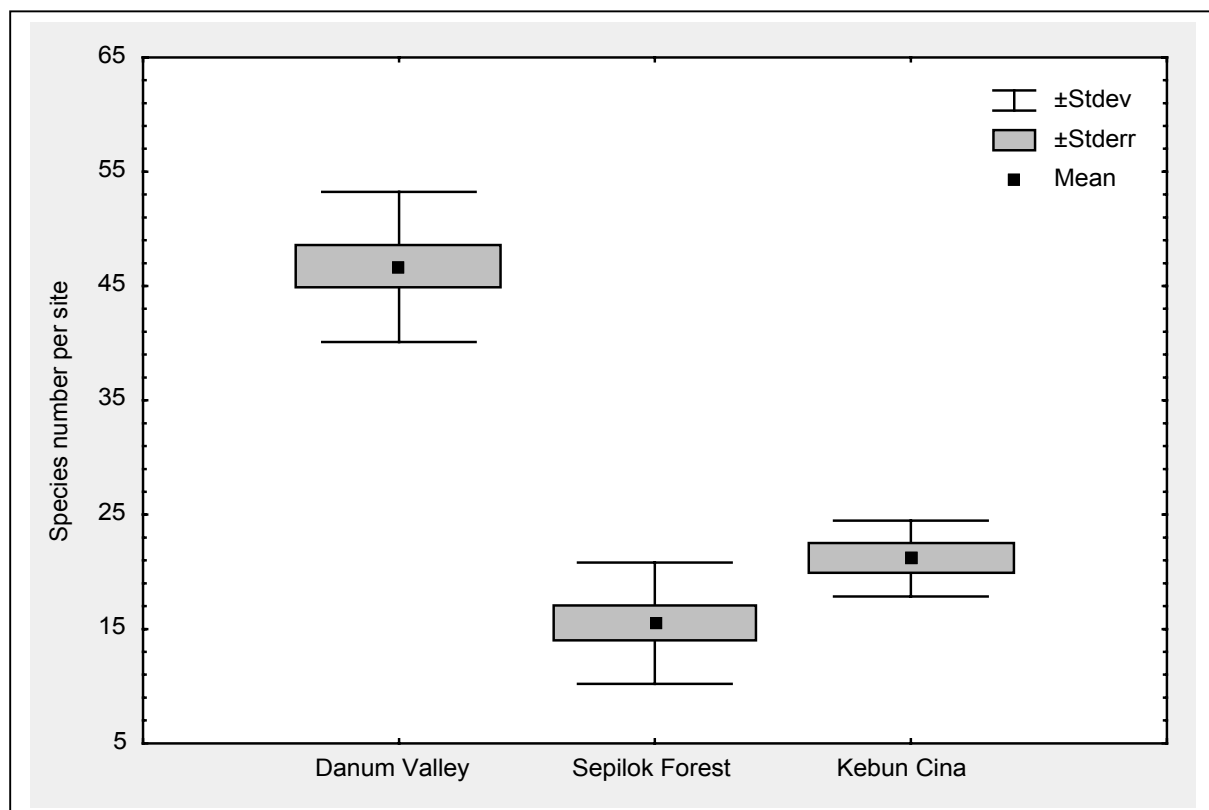
Fig. 44 Box-Whisker plot of the species number per site in the three different forests.

8.3.8   Species density in the forest types

The lowest spatial scale is represented by the number of ant species collected in one square meter of leaf litter. For Danum Valley and Sepilok Forest only the spatial replicates were used and the Kebun Cina Forest samples were standardised for sample size by multiplying the

values by 2. The shape of the resulting species distributions of the three primary forests was different (Fig. 45): the curve of Danum Valley was bell-shaped, whereas in Sepilok Forest and Kebun Cina Forest the distributions were skewed to the left. Ten species were collected in an average square meter in Danum Valley, in Sepilok Forest and Kebun Cina this value decreased towards three and four species. In Danum Valley, ants were recorded in every sample, in Sepilok 18 out of 120 samples were found without ants, in Kebun Cina four.
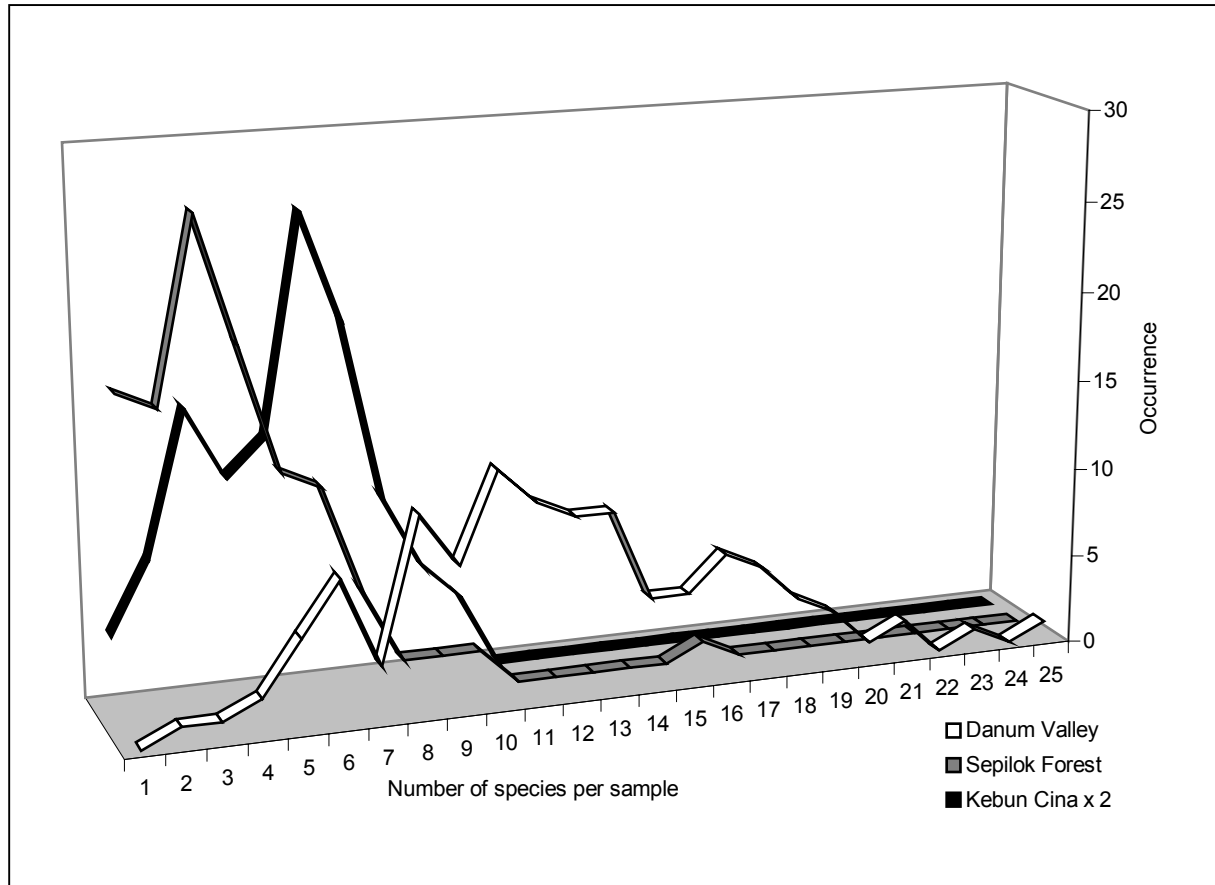
Fig. 45 Species density distribution per m². The number of ant species occurring in the 1-m²-unit samples in the different forests. DVCA, SFR and KCFR (corr. x 2).

8.3.9   Multidimensional scaling and cluster analysis

For an analysis of the community structure, the two independent spatial replicates in Danum Valley and Sepilok Forest and the one plot in Kebun Cina were included. The Steinhaus similarity index was calculated (see General Methods and Appendix) and the resulting matrix analysed with MDS (Fig. 46).

The Danum Valley plots are situated adjacent to each other as well as the replicates of Sepilok Forest. The position of the Kebun Cina ant community is closer to Sepilok K*99 than any other plot. The two-dimensional MDS graph explains all the variation (100%, stress: 0), dimension 1 accounted for 94.3% and dimension 2 for 5.7%. A MANOVA showed significant differences between the three forests along dimension 1 ($df_{effect} = 2$, $df_{error} = 2$, $F = 22.70$, $p < 0.05$; dimension 2 n.s.), but a Scheffe post-hoc test did not reveal any significant differences due to the low number of replicates within the forest types (one or two plots).
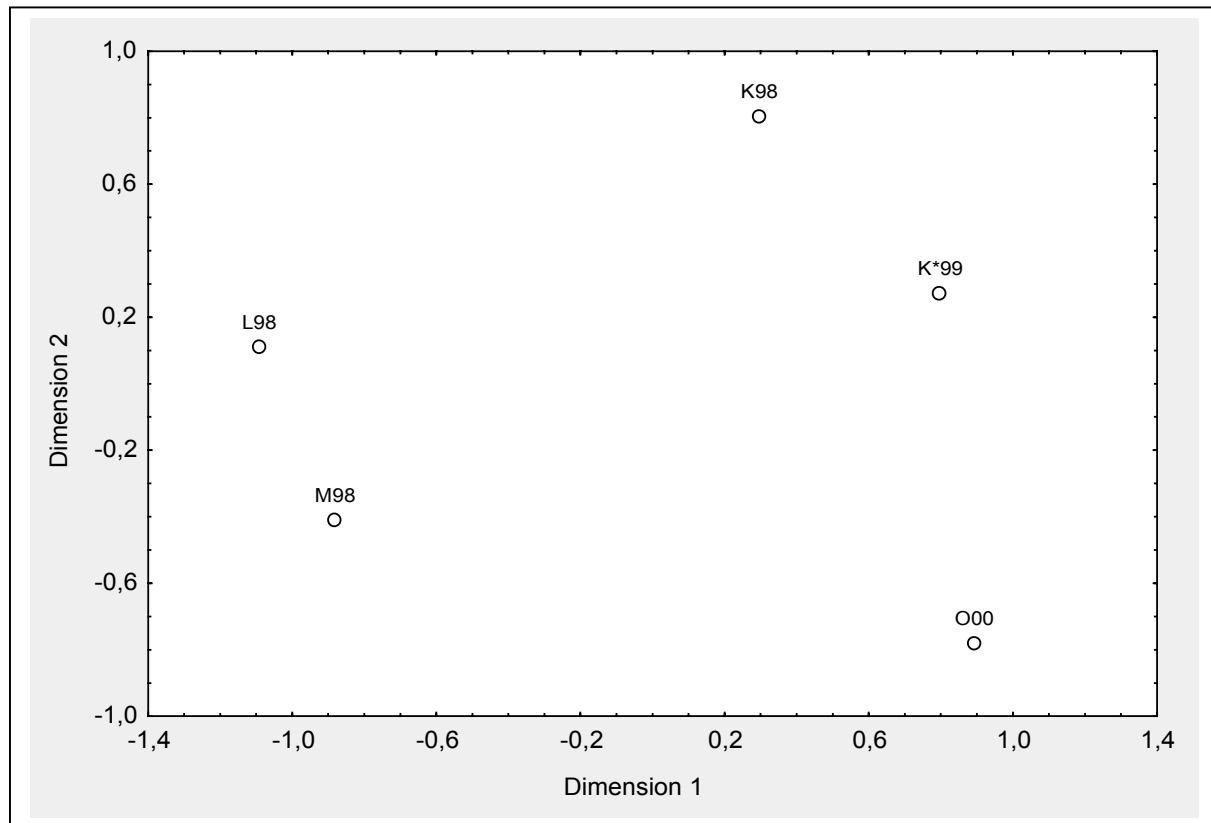
Fig. 46 MDS ordination (based on the Steinhaus index) of the ant communities of the different plots (two dimensions, stress: 0). The DVCA plots (L98, M98) are separated from the SFR (K98, K*99) and KCFR (O00) plots along dimension 1 (MANOVA, p << 0.05).

8.3.10 Cluster analysis

The dissimilarity values (1 - Steinhaus index = Bray Curtis index) were calculated for each comparison and a cluster analysis was performed. UPGMA and Single Linkage were used as clustering algorithms (see General Methods).

The UPGMA dendrogram (Fig. 47) exhibits the high similarity of the Danum Valley plots L98 and M98. The Danum Valley communities are slightly more similar to the Kebun Cina Forest community than to the Sepilok Forest community. The Sepilok plots are more similar , but closely related to the Kebun Cina plot. The same pattern was evident in the Single Linkage dendrogram (not displayed) with the branching points at a lower distance level due to the underlying algorithm which is used for pairwise comparisons (Krebs, 1989) (see General Methods).
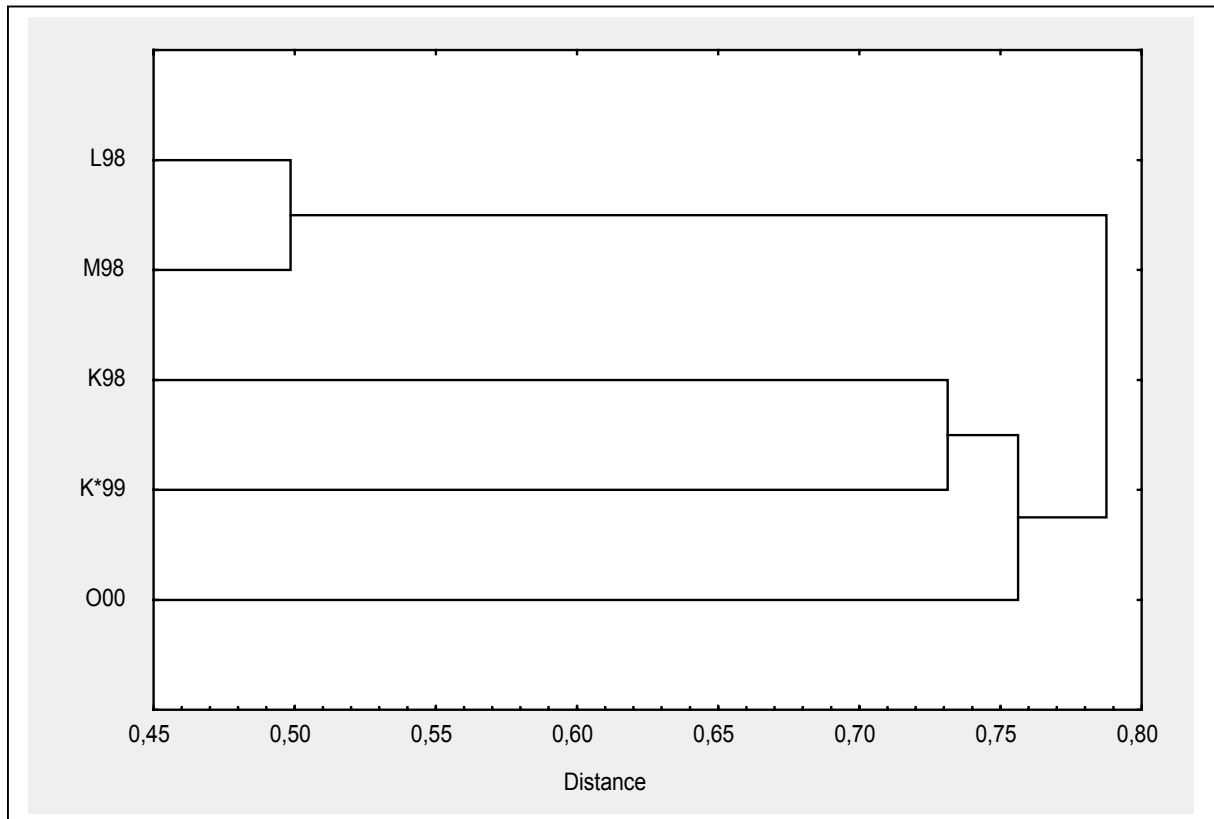
Fig. 47   UPGMA dendrogram using 1 - Steinhaus as distance measure.

8.3.11 Widely distributed and restricted species

The abundance distributions in the spatial replicates were analysed for an assessment of the distribution of species between the different forest types (total species number N = 145). Typical common species had to occur among the ten most abundant species (rank 1-10) in both plots in Danum Valley and Sepilok Forest and in the single plot in Kebun Cina. 13 species could be identified as common in the different forests (Tab. 30).

Tab. 30   Species found among the ten most abundant species in each forest plot. Two species are considered generalists as they occur in all communities.

Species	Danum Valley	Sepilok Forest	Kebun Cina	Type
Pachycondyla b	x	x	x	Generalists
Tetramorium a	x	x	x	
Hypoponera e	x			Large area
Strumigenys juliae	x			
Ponera e	x			
Pheidole clypeocornis	x		x	
Paratrechina e		x	x	
Lophomyrmex bedoti		x	x	
Crematogaster a			x	
Pheidole plagiaria			x	
Strumigenys aechme			x	
Monomorium a			x	
Oligomyrmex c			x	Small area

Two of the most abundant species were widely distributed and present in all primary forests *(Pachycondyla b, Tetramorium a)*. Four common species were found with higher abundances restricted to Danum Valley (*Hypoponera e, Strumigenys juliae, Ponera e*), one species to Sepilok Forest *(Paratrechina e)* and five common species were found in Kebun Cina (*Crematogaster a, Pheidole plagiaria, Strumigenys aechme, Monomorium a, Oligomyrmex c)*. *Lophomyrmex bedoti* and *Paratrechina e* were recorded among the 10 most common species in Sepilok and Kebun Cina, *Pheidole clypeocornis* was shared between Danum Valley and Kebun Cina. Another aspect for describing the communities is the presence of species in only one forest and their absence in others: 61 species were restricted to Danum Valley, four to Sepilok Forest and nine to Kebun Cina. Most of these species discovered in one forest were collected in low abundances (in 1-5 m²) except for *Hypoponera f, Ponera d, Vollenhovia d, Myrmecina b, Tetramorium neshena, Solenopsis a, Strumigenys koningsbergeri* and *Pheidole a* in Danum Valley and *Meranoplus c* in Kebun Cina. These species were found in more than 10% of the collected samples. 23 of the 145 species in this comparison (15.8%) were found in all forests in variable abundances.

8.3.12 Seasonality

To account for seasonal changes in the litter ant community, resampling of the same transect took place in the Danum Valley plot L and Sepilok Forest plot K in 1999. In 1998 the weather was very dry due to an ENSO event which reached its peak from March to May 1998. In 1999 rainfall exceeded mean monthly records and reached 124% of the yearly average in DVCA (see Study Sites).

Weather conditions can alter the distribution of ants and result in differences in community composition. There was some variation found in the different years when comparing the estimators and species numbers (Tab. 26): the resampling in Danum Valley showed a lower species number compared to the previous year but still within range of the forest type. In Sepilok Forest the 1999 sample showed a higher species number than in 1998. But it is remarkable that K*, sampled also in 1999, exhibited the lowest species number collected in Sepilok Forest. The species accumulation curves of the different years performed in a similar way (Fig. 40). When the resampled plots were compared regarding their diversity, L99 in Danum Valley showed slightly lower diversities. In Sepilok Forest, diversities were very similar, in the Renyi family (Fig. 43) the lines of K98 and K99 did even cross each other and the communities were therefore non-comparable. The most interesting point in the comparison of the same plots sampled in different years is community composition. Again a Steinhaus similarity matrix was calculated for MDS.

The three different forest types form distinct groups in the MDS diagram (Fig. 48). The positions of L98 and L99 are almost identical, indicating the high similarity in the species composition of the communities. In comparison, the resampled plots of Sepilok Forest are further apart from each other. Kebun Cina is closer situated to Sepilok Forest than to Danum Valley. The two dimensions explain 96.8% of the variation in the data, dimension 1: 87.8% and dimension 2: 9.0%. The Danum Valley plots are distinctly separated from the plots in Sepilok and Kebun Cina along dimension 1 (MANOVA: $df_{effect} = 2$, $df_{error} = 4$, $F = 20.21$, $p < 0.01$; dimension 2 n.s.; Scheffe post-hoc test: differences between Danum Valley-Sepilok: $p < 0.05$, Danum Valley-Kebun Cina: $p < 0.01$, Sepilok-Kebun Cina: n. s.).
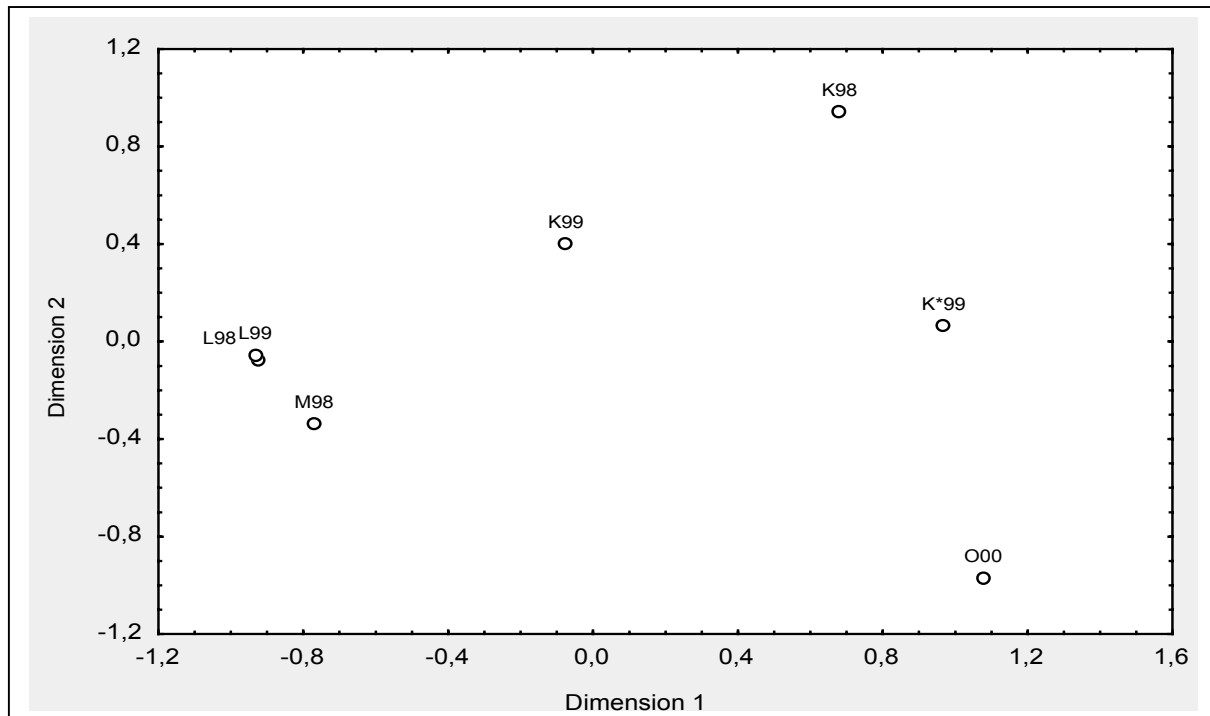
Fig. 48 MDS ordination (based on the Steinhaus index) of the ant communities including the plots resampled in 1999 (two dimensions, stress: 0.032). The DVCA plots (L98, L99 and M98) are separated from the SFR (K98, K99, K*99) and KCFR (O00) plots along dimension 1 (MANOVA, p < 0.01).

The cluster (UPGMA) analysis shows a higher similarity of the Danum Valley plots of the following years than the Sepilok Forest plots.
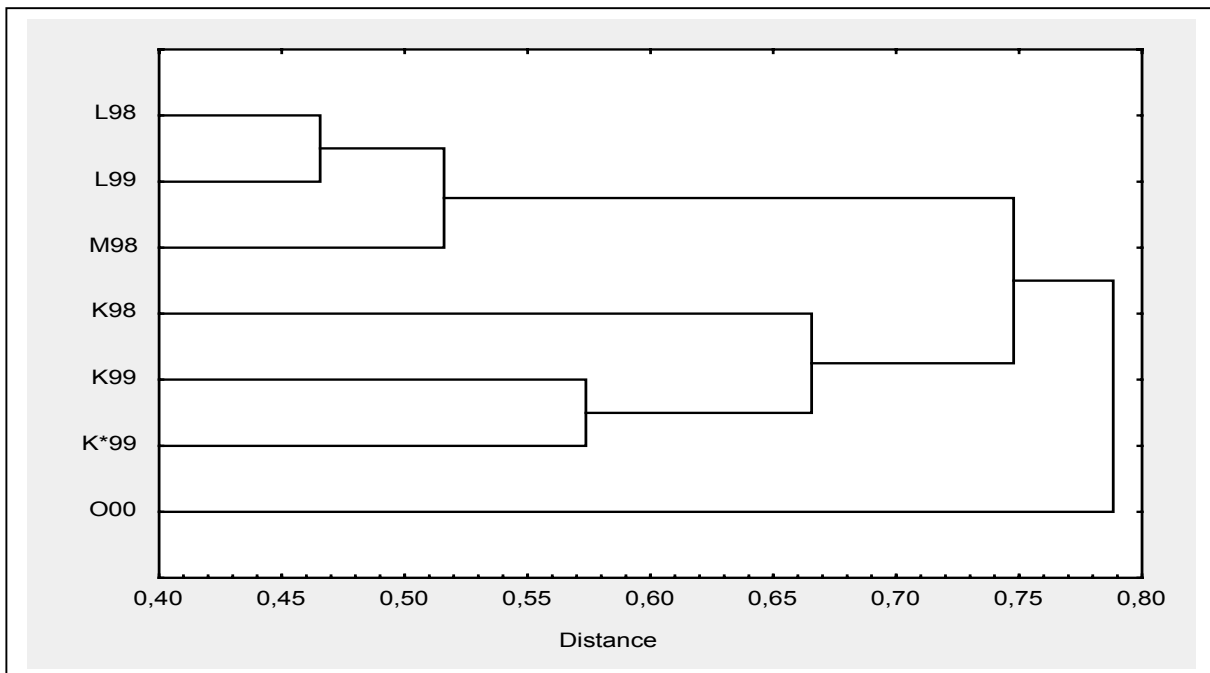
Fig. 49 UPGMA dendrogram based on 1 - Steinhaus as distance measure including the plots resampled in 1999.

Kebun Cina forms the outgroup with a lower distance to the Sepilok Forest cluster. A Single Linkage dendrogram showed no difference in its pattern and is therefore not displayed.

8.4 Discussion

8.4.1 Taxonomic structure of the total community

The taxonomic structure of the leaf litter ant community in this analysis of the primary forests of different sizes largely resembled the one recorded in the comparison of primary and logged over forest (see previous chapter). The number of genera as well as the dominant genera were identical and only one more species was collected. This is amazing at a first glimpse as total sample size was substantially lower with 420 m² instead of 900 m². But the Danum Valley samples determine the taxonomic composition of the total ant community, with 179 species recorded in 180 m², which lead to the similarity in faunal composition in both analyses. Therefore the fauna of the different primary forests is in its taxonomic composition also comparable to results from other inventories in Southeast Asia as was obvious in the previous chapter.

8.4.2 Sampling efficiency

General sampling efficiency was high and sufficient for this study because a taxonomically comparable total fauna was collected as in other investigations in Southeast Asia. But for a comparison of communities of different forests we need to sample those to a similarly high degree (Colwell & Coddington, 1994). This sampling efficiency can be inferred from species richness estimators and the shape of the species accumulation curves of the different forests and plots.

8.4.2.1 Species richness estimators

Estimated species richness was closest to the observed species numbers in the Danum Valley plots which lead to high values of sampling efficiency in the various estimators. The lowest values for sampling efficiency in the different estimators were obtained in plots K99 and K98 in Sepilok Forest. This is due to the high proportion of unique species (K98: 22 of 49 spec. (44.9%); K99: 28 of 61 spec. (45.9%)) in contrast to the species rich plots in Danum Valley (e.g. L98: 27 of 105 spec. (25.7%)). Since the Chao2 estimator reacts especially sensitive to uniques, it hence produced high species richness estimates for K98. Generally, sampling efficiency values were higher in Bootstrap and MMMean (efficiency > 80%, except K98), followed by ICE, Jack1 and Jack2, where differences in sampling efficiency between plots became more pronounced due to the underlying mathematics (see General Methods, Appendix). The means of all six estimators of the plots were located between 73.1% and 83.9%, except for K98 and K99 with 64.1% and 66.8%. Their mean sampling efficiencies did not reach higher values due to the influence of the low estimates of Chao2. Values of sampling efficiency were similar to those recorded along the forest disturbance gradient.

8.4.2.2 Species accumulation curves

The species accumulation curves of the Danum Valley plots were situated above the curves of Sepilok Forest and Kebun Cina, and did not show differences in performance. The Danum Valley curve showed the highest increase at the beginning of sampling. Species accumulation

curves in the plots and forests reached a high degree of saturation. The increase in species number in the accumulation curves of the three forests in the last 10 samples was between two and three species. This was also the case in Kebun Cina where only 60 m² were sampled in total.

In conclusion, the applied sampling method yielded a high number of the present species in the different forests as confirmed by a similarly high sampling efficiency and saturation in the species accumulation curves.

8.4.3   Rank abundance distribution

All rank abundance distributions followed the log series model and were therefore generally similar in appearance. The Danum Valley distributions were over most ranks higher in abundances and displayed a longer tail due to higher species numbers. Differences existed in the number of uniques and rare species: the plots of Sepilok Forest and Kebun Cina always demonstrated similarly low numbers compared to the large primary forest of Danum Valley.

This result is different from that of the logged over forests of Deramakot in the previous chapter which revealed a similar or even higher number of unique and rare species compared to Danum Valley. However, with lower species numbers, the plots in the smaller forests included proportionally more unique and rare species in the community (Rare species: Danum Valley plots, mean: 57.1%; Sepilok Forest plots, mean: 72.3%, Kebun Cina: 64.4%). Compared to the logged over forests the proportions of rare and unique species are even higher in the smaller primary forests. Contrary to unique and rare species the most common species in Kebun Cina and Sepilok were present in a similar number of samples as those in Danum Valley. Therefore the curves of the smaller primary forests are compressed in shape, even more than the secondary forest rank abundance curves, directly affecting the eveness.

8.4.4   Species number, density and α-diversity

The absolute measure of diversity, species number, decreased from an average of 101 species in 60 m² in Danum Valley to 48 species in the plots of the two smaller primary forests (47.5%). The number of species of the single Kebun Cina plot was intermediate to those recorded in the different plots in Sepilok Forest. Species diversity was here significantly lower for all indices compared to Danum Valley. The Kebun Cina plot was significantly lower in diversity for all indices compared with the most species rich plot in Sepilok, K99, but not distinguishable from K*99, the plot in Sepilok with the lowest species number. As expected from the rank abundance distributions, significantly lower eveness values were detected in Sepilok. Due to the more compressed shape of the distributions the values were lower than those of the logged over forests of Deramakot. All α-diversity indices produced noticeably lower values for the smaller fragments of primary forest compared to the plots of the most disturbed logged over forest in Deramakot. The diversity ordering (Renyi index) clarified the difference between the Danum Valley plots and the plots in the smaller forests by higher values over all scale parameters and revealed similar diversities in Kebun Cina and Sepilok K*99. At the smaller spatial scale of sampling sites, the pattern was confirmed by displaying significantly lower species numbers in Sepilok and Kebun Cina, from an average of 46 species in Danum Valley to 16 or 21 species. The species numbers at sampling sites in the fragments were also lower than those recorded in average in the logged over forests (22 to

31 species). The smallest scale in the analysis, the density of ant species per square meter, clearly showed the difference between the forest fragments and Danum Valley and suggested a tremendous thinning in those forests, even more pronounced than in the logged over forests of Deramakot, where average species densities were higher. This thinning of the community, where ants were absent in up to 15% of the samples (Sepilok), is one reason for the loss of species in the forest fragments at higher spatial scales.

8.4.5   Community composition

The complementarity of the communities of the different primary forests was analysed with MDS and cluster analysis (see General Methods). In both diagrams the Danum Valley plots were more similar and distinctly different from the plots of Kebun Cina and Sepilok Forest. The Sepilok Forest and Kebun Cina plots were related to each other at a much higher level, implied by the smaller distance in the cluster analysis. The splitting of the forest groups can be explained by studying the distribution patterns of common and rare species.

8.4.6   Widely distributed and restricted species

Only two of the common species were widely distributed and found as generalists in all three forests. Interestingly these two species (*Pachycondyla b* and *Tetramorium a*) were also among the generalists in the comparison of forests along a disturbance gradient. Most of the common species were only found in one forest which lead to a separation of the plots in community analysis. *Lophomyrmex bedoti* and *Paratrechina e* were recorded among the most common species in the two fragments of Sepilok Forest and Kebun Cina, producing a tie between them. Both species were among the common species in the logged over forests of Deramakot. The number of common species is highest in Kebun Cina, simply because there was no replicate and the abundance pattern of species could not be compared to a second community. Therefore all common species (rank 1-10) were included. However, it is interesting to notice, that two other common species in Kebun Cina, *Crematogaster a* and *Oligomyrmex c* were also common in the logged over forests.

The number of species restricted to one forest was especially high in Danum Valley with 61 species, producing a clear separation in community comparison to the fragments. Only a few species were found to be restricted to the smaller forests, producing subsets of the large primary forest of Danum Valley with low species numbers and variations in abundances on the community level. The species restricted to Danum Valley also included eight species with abundances over five samples. This was only the case in one species in the logged over - primary forest comparison and is another indication of the higher level of thinning in the forest fragments.

8.4.7   Seasonality

The resampling in 1999, the wet year after the ENSO event in 1998 (see Study Sites) produced a highly similar community in Danum Valley with nearly overlapping positions in the MDS graph and low distances in the cluster dendrogram. Since the difference between the two plots M and L was higher, it can be concluded that temporal variation was extremely low and overruled by spatial variation in Danum Valley. The temporal replicate K99 in Sepilok Forest showed a large distance to K98 in the MDS plot and was even more similar to K*99 in the cluster dendrogram. Temporal variation might be more influential in Sepilok Forest and

possibly related to a few species in the community which showed enormous fluctuations in abundance. *Pheidole annexus,* for example increased dramatically in its presence at tuna baits in 2000 compared to 1999 when it was almost absent (T. Bickel pers. comm.). As the leaf litter ant community of Sepilok Forest consists of fewer species, changes in abundance have a higher impact on similarities between the plot communities. Although resampling produced a very distinct community within Sepilok Forest, the differences between the ant communities of Danum Valley and Sepilok Forest as well as Danum Valley and Kebun Cina were significant. The communities of the two smaller fragments could not be separated due to their high similarity.

Evidently the large primary forest of Danum Valley was more species rich and diverse than the smaller primary forest fragments of Sepilok and Kebun Cina over all spatial scales analysed, from forest types to square meter. The community composition was different due to a high proportion of rare restricted species in the large Danum Valley forest and common species only present in one forest. The leaf litter ant communities of the fragments resembled thinned subsets of the larger primary forest with species present at lower densities. The ant communities in the fragments were similar in species richness and diversity and closely related in community composition.

On the plot level the number of species in the fragments was reduced to 47.5% of the Danum Valley level. This reduction of species could be the result of a different local species pool or an effect of fragmentation. A few arguments might convince the reader that these leaf litter ant communities are drawn from an identical local species pool: (1) Soils and forest type of Sepilok Forest and Kebun Cina are similar to Danum Valley, the large primary forest situated in a distance of 100 km to both fragments. (2) Distances between the forests (see Study Sites) did not translate into proportional distances in MDS or cluster analysis but were similar between Sepilok and Kebun Cina and Sepilok and Danum Valley. (3) The ants of the lower vegetation showed only low differences in β-diversity (Gossner, 1999). (4) If we accept the arguments of the previous chapter that the leaf litter ant communities of Deramakot Forest and Danum Valley are drawn from the same local species pool then these arguments should also apply to Sepilok Forest and Kebun Cina as they are situated in the same region in East Sabah (Fig. 1). If the similarity of the local species pool were accepted, the reduction of species to 47.5%, the decrease of density and the changes in community composition in the smaller forests are a result of fragmentation.

Influences of fragmentation on the ant community were also obvious in other studies. In fragments of tropical rain forest in Venezuela, the density of nests of the genus *Atta* increased due to reduced predation by a lower armadillo density (Rao, 2000). In contrast, army ants were among the first to disappear from small forests, because they need large, continuous areas (up to 30 ha) for foraging (Franks & Fletcher, 1983). Temperate forest fragments showed differences in community composition due to the dispersal mode of ant species (Punttila, 1996). So far, the most intensive study on ant community changes in forest fragments was conducted in Amazonia in 100 ha forest remnants (Carvalho & Vasconcelos, 1999). The study concentrated on twig nesting ants (52 species), a small proportion of leaf litter ants. Findings on species richness and density were very similar to the Sabah study: in contiguous forests species richness and abundances were significantly higher and a greater

nest density was found for most species (65.8%). It is suggested in the study that populations of twig nesting ants are maintained by immigrants from external source populations and isolated populations are therefore extinction prone. This should be especially the case if the surrounding matrix consists of pasture or open habitat instead of secondary regrowth forest.

Forest fragmentation studies concentrated on a range of other taxa, although studies in the tropics in general are rare and only one experimental set up exists in Brazil (BDFFP, Debinski & Holt, 2000). There, a very different composition of the leaf litter insect fauna was observed in isolated forest patches (Didham, 1996; Didham, 1997). The beetle community revealed a lower species richness and a different composition in 100 ha fragments (Laurance & Bierregaard, 1996). In the BDFFP study the butterfly community of the fragments lost many species, but in the end showed higher species richness than the contiguous forest due to open habitat species that invaded the fragments (Gascon, 1998). On islands created after the building of a dam in Venezuela, butterflies decreased in abundance and in species richness in some fragments, depending on the distance to the contiguous forest. Colonisation seemed to be reduced after distances of > 1 km from the source and was especially severe for forests specialists (Shahabuddin & Terborgh, 1999). Fragmentation also resulted in non-random extinction of populations and species of butterflies in Europe depending on their dispersal mode of the species (Thomas, 2000).

In vertebrates, birds were often analysed in fragmentation studies. Insectivorous understory birds declined in abundance and species richness in small forest fragments (1-10 ha) in Brazil, and the first to disappear were army ant followers (Gascon, 1998; Stouffer, 1998; Stouffer & Bierregaard, 1995). One possible factor for the decrease in abundance and density of many species was higher nest predation in fragments as found in Colombia and Malaysia (Arango-Velez & Kattan, 1997; Cooper & Francis, 1998). Fragmentation did not result in a species loss in the frog community in the BDFFP project, but composition was substantially altered in forest remnants due to invasions of matrix species (Gascon, 1998). In a study of different Virgin Jungle Reserves in Malaysia, medium sized mammal species were absent from forest fragments below 160 ha, depending on the surrounding vegetation (Laidlaw, 1996; Laidlaw, 2000). Mammal density was also lower in fragments of Atlantic forest in Brazil, related to a shortage of food and higher predation pressure. Forst fragments need to exceed 20 000 ha to support the viable population size (> 500 individuals) in five mammal species studied by Chiarello (2000).

Studies on the effects of fragmentation on the remaining vegetation showed a change in community composition and decrease of species richness (Fox *et al*., 1997), higher mortality (300-800%) due to wind and changes in microclimate, an increase in gaps (Laurance, 1998b) and a decline in tree seedlings in smaller fragments (Benitez-Malvido, 1998). In isolates of dry forest in Argentina a significant decline in fruit set was measured implicating a mean decrease in pollination levels of 20%. Possible changes in ecosystem function due to altered animal communities in forest fragments are summed up by Didham (1996), although hard data are still scarce.

Most of the above mentioned studies were conducted within the BDFFP project in Brazil. The largest forest fragment size there is 1 000 ha (Debinski & Holt, 2000), but most forest islands are of smaller size. The interesting result of my study in Sabah is that even a fairly large sized forest fragment exceeding 4 000 ha could not support a high proportion of leaf litter ant

species of a contiguous primary forest and fragmentation had a more drastic effect than disturbance due to selective logging (see previous chapter).

This is in contrast to studies of stingless bees in Sepilok Forest and Danum Valley (T. Eltz) where nest densities increased from 0.5-0.7 nests ha^{-1} in Danum Valley to 16.2 nests ha^{-1} in Sepilok Forest. Stingless bees seemed to profit from forest fragmentation in Sepilok as they gained access to new plentiful food sources in the agricultural surroundings. Community patterns in the ants of the lower vegetation were analysed in the same study sites in 1998 (Gossner, 1999). M. Gossner detected a reduction in species richness from 135 species in Danum Valley to 82 species in Sepilok Forest (60.7%), a decrease in nest density and profound changes in the community composition. The Sepilok community also showed a lower species number than the different logged over forests of Deramakot (mean: 108 species) and the general patterns detected in the leaf litter ant communities were confirmed. Other evidence of immense effects of forest fragmentation on forest ants is coming from an even smaller forest isolate in Sabah: in the Labuk Road Forest Reserve (46 ha with a forest core of ca. 10 ha), in proximity to Sepilok Forest, 40 species of ants were recorded using litter sifting (T. Bickel, pers. comm.). Additionally, a change in general ant activity was observed: in Danum Valley tuna baits were detected and occupied by ants within 10 minutes; in Labuk, ants were absent at most baits even after an hour and instead birds were observed feeding at the baits on the forest floor. This indicates a severe and extreme reduction in the density and activity of litter-dwelling ants in this forest fragment. It has been noted that circular forest isolates smaller than 100 ha have no real forest interior anymore (Laidlaw, 1996).

Interestingly, I did not find huge differences between the number of ant species in the plots in Sepilok Forest or Kebun Cina, although the latter covers only 146 ha. The litter ant community of the smallest fragment, Labuk Road with almost no forest interior also yielded 40 litter ant species. A few forest species common in logged over forests increased in abundance in forest fragments, notably *Lophomyrmex bedoti, Paratrechina e, Crematogaster a* as well as *Oligomyrmex c* and a group of generalistic species; but most true forest species become rare in the isolates. Additionally, there is a set of species that is possibly also present in the matrix of regrowth, logged over forest and fruit plantations around the fragments including invasive tramp ants. In Labuk Road Forest Reserve at least three tramp ants (Schultz & McGlynn, 2000) were recorded: *Monomorium pharaonis, M. floricola* and *Anoplolepis gracilipes*, the last two neither present in Sepilok Forest nor in Kebun Cina. The increasing invasion of tramp species and ants of the surrounding agricultural matrix with smaller fragment size keeps the recorded species number of all studied forest fragments at a similar level although size varies considerably. Therefore an analysis of community composition is more informative than the comparison of mere species numbers.

As the decline in abundance in some ant species in the smaller forest fragments was obvious, the question arose, if this reflects a reduction in population densities and affects the genetic diversity of species (Didham, 1996; Saunders, Hobbs & Margules, 1991). Under the supervision of J. Gadau, T. Bickel analysed the genetic variability of two ant species which showed a decline in abundance from the contiguous forest of Danum Valley to the smallest fragment of Labuk Road Forest: *Odontomachus rixosus* and *Pheidole annexus*. In both species nucleotide diversity is reduced in the smaller fragments however the degree of this relationship is related to a species specific dispersal pattern and colony structure. Although

this is just a first attempt to quantify the genetic loss in tropical forest remnants, the results are alarming and further examinations of this phenomenon are urgently needed.

Unfortunately, the species richness and community patterns in other animal or plant groups in Sepilok Forest or other forest fragments in Sabah compared with those of larger primary forests in the region are unstudied up to now. If the pattern observed in ants of the leaf litter and lower vegetation are confirmed in other groups and different forest fragments, large areas of Sabah would have lost a major portion of their biodiversity as most of the remaining primary forest is conserved in small to medium sized Virgin Jungle Reserves, especially in the lowlands in the east with Sepilok Forest presenting one of the bigger fragments. This rate of biodiversity loss in comparatively large fragments contradicts estimates, that even isolates < 100 ha can retain a relatively large proportion of their biodiversity even decades after isolation (Turner & Corlett, 1996).

The fragmentation studies in Brazil and elsewhere revealed, that the matrix habitat surrounding the forest isolate is important for the remaining species richness in the fragment as it allows or prevents dispersal from distant source pools and colonisation of the isolate (see above). In East Sabah, large areas of rain forest have recently been clear cut and transformed into oil palm plantations which now separate forest isolates. The following chapter analyses the ant community found in oil palm plantations to evaluate their status as a dispersal barrier between forest fragments.

9   Ant Communities in Oil Palm Plantations

9.1   Introduction

The lowland rain forests of Sabah have been a target of large scale logging operations during the last decades because of the commercial value of dipterocarp trees and thus virgin forest is almost depleted outside conservation areas. A substantial part of the area formally covered by extensive forests has been converted into production forest of some exotic tree species which can be used for pulp and paper production. Large scale plantation forestry started in Sabah in 1974 (Chey, Speight & Holloway, 1992). By 1999 about 138 400 ha, ca. 2% of Sabah's land area were planted with forest plantation species (Chung *et al.*, 2000). Half of this area is now covered by the fast growing exotic tree species *Acacia mangium.* In the last 30 years the conversion of forest to agricultural land has also expanded rapidly, especially the establishment of plantations of the oil palm, *Elaeis guineensis*, a native wetland species from West Africa.

The oil palm was introduced into Southeast Asia in 1848 through Bogor Botanic Gardens, where one of the four original 'mother' palms can still be seen (MacKinnon *et al.*, 1996). The valuable crop serves the fastest growing industry in the state: in 1995 it accounted for 65% of the total crop area in Sabah, generating an income of US$ 0.6 billion for only one year (Chung *et al.*, 2000). Oil palm plantations are today stretching all over the flat terrain on the east coast and most of the lowland rain forest has been converted into a monoculture of immense dimensions. Oil palm plantations are only commercially viable on a large scale because the fruits are perishable and need to be processed quickly after harvesting (MacKinnon *et al.*, 1996). In 2000 about 1 million ha were covered by oil palm plantations, ca. 15% of the total land area of Sabah. Oil palm monocultures have to be well maintained with regular pruning, manuring and pest control (Chung *et al.*, 2000). Harvesting and pruning can be conducted as frequently as every 10 days, manuring occurs twice a year and herbicides are applied up to three times a year while insecticides are used whenever considered necessary.

It has been estimated that by 1990 24% of the lowland tropical rain forest on Earth had been cleared to create agricultural land (Turner & Corlett, 1996). The remaining wooden debris and some trees catch fire easily, especially in dry ENSO years. The extensive fires in Borneo in 1998 were mostly associated with agricultural and land clearing operations (Cao, 2000; Chazdon, 1998; Whitmore & Sayer, 1992), in Sabah often related to the establishment of oil palm plantations.

The forested land is completely cleared of vegetation and then often terraced for the establishment of an oil palm plantation. The soil in the plantations lacks a thick humus and leaf litter layer because of erosion of the top soil associated with high surface water runoff, which reaches more than double the values measured on land under forest cover (MacKinnon *et al.*, 1996). Together with high temperatures especially in the young, open plantations and compacted soils due to the use of heavy machinery, the habitat for ground dwelling ants is very different from the forest interior and one expects changes in the community composition.

9.2   Methods

Ground dwelling ants were collected in four oil palm plantations: in the Mayvin oil palm estate and plantations near Tawai Hills Forest Reserve, Deramakot Forest Reserve and Sepilok Forest Reserve (Fig. 50).
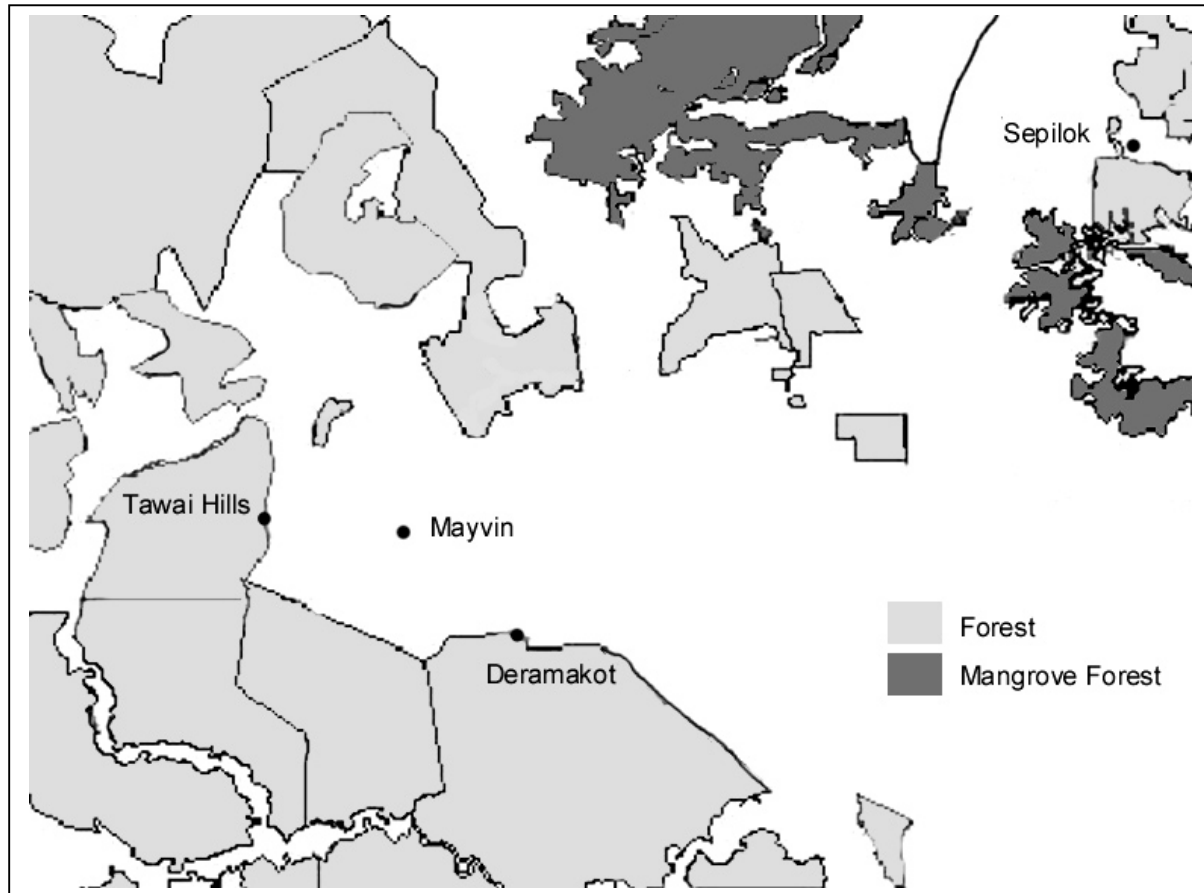
Fig. 50   Location of the oil palm plantations where the ground dwelling ant fauna was sampled. 'Forest' comprises primary and logged over forest. Most of the remaining non forested landscape is covered by oil palm or forest plantations.

Mayvin estate is situated in the core of a very large plantation area between the village Telupid and DFR. The oil palm plantation where sampling was undertaken is about 8-10 years old with palm trees reaching 8 m in height. Undergrowth existed in the form of various grasses and herbs (e.g. *Panicum* spp*., Mimosa pudica*), distance to the Tawai Hills Forest Reserve is about 2 km. The Tawai transect stretched from the logged over forest of the Tawai Hills Forest into an oil palm plantation. This plantation was 5-7 years old, palm trees were about 3-5 m in size, the undergrowth was open and bare ground mostly visible. The same situation was present in the Deramakot transect, which stretched from DFR into a plantation. The Sepilok transect ran from the forest entrance to research plot K* (see Fig. 5) into an old abandoned oil palm plantation (ca. 15-20 years). The palm trees reached up to 10 m in height, and various bushes, herbs and saplings were present forming a comparably dense undergrowth. However there was no substantial leaf litter layer present inside this plantation as well.

Due to the absence of leaf litter in oil palm plantations it was impossible to use litter sifting and Winkler-extraction as a quantitative sampling method for ants. Alternatively I therefore attracted ground dwelling ants with baits consisting of canned tuna in oil and collected them manually. Baits were left for 2 h to attract ants and were checked every 30 min. Baiting was conducted along transects of various lengths (Tab. 31).

Tab. 31   Configuration of the oil palm plantation transects.

Plantation transects	Number of bait sites	Transect length (m)	Distance between bait sites (m)
Sepilok 1	10	250	25
Sepilok 2	15	150	10
Sepilok 3	15	150	10
Tawai 1	15	500	50
Tawai 2	15	150	10
Tawai 3	10	1 000	100
Deramakot 1	15	150	10
Deramakot 2	10	1 000	100
Mayvin 1	10	200	20

In all plantations with forest contact, two bait sites were established within the forest and 13 in the oil palm plantation. The transects were 150 m in length with bait sites every 10 m. Additionally, ants were sampled in 1 000 m transects with bait sites every 100 m in Deramakot and Tawai and 500 m transects with a distance of 50 m between bait sites in Tawai to cover the variation in the present ground dwelling ant community over a longer distance. The core area of Mayvin was sampled along a 200 m transect with baits every 20 m. All transects followed a trail or dirt road into the plantation except for the Sepilok 3 transect which was established by cutting through dense vegetation. Tuna baits were placed at a distance of 5, 10 and 15 m from the access trail/road to avoid possible disturbance by humans or machinery. All oil palm plantations were sampled between March-April 1999 and 2000.

9.3   Results

9.3.1   Taxonomic structure of the total community

The total ground ant community collected in the oil palm transects including forest interior bait sites consisted of 41 species in 20 genera and four subfamilies (Tab. 32).

Tab. 32   Species and genera number (proportions of total in %) in the different subfamilies in the community of ground dwelling ants in oil palm plantations.

Subfamilies	Genera	Species
Myrmicinae	11 (55.0)	20 (48.8)
Formicinae	4 (20.0)	10 (24.4)
Ponerinae	3 (15.0)	3 (7.3)
Dolichoderinae	2 (10.0)	8 (19.5)
Total	**20**	**41**

Most species and genera were found in the Myrmicinae, followed by Formicinae, Dolichoderinae and Ponerinae. No individual of the subfamily Cerapachyinae was collected in the plantation transects. When the ant genera were ranked after the number of species

included (Tab. 32) six genera comprise more than 5% of all species *(Paratrechina 7, Technomyrmex 5, Pheidole 4, Dolichoderus 3, Tetramorium 3, Monomorium 3).* 12 of the 20 genera included only one species.

Tab. 33 Ranking of the ant genera in the oil palm plantation community according to the number of species included. The proportion of species number of the genus to total species number is given in %. Ants collected at forest bait sites are included.

Genus	Number of species	%	Genus	Number of species	%
Paratrechina	7	17.1	*Anoplolepis*	1	2.4
Technomyrmex	5	12.2	*Crematogaster*	1	2.4
Pheidole	4	9.8	*Diacamma*	1	2.4
Dolichoderus	3	7.3	*Lophomyrmex*	1	2.4
Monomorium	3	7.3	*Myrmicaria*	1	2.4
Tetramorium	3	7.3	*Odontoponera*	1	2.4
Pheidologeton	2	4.9	*Oecophylla*	1	2.4
Recurvidris	2	4.9	*Pachycondyla*	1	2.4
Acanthomyrmex	1	2.4	*Solenopsis*	1	2.4
Acropyga	1	2.4	*Strumigenys*	1	2.4

9.3.2 Species accumulation curves and species richness estimators

Species accumulation curves were calculated for ants collected only at bait sites inside the oil palm plantations to get an estimate of sampling efficiency (Fig. 51). For comparison, data of tuna baiting within Danum Valley primary forest with a similar sampling design were included (data kindly provided by T. Bickel).
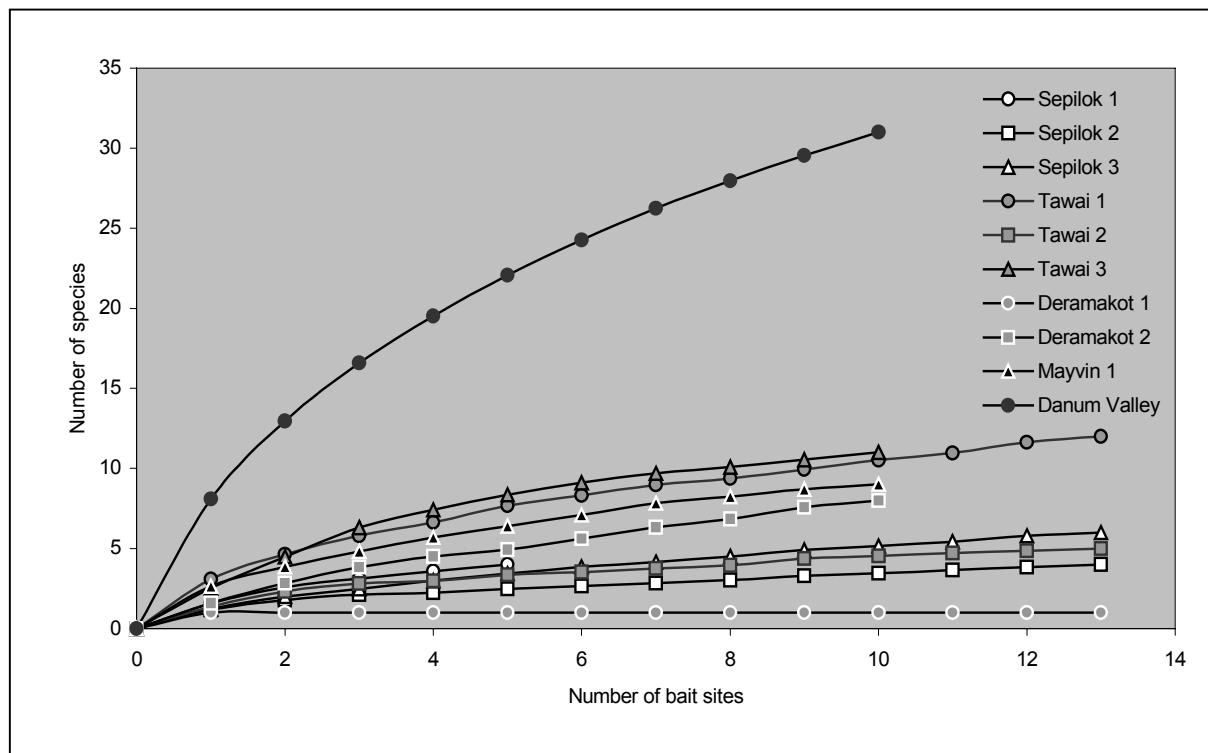
Fig. 51 Species accumulation curves for the different oil palm transects (only bait sites inside the plantations were included) and one transect in the primary forest of Danum Valley for comparison.

The randomised species accumulation curves of the oil palm plantations were always flatter than the accumulation curve of the primary forest, yielding far lower species numbers. The increase in species over bait sites was low in all plantations. In the Deramakot 1 transect only one species was recorded in all 13 bait sites.

For an additional analysis of sampling efficiency, the various species richness estimators (see General Methods) and their means were calculated for all transects. The values of sampling efficiency in the plantations reached a similar level as in the primary forest (Tab. 34). Although there were differences between the estimators, especially with the Chao2 estimator producing a very low value for the Deramakot 2 transect, the mean values of sampling efficiency were generally between 65-75%. This indicates a relatively intensive coverage of the ground dwelling ant community inside the oil palm plantations without many additional species to be expected with subsequent sampling.

Tab. 34 **Observed and estimated species and sampling efficiency *(%)* of the ant communities in the different oil palm plantation transects, the primary forest of DVCA and the total number of all bait sites in the oil palm plantations.**

Transects	Obs. spec.	ICE		Chao2		Jack1		Jack2		Bootstrap		MMMean		Mean	
Sepilok 1	4	7	*(57.1)*	6	*(66.7)*	6	*(66.7)*	6	*(66.7)*	5	*(80.0)*	6	*(66.7)*	6	*(66.7)*
Sepilok 2	4	7	*(57.1)*	5	*(80.0)*	6	*(66.7)*	8	*(50.0)*	5	*(80.0)*	4	*(100.0)*	6	*(66.7)*
Sepilok 3	6	17	*(35.3)*	13	*(46.2)*	10	*(60.0)*	13	*(46.2)*	7	*(85.7)*	8	*(75.0)*	11	*(54.5)*
Tawai 1	12	19	*(63.2)*	21	*(57.2)*	18	*(66.7)*	21	*(57.2)*	14	*(85.7)*	15	*(80.0)*	18	*(66.7)*
Tawai 2	5	8	*(62.5)*	7	*(71.4)*	7	*(71.4)*	8	*(62.5)*	6	*(83.4)*	6	*(83.4)*	7	*(71.4)*
Tawai 3	11	14	*(78.6)*	15	*(73.4)*	15	*(73.4)*	16	*(68.8)*	13	*(84.6)*	18	*(61.1)*	15	*(73.4*
Deramakot 1	1	1	*(100.0)*	1	*(100.0)*	1	*(100.0)*	1	*(100.0)*	1	*(100.0)*	1	*(100.0)*	1	*(100.0)*
Deramakot 2	8	17	*(47.1)*	21	*(38.1)*	13	*(61.5)*	16	*(50.0)*	10	*(80.0)*	13	*(61.5)*	15	*(53.3)*
Mayvin 1	9	14	*(64.3)*	10	*(90.0)*	12	*(75.0)*	11	*(81.8)*	11	*(81.8)*	12	*(75.0)*	12	*(75.0)*
DVCA	31	49	*(62.2)*	47	*(65.9)*	45	*(68.8)*	52	*(59.6)*	36	*(86.1)*	41	*(75.6)*	45	*(68.8)*
Total oil palm	**23**	**38**	***(60.5)***	**73**	***(31.5)***	**33**	***(69.7)***	**48**	***(47.9)***	**27**	***(85.2)***	**25**	***(92.0)***	**41**	***(56.1)***

9.3.3   Total estimated species richness of the plantation

The species richness estimators for the oil palm bait sites are listed in Tab. 34. The oil palm plantation ant community attracted at tuna baits comprised 23 species. If the Chao2 estimator is excluded due to its bias towards unique species which became already obvious in the previous chapters, the highest estimate for oil palm plantation ant species collectable with tuna baits on the ground was 48, the lowest 25 species. The slope of the species accumulation curve for all bait sites within the oil palm plantations (Fig. 52) was getting flatter at the end of sampling, increasing in only one species in the last 10 bait sites (30 baits). This confirms the results obtained from the species richness estimators of the transects, that additional sampling in oil palm plantations would produce only a small number of new species.
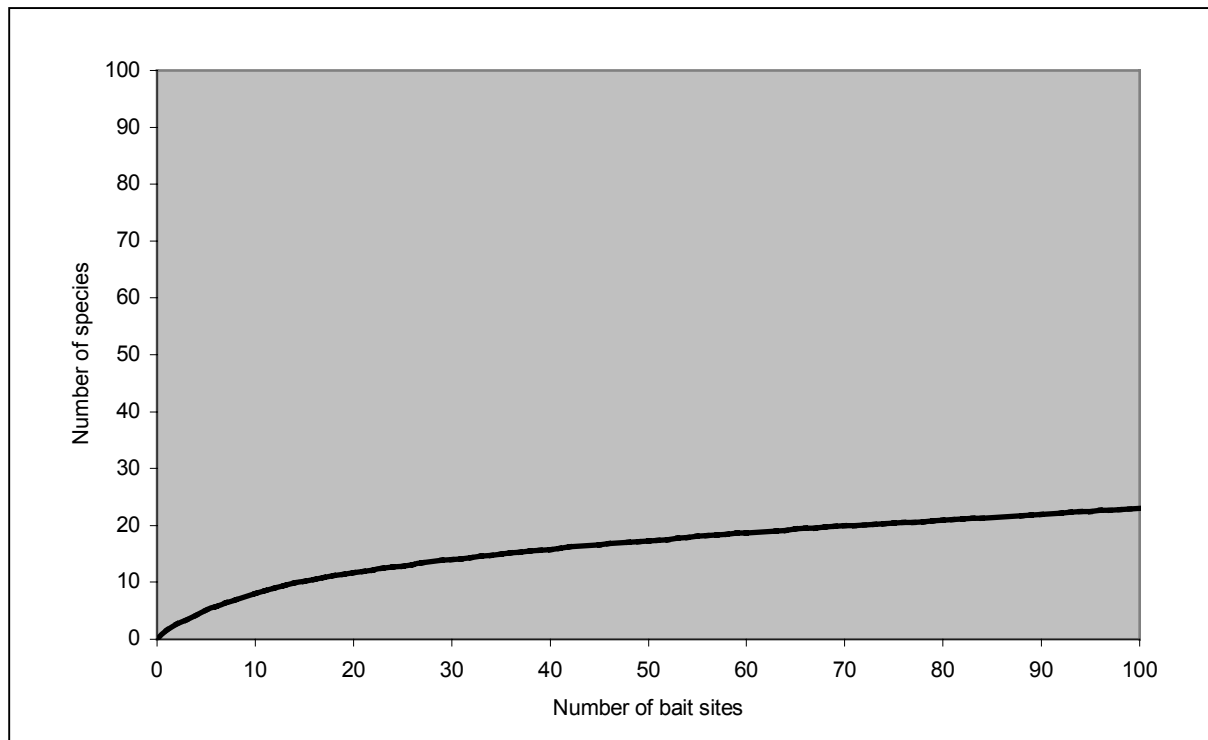
Fig. 52   Species accumulation curve of all bait sites within oil palm plantations (N = 100).

9.3.4 Species numbers in plantation areas and transects

For an analysis of the species numbers in the oil palm plantations, the bait sites situated within the forests were excluded. Although the number of bait sites was different among the different oil palm plantations, species numbers approached similar values (Tab. 35).

Tab. 35 Number of species in the different plantation sites. The bait sites in the forest are excluded.

Plantations	Number of bait sites	Number of species
Tawai	36	15
Sepilok	31	11
Deramakot	23	8
Mayvin	10	9

The similarity in species number became even more obvious when the different transects in the plantation areas were analysed (Tab. 36), although the longer transects (500-1 000 m) yielded more species.

Tab. 36   Number of species in the different oil palm plantation transects. The bait sites situated in the forest were excluded.

Plantation transects	Number of bait sites in the plantation	Number of species
Sepilok 1	5	4
Sepilok 2	13	4
Sepilok 3	13	6
Tawai 1	13	12
Tawai 2	13	5
Tawai 3	10	11
Deramakot 1	13	1
Deramakot 2	10	8
Mayvin 1	10	9

9.3.5   Comparison of oil palm plantation with the forest communities

After the transect bait sites situated inside the forests were excluded total species number decreased to 23 in 14 genera inside the oil palm plantations. Even if 13 of the 23 species discovered in the oil palm plantations were also collected on the forest floor (Tab. 37), most of them were only present at very few of the 100 bait sites, except for *Technomyrmex g*.

Tab. 37   Ant species collected in the oil palm plantations, their occurrences at the bait sites in the plantation and in Winkler litter samples in all forests.

Species	Plantation (Number of bait sites)	All forests (Number of litter samples)
Anoplolepis gracilipes	70	-
Dolichoderus k	17	-
Odontoponera denticulata	11	-
Monomorium f	4	-
Dolichoderus i	3	-
Technomyrmex i	3	-
Dolichoderus g	1	-
Oecophylla smaragdina	1	-
Paratrechina l	1	-
Crematogaster f	1	-
Recurvidris a	1	9
*Pheidole d**	1	9
Technomyrmex g	11	11
Pheidole sarawakana	2	20
Tetramorium noratum	1	32
Technomyrmex a	1	64
Monomorium a	2	70
Solenopsis a	1	115
Pheidole c	7	103
Pachycondyla b	2	276
Lophomyrmex bedoti	6	279
Monomorium floricola	10	excluded
Paratrechina h	1	362

Half of these species were frequently collected in the forest leaf litter and some have been characterised as common species in the previous chapters: *Monomorium a* was among the ten most abundant species in Kebun Cina, *Pachycondyla b* and *Paratrechina h* were recognised as generally common in the forest leaf litter of all forests, and *Lophomyrmex bedoti* was
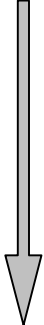
recorded in all logged forests in Deramakot and the forest fragments of Sepilok and Kebun Cina in high abundances. Although *Monomorium floricola* was excluded from the analysis in the previous chapters due to its contamination of the Winkler bags (see General Methods) it was sighted in the logged over forests.

Among the ten species of the oil palm plantation that were never recorded inside the forest *Anoplolepis gracilipes* was the most abundant species, collected at 70 out of 100 bait sites. It was present in all oil palm plantations and tended to numerically dominate baits. It was followed by *Dolichoderus k* and *Odontoponera denticulata*. *Oecophylla smaragdina*, the green ant was collected only at one bait site, because it seldomly forages on ground level, although the species is widely distributed in older oil palm plantations.

9.3.6 Gradient of species number from forest interior towards oil palm plantation

In order to compare the characteristics of the ground dwelling ant community, bait sites were established in the oil palm plantations and neighbouring forests except for Tawai 3, Deramakot 2 and Mayvin 1. Higher species numbers were obvious at the forest bait sites in Sepilok 1 and Deramakot 1 (Tab. 38). Species number at forest baits was in average 2.8 +/- 1.9 and at plantation baits 1.7 +/- 1.2. Most species attracted by the forest baits were not collected in the oil palm plantations. In the Sepilok 2 and Deramakot 1 transect only one species was recorded at the bait sites: *Anoplolepis gracilipes.*

Tab. 38   Number of species at the different bait sites in the transects. Forest baits sites are shaded in grey.

Bait site	Sepilok 1	Sepilok 2	Sepilok 3	Tawai 1	Tawai 2	Tawai 3	DFR 1	DFR 2	Mayvin 1	
1	5	1	1	3	3	3	1	1	2	**Forest**
2	8	1	2	3	1	3	4	1	1	**interior**
3	4	1	1	4	1	2	1	1	2	
4	2	2	1	4	4	4	1	5	4	
5	3	1	1	4	1	3	1	1	1	
6	3	1	3	2	1	1	1	1	1	
7	2	1	2	1	1	3	1	2	4	
8	2	1	2	5	2	1	1	1	6	
9	1	1	1	0	1	2	1	1	2	
10	0	1	1	1	1	6	1	2	1	
11		1	0	3	1		1			
12		1	1	1	1		1			
13		2	1	2	2		1			
14		1	1	3	1		1			**Oil palm**
15		1	2	3	0		1			**plantation**

9.4   Discussion

9.4.1   Taxonomic structure of the total community

Compared to the litter ant communities of the previous chapters, which were very similar in genus and species number to other inventories in tropical rain forests in Southeast Asia, the taxonomic composition of the fauna recorded along the oil palm plantation transects decreased drastically from 186 species in 48 genera to 41 species in 20 genera. No

Cerapachys species was recorded in the plantation, reducing the number of subfamilies to four. The change in taxonomic composition is most remarkable in the subfamily Ponerinae where only 3 instead of 14 genera and 3 compared to 38 species were recorded in the plantations. Ponerinae decreased in their proportion of genera in the community from 29.1% in the forest litter to 15.0% and in species from 20.3% to 7.3%. In contrast, the Formicinae increased in their proportion from 4.6% to 20.0% in genera and 10.7% to 24.4% in species (compared with the communities in the previous chapters). *Diacamma* and *Odontoponera* were present in the bait fauna of the oil palm plantations but excluded from the forest litter fauna due to their size (see General Methods). *Dolichoderus* is a vegetation ant genus typical of the forest and was therefore also not included in the previous analysis (see General Methods). The genera *Oecophylla* and *Anoplolepis* were only recorded in the oil palm fauna. Although *Pheidole* and *Tetramorium* were still present among the most species rich genera (including over 5% of the species), a shift in the proportions of genera compared to the forest interior became obvious: *Paratrechina* and *Technomyrmex* became especially important in the oil palm plantation and the Dacetine genera *Strumigenys* and *Pyramica* were not among the species rich genera anymore. Only one species of *Strumigenys* was collected, *Pyramica* was absent in the plantations. This might either be due to the fact that Dacetine ants are only rarely attracted by tuna baits (pers. observ.) or the restriction of their nests to the leaf litter layer (Brown, 2000), which is absent in the plantations.

9.4.2   Species accumulation curves and species richness estimators

Sampling efficiency was high in every single transect. The Bootstrap and MMMean estimators produced highest sampling efficiency and Chao2 the lowest. ICE, Jack1 and Jack2 were as before intermediate in their estimates. The mean values of sampling efficiency were similar to the bait community in Danum Valley and slightly lower than in the Winkler method studies. Together with the flat slopes of the accumulation curves at the end of sampling the high efficiency and low species number in the transects became obvious.

9.4.3   Total estimated species richness of the plantation

Estimates of the species richness of the oil palm ant community ranged from 25 to 48, not including the Chao2 value. The high estimates of species richness are due to a few dominant species and many species collected only once. The accumulation curve for the total oil palm community with an increase of only one new species in the last 30 baits clearly indicated a high sampling efficiency for this community. Hand collecting in the oil palm plantation during the bait experiment did not reveal any species not recorded at the baits. Because sampling was conducted in four different oil palm plantations in two years representing spatial and temporal replicates, the community of this habitat was extensively sampled in this study and should reflect a general picture of the situation all over Sabah.

9.4.4   Species numbers in plantation areas and transects

The number of species in the different transects did not vary much between the plantations. This was unexpected as the Sepilok, Tawai Hills and Deramakot transects were directly connected to forest, in the case of Sepilok even a primary forest, and forest ants could have established their nests in the plantation. Instead species numbers were similar to the Mayvin transect situated in the core of an oil palm plantation. Even age and vegetation structure had

no effect on ant species number. The abandoned Sepilok plantation with old palms, dense vegetation and no mechanical or chemical treatment produced as little ant species as recorded in the young plantations near Tawai Hills, where the ground had been completely cleared of forest 4-5 years before sampling. More species were only recorded in the three longer transects in the oil palm plantation (500 and 1 000 m).

9.4.5   Comparison of oil palm plantation with the forest communities

Only 13 of the 186 species (6.9%) recorded in the forest leaf litter (see previous chapters) were present in the oil palm plantations. This represents a tremendous reduction in species richness. Furthermore, most of these forest species were only occasionally collected in the plantations with the exception of *Technomyrmex g*, which was encountered at 11 of 100 bait sites. The forest species encountered in the plantation were generalistic litter ant species as *Pachycondyla b* and *Paratrechina h* or species commonly found in fragments *(Monomorium a)* or generally disturbed forest *(Lophomyrmex bedoti)*. But even *L. bedoti,* recorded in high abundances in the most disturbed logged over forest in Deramakot was not really abundant in the oil palm plantation (6 of 100 bait sites). The oil palm plantation ground ant community was characterised by three common species only: *Dolichoderus k*, *Odontoponera denticulata*, the sister species of *O. transversa*, a species mostly recorded from the forest interior and *Anoplolepis gracilipes*, present in all plantations at 70% of the total bait sites. *A. gracilipes* has been recognised as a tramp species (Schultz & McGlynn, 2000).

The geographic spread of tramp species is tied to human activities. *A. gracilipes* was originally confined to East Africa but from 1960 onwards a fast extension of its range over Madagascar and along the African coast into the Indian subcontinent took place (B. Bolton, pers. comm.). The ant reached Southeast Asia at the beginning of the 1980s and was soon recognised as an invasive species which moves into natural habitat and outcompetes native ant species (Schultz & McGlynn, 2000). Another tramp species, *Monomorium floricola* (Delabie *et al*., 1995; Schultz & McGlynn, 2000) was fairly common in the oil palm plantation, but was also recorded in logged forest interior. The other ant species restricted to oil palm plantations were only occasionally encountered, suggesting the formation of exclusive territories of the most abundant species.

9.4.6   Gradient of species number from forest interior towards oil palm plantation

From the species numbers at the bait sites along the transects, the difference between forest interior and oil palm plantation became especially obvious in the case of the Sepilok 1 transect, where much more species were collected inside the forest. The decrease in species number is very sharp and amazing in this case as the abandoned plantation supports a dense undergrowth where one would expect more ant species to be present. Not only was the species number slightly higher at the bait site inside the forest but also the composition of the community there was very different. The total fauna collected in this study consisted of 41 species, but 23 were only found in the oil palm plantation. This leaves 18 species recorded at the 15 forest bait sites. The fact, that 43.9% of all species were recorded at 13.0% of the total bait sites serves as another argument for the severe decrease in species number in the plantations. It is also interesting to realise the domination of *Anoplolepis gracilipes* in Sepilok 2 and Deramakot 1, where it is the only species recorded at most of the bait sites.

In summary the oil palm plantation ground ant community was severely reduced in species richness, regardless of age or undergrowth cover and 50% consist of species that were not recorded in the forest. Forest interior species were mostly common generalists or species typical of disturbed habitat, but they did not reach high abundances in the plantations. The community is characterised by the occurrence of tramp species and a few dominant species, especially *Anoplolepis gracilipes*.

Hitherto existing studies on ant communities in plantations were conducted in comparatively shady cacao plantations. In Peninsular Malaysia in 18 cacao plantations only 39 species of ants were recorded (Maryati & Chung, 1995). The composition at subfamily level revealed 14 species in the Formicinae (35.8%), 11 species in the Myrmicinae (28.2%) and only 5 species belonging to the Ponerinea (12.8%). This reduction in ponerine ant species number in the cacao plantations is similar to that of the examined oil palm monocultures. In Bahia cacao plantations, including old and abandoned plantations, only 69 species were recorded in the leaf litter ant community (Delabie & Fowler, 1995). In Costa Rica plantations of various crop showed a reduced diversity and a species richness of less than 50% of a forest ground ant community (Roth & Perfecto, 1994). The transition from primary forest to plantation or pasture severely affected the ant community in Peru. In this anthropogenic habitat only 50% of the species compared to a primary forest were present (Verhaag, 1991). In the Atlantic rain forest of Brazil, a transect from open grassland into a forest fragment revealed highest species richness in the forest interior and lowest in the open, with a clearly distinct set of species (Majer, Delabie & McKenzie, 1997).

Apart from the dramatic reduction in species richness and diversity compared to forests, the plantation ant communities were also characterised by a few dominant ant species, with some tramp species in this group. Four ant species were found to be dominant in Bahia in cocoa plantations and two of those have been recognised as tramp species (Delabie & Fowler, 1991; Delabie & Fowler, 1995). Six species were dominant in the community and occurred in frequencies of over 50% in the Malaysian cacao plantations (Maryati & Chung, 1995). One of those, *Anoplolepis gracilipes*, was also recorded among the dominant species in the oil palm plantation and was generally found to be a dominant species in many ant communities in disturbed habitat all over the world (Majer, 1993). *A. gracilipes* forms polydomous colonies with many nests which are connected with routes and multiple queens present in each nest on Okinawa (Yamauchi & Ogata, 1995). There, open land was predominantly occupied by tramp ants and forest contained endemic species. Another species recorded in the oil palm plantations in Sabah, *Monomorium floricola*, was among the dominants in the Costa Rica cacao plantation study (Roth & Perfecto, 1994) and also in the open grassland in Brazil (Majer *et al*., 1997).

Generally, the community pattern in the oil palm plantations was very similar to those recorded in the other studies, although species reduction seemed to be more severe. The few numerically dominant species in the plantations occupied large territories which was especially obvious in the 1 000 m transects. *Anoplolepis gracilipes* and *Dolichoderus k* were alternatingly recorded over a few hundred meters. Large dominant territories were also recorded in the weaver ants (genus *Oecophylla)* (Hölldobler, 1983; Hölldobler & Wilson, 1977a; 1977b) leading to the theory of an arboreal ant mosaic in plantations (Hölldobler,

1986; Hölldobler & Wilson, 1990; Majer, 1976), which was recently disputed to occur in primary rain forests (Floren & Linsenmair, 2000). The ground ant community in the oil palm plantation with its reduced diversity and few dominant species agrees well with the dominance-impoverishment rule (Hölldobler & Wilson, 1990): 'the fewer the ant species in a local community, the more likely the community is to be dominated behaviourally by one or a few species with large aggressive colonies that maintain absolute territories'. This kind of community structure is explained by a physically harsh habitat which supports only a few generalistic species expanding ecologically and occupying a wide range of nest sites and food items. The most influential factor on the distribution of ants as well as their competitive performance in an experimental study in Puerto Rico was microclimate (Torres, 1984). Forest ants had a lower tolerance to high temperature than ants from non-forested areas. In general, ponerine ants withstood high temperatures less well than ants in the subfamilies of Formicinae, Myrmicinae and Dolichoderinae. This might be one reason for the change in community composition with the reduction of the Ponerinae subfamily in the oil palm plantation compared to the forest interior. Another feature of the open habitat was the occurrence of more aggression: interspecific combats were recorded at 6% (N = 464) of the baits in forest and at 38% (N = 1 056) of non-forested habitat (Torres, 1984).

The species richness and diversity of animal communities were also measured in other taxa in different types of plantations: in a comparison of the beetle communities of primary, secondary, plantation forests and oil palm plantations (Chung *et al*., 2000) found lowest abundances and species richness and a very different community structure with a few numerically dominant species in the oil palm plantation. Trophic guilds were very different and presumably instable due to the heavy maintenance work including pruning, manuring and pest control (Chung, 1997). Species richness was higher in *Acacia mangium* plantations with a dense undergrowth and less maintenance. Forest plantation kept a considerable proportion of the moth fauna (Chey *et al*., 1992), although *Acacia* plantations had lower species numbers (726 spec.) compared to *Eucalyptus* plantations (872 spec.) or secondary forest (1 048 spec.) (Chey, Holloway & Speight, 1997), and showed the lowest diversity (Holloway, Kirk-Springs & Chey, 1992). The heaviest impact on the moth community was due to clearance before planting (Intachat *et al*., 1997) and a loss of indigenous plant species in the vegetation. Undergrowth species diversity was the only correlate to geometrid moth diversity in a study along a disturbance gradient in Sabah (Beck *et al*., in press). In a study on mammals, forest plantations produced a massive loss of diversity and only a few of the most adaptable species were recorded in *A. mangium* plantations (14%) (Laidlaw, 1996).

All these studies are in concordance with the pattern observed in the ground living ants in oil palm plantations. Unfortunately, except for beetles, no group was studied in oil palm plantation so far, but we are safe to assume that the reduction in species richness and diversity is more pronounced than in forest plantations. It becomes very clear, that conversion into oil palm plantations alters ground ant and beetle communities dramatically with extreme reductions in diversity, a numerical dominance of a few species and in the case of ants the introduction of aggressive tramp species into the system which seem to establish large exclusive territories. The large scale establishment of oil palm plantations in Sabah produces a decline in ant diversity over a huge area. This loss of biodiversity should caution us against preliminary conclusions drawn from a few samples in one site, that the global loss of species

resulting from tropical deforestation may be an exaggeration of environmental activists (Belshaw & Bolton, 1993).

But oil palm plantations are also affecting the litter ant species of the forest interior because they form a very efficient dispersal barrier. The queens of forest ants may be killed by high temperatures during dispersal from forest remnants into plantations and/or are in most cases unable to establish colonies in the harsh conditions encountered there. This leads to a very effective isolation of many primary forest fragments that persist in the form of small Virgin Jungle Reserves in a matrix of oil palm monocultures in the lowlands of Eastern Sabah.

10 Correlation with Environmental Parameters

10.1 Introduction

So far we observed a decline in species richness, diversity and composition of leaf litter ant communities along the gradients of forest disturbance and size. In search of causal factors for the observed pattern I examined the effect of different environmental parameters on the ant communities (see Microclimate and Leaf Litter).

Ant communities are composed of populations of different species, which are clearly regulated by three factors: (1) competition, (2) resources and (3) climatic conditions (Brown, 1973; Hölldobler & Wilson, 1990). (1) Competition, inter- or intra-specific regulates the access to resources. Due to small colony sizes of leaf litter ants in tropical rain forests not allowing domination of neighbouring colonies, interspecific competition by dominant species is supposedly absent (Kaspari, 1996a). Additionally, the litter used as nest material is continually rotting in the humid surroundings of a tropical rain forest which prevents the ants from establishing large, stable territories (Kaspari, 2000). (2) Resources for ant colonies are items used and depleted, such as food or nest sites. The distribution of resources is influenced by (3) climatic conditions like temperature and humidity. Nest sites, for example, might be too dry or wet and therefore not be usable although structurally acceptable. Foraging for food resources might also be limited by abiotic factors, for example if the leaf litter becomes too wet after heavy rains (Hölldobler & Wilson, 1990).

In order to find an explanation for the differences in ant species number in the study sites, conditions like soil and leaf litter humidity and temperature were measured as well as the leaf litter volume, a possible resource for leaf litter ants. Correlation analysis might provide us with an idea if and to which degree these variables affect the composition of leaf litter ant communities in tropical rain forests in Sabah.

10.2 Methods

The data for regression analysis have already been presented in the chapters on microclimate and leaf litter volume. Species numbers are obtained in the chapters on Forest Disturbance and Forest Size.

10.3 Results

10.3.1 Total species number:

To obtain the leaf litter ant species numbers and total volume of leaf litter per plot, the number of ant species was counted and the volume of leaf litter measured in every sample. These data exist for all plots (Danum Valley, the different forest types in Deramakot, Sepilok and Kebun Cina). A regression analysis was performed, which shows a highly significant correlation between species number and total leaf litter volume per plot ($df = 17$, $F = 9.68$, $p < 0.01$, $r^2 = 0.37$). In plots with higher litter volume, more species were recorded. Kebun Cina and two of the Sepilok plots are situated below the regression line, indicating that for the amount of leaf litter more ant species were expected.

$y = 1.22x + 42.33$
$r^2 = 0.37$
$p < 0.01$
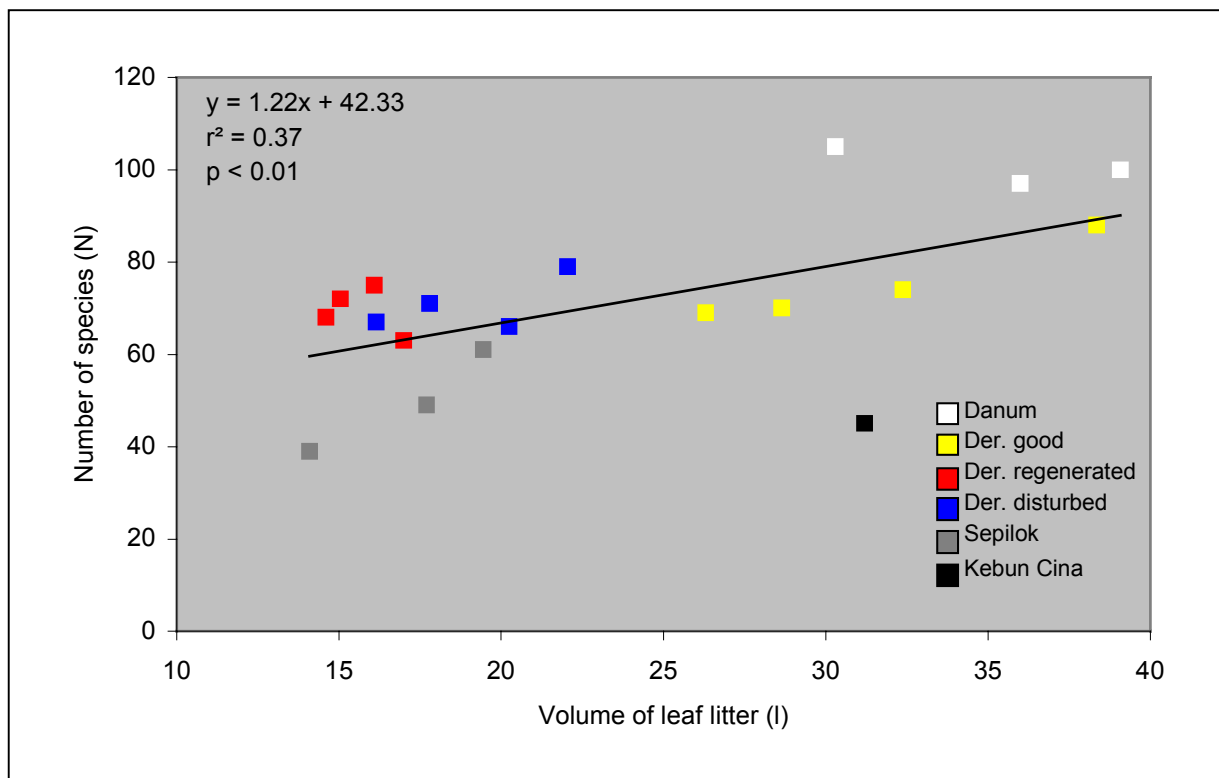
Fig. 53   Correlation of number of species and volume of leaf litter per plot (all replicates included).

10.3.2 Species number at the sampling sites

In 1999 microclimate was measured in the plots sampled to obtain temporal replicates. These were plot L in DVCA, plots A, E and H of the three different forests in DFR and plot K in SFR. Significant differences in temperature and humidity have been detected between the plots (see Environmental Parameters) as well as lower species numbers in DFR and the forest fragments (SFR and KCFR) in comparison to DVCA (chapters on Forest Disturbance and Forest Size). I performed a multiple linear regression analysis to assess the effect of habitat variables on species richness at a sampling site. The following independent variables were used:

- Mean litter volume (per 10 m²)
- Mean soil humidity
- Minimum soil humidity in the afternoon
- Mean litter humidity
- Minimum litter humidity in the afternoon
- Soil temperature
- Maximum soil temperature in the afternoon
- Litter temperature.

All statistical calculations were performed with the program Statistica 5.5 (StatSoft, 2000). A stepwise forward multiple regression of these variables with species number at the sampling sites was significant ($r_{mult} = 0.84$, $r^2 = 0.70$, $F_{3,26} = 20.38$, $p \ll 0.001$). The variables with most explanatory power were mean leaf litter humidity (partial correlation coefficient $\rho = 0.33$, $p = 0.047$), leaf litter volume ($\rho = 0.43$, $p = 0.002$) and leaf litter temperature ($\rho = -0.26$, $p = 0.071$ n.s.).
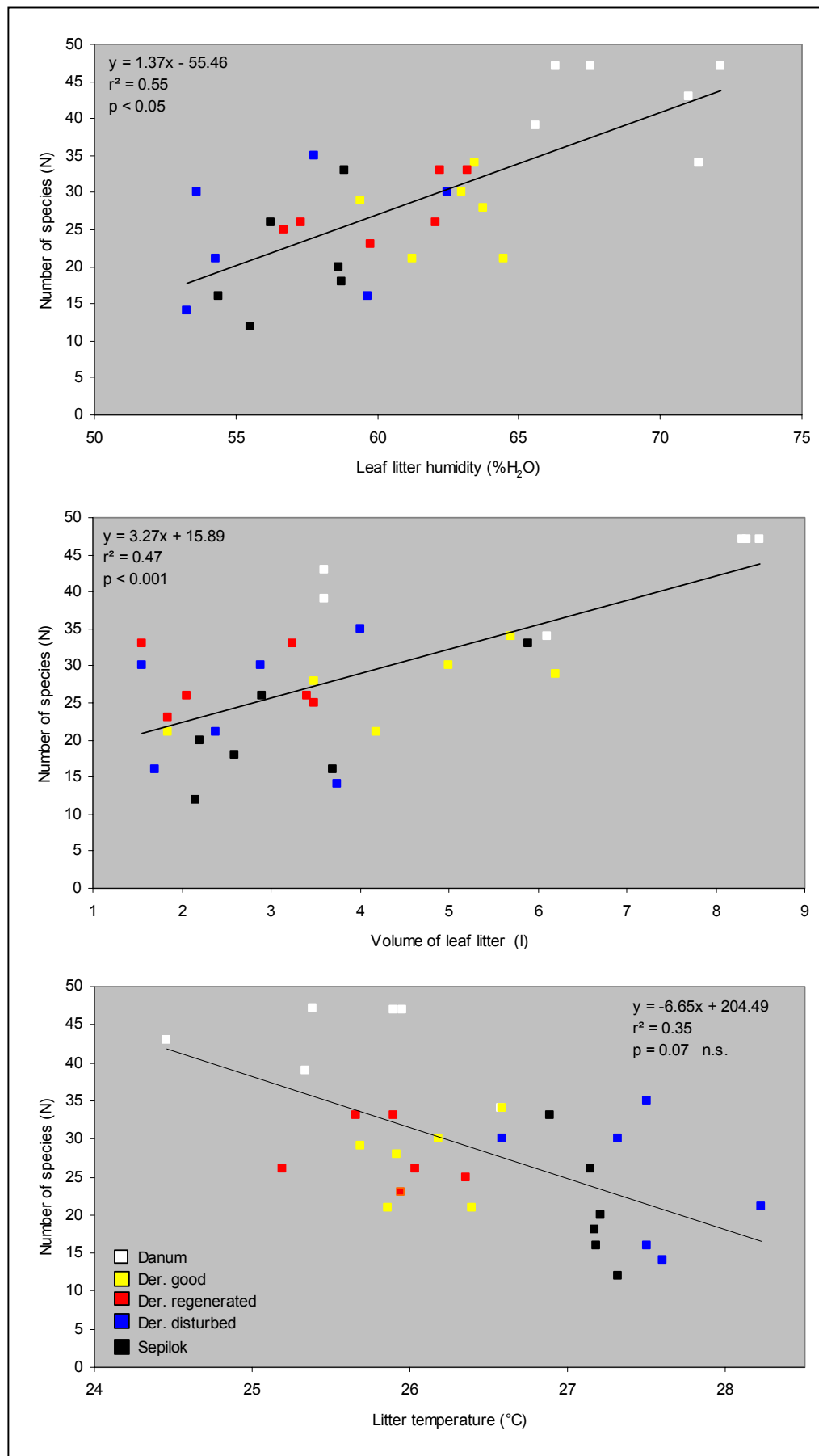
Fig. 54 Correlations of leaf litter humidity, volume and temperature with species number at the sampling sites.

Subsequently, I calculated linear regressions for the three variables (Fig. 54). All regressions were highly significant: species number and leaf litter humidity ($r^2 = 0.54$, $F_{1,28} = 32.97$, $p < 0.001$), species number and litter volume ($r^2 = 0.47$, $F_{1,28} = 24.97$, $p < 0.001$) and species number and leaf litter temperature ($r^2 = 0.35$, $F_{1,28} = 15.36$, $p < 0.001$).

The sampling sites of Danum Valley revealed highest litter humidity values and species numbers. Lowest humidity levels were recorded in Deramakot disturbed and Sepilok, with lower species numbers in the dry sites in Sepilok. The mean leaf litter volume regression showed high mean litter volumes and species numbers at three sites in Danum Valley while the three others revealed lower mean litter volumes but similar high species numbers. Lowest mean litter volumes per site were recorded in the disturbed and regenerated forests of Deramakot and Sepilok. The temperature regression showed lowest temperatures and high species numbers in the Danum Valley sites; highest temperatures in the leaf litter were measured in the disturbed sites of Deramakot followed by Sepilok Forest.

10.3.3 Species number and area

The size of a forest and the degree of isolation are among the parameters that have theoretically and often empirically an influence on the species richness of a forest fragment (Mac Arthur & Wilson, 1967; Saunders, Hobbs & Margules, 1991). Data on the degree of isolation and the time scale of fragmentation in the area were not available, contrary to area measurements of the forest fragments (see Study Sites). Nevertheless, Sepilok has at least been isolated since the 1960s when it was surrounded by rubber plantations (Fox, 1973). A correlation of forest size and mean number of species recorded in a plot (Danum Valley and Sepilok Forest N = 3, Kebun Cina N = 1) was highly significant ($r^2 = 0.99$, $F_{1,2} = 8\,987.95$, $p < 0.01$; Fig. 55).
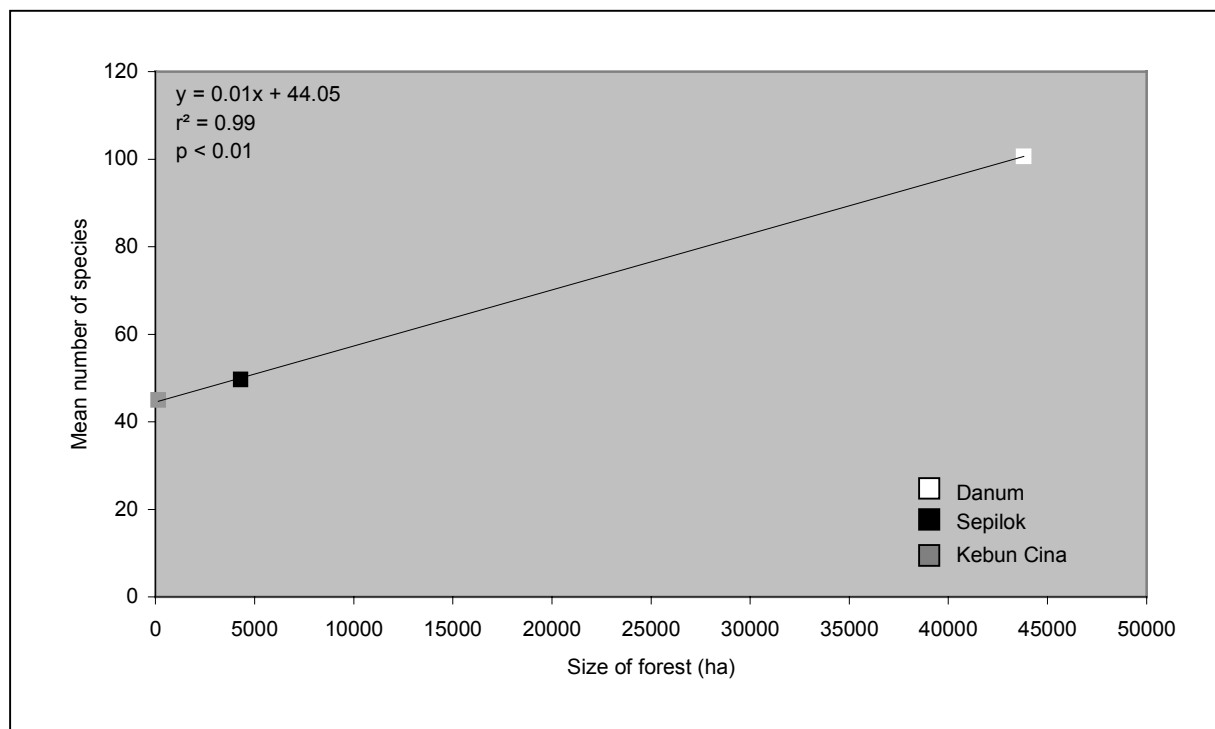
Fig. 55 Correlation of size of forest area with mean number of ant species per plot (DVCA and SFR N = 3, KCFR N = 1).

10.4 Discussion

10.4.1 Leaf litter volume

The leaf litter volume measured in this study is the fine leaf litter that falls through a sieve with 1 x 1 cm mesh size. It is fine leaf litter in contrast to other studies where biomass or depth is measured, but it can be assumed that the fine leaf litter volume correlates with all other measurements and might be an even better estimator of the habitat heterogeneity for ground dwelling ants (see Leaf Litter).

Leaf litter volume was significantly positively correlated with species number on the larger scale of plots (60 m²) as well as with sites (10 m²). In contrast, litter depth was not found to significantly affect litter ants species richness in Brazilian cocoa plantations (Delabie & Fowler, 1995) and litter amount was also not correlated to ant diversity in Costa Rica (Roth & Perfecto, 1994), probably due to difficulties in making accurate measurements in highly variable habitats and sites. The measurement of the heterogeneity of the litter habitat is not a simple task and needs, as well as the sampling of the litter ant community, a large sample size and scale. I would like to point out that the amount of leaf litter can be measured without any additional efforts in the Winkler method as it is the substrate transferred in and out of the extractors.

The correlate leaf litter is the habitat of leaf litter ants and it is therefore not amazing that species number correlates with its volume. The litter layer provides nest sites for many ant species nesting in cavities in twigs or fruits, between leaves or in large decaying logs in humid tropical rain forest (Kaspari, 2000). Here the fraction of species nesting in litter is largest (Wilson, 1959). Suitable nest sites were the mediating resource for the ant community in a temporal forest in Vermont (Herbers, 1989) and limited local patchiness of the twig nesting ant community in four neotropical forests (Kaspari, 1996b). In this community the number of nest sites doubled with the addition of bamboo twigs in the leaf litter. Apart from providing nest sites, the leaf litter is also the habitat where ants forage and it might be a correlate of food availability (Delabie & Fowler, 1995) with more prey related to a thicker litter layer. Litter is also a correlate of microclimate, because a thick layer buffers temperature and humidity much better than a thin layer.

10.4.2 Temperature

The two measured variables of microclimate itself, leaf litter temperature and humidity, were good correlates of species number at the sites. The effect of temperature in the leaf litter layer on species number was especially obvious in a comparison of the cool and species rich Danum Valley sites and the hot and species poor sites in Sepilok Forest and Deramakot disturbed. The variation of species number, especially in the hotter sites might be due to the fact, that ants were sampled over a larger area, covering more microhabitats whereas leaf litter temperature was measured at only two locations.

Direct measurements of temperature and ant species richness in tropical forests are scarce. In Costa Rica soil temperature was not correlated to ant diversity (Roth & Perfecto, 1994), although this was again discussed as a measurement artefact due to low sample size. Temperature affects ants in their distribution be it on a latitudinal (Kusnezov, 1957) or altitudinal gradient (Brown, 1973; Brühl, Mohamed & Linsenmair, 1999) as well as in their

behaviour (Roces & Nunez, 1989). Temperature also has a great influence on the nest site where the brood develops, although an ant colony can control its nest temperature by various mechanisms (Hölldobler & Wilson, 1990). Soil living ants for example are able to control the temperature inside the nest by shifting chambers to a greater depth, if temperature is getting higher (Hölldobler & Wilson, 1990; Petal, 1978). Ant species in tropical forests usually utilise small pieces of rotting wood and the leaf litter itself as a nest site, only a few nest entirely in the soil (Brown, 2000; Hölldobler & Wilson, 1990). Nest shifting is very risky for litter living ants and has been the cause of high colony mortalities in twig nesting ants (Byrne, 1994).

Ground temperature might be a critical parameter for a suitable nest site, especially during midday when maximum temperatures within sunflecks can reach 40-45°C in the litter within minutes (Levings, 1983; Torres, 1984). In a laboratory experiment Southerland (1988) could demonstrate that higher temperatures increase the death rate in *Aphaenogaster rudis* workers significantly. But high surface temperatures also limitate the colony and foraging activity. Forest ants showed a low tolerance to 45°C compared to open habitat species and especially ponerine ants performed less well in higher temperatures (Torres, 1984). Levings (1983) observed several ant species which died when caught foraging in a sun fleck. The occurrence of places suitable for nesting or foraging is a result of interactions between temperature and desiccation (Levings, 1983).

10.4.3 Humidity

Mean humidity levels in the leaf litter were positively correlated with ant species richness at the sites, although only recognised as a trend in the stepwise regression model. The effect of humidity was especially obvious when comparing the wet and species rich sites of Danum Valley with the dry and species poor sites of Deramakot disturbed and Sepilok Forest. Positive correlations between litter moisture and the abundance of ants and other groups of soil arthropods such as Coleoptera, Collembola, Homoptera, Isoptera and Diplopoda have been demonstrated in Panama (Levings & Windsor, 1984). More ant species and individuals were recorded in wetter places (Levings, 1983). Moisture availability is an important contributor to species richness by affecting foraging activity. Smaller ants tend to be more active in cooler and moister microclimates, larger ants tend to be microclimate generalists (Kaspari, 1993). In a watering experiment during the dry season on Barro Colorado Island ant activity and foraging time increased significantly in the wet treatments (Levings, 1983). But humidity might also influence the distribution of nest sites as demonstrated in Panama, where dry sites had lowest nest densities (Levings, 1983), although there exist different control mechanisms to keep moisture levels in ant colonies at a relatively constant level (Hölldobler & Wilson, 1990). An increase in food availability was also recognised by Levings (1983): higher abundances and activity levels in some soil arthropods were recorded with higher moisture levels increasing the prey availability for ground dwelling ants.

Although it is impossible to separate the direct and indirect effects of leaf litter volume and microclimate, it could be illustrated that both have an influence on ant species number in the leaf litter. Additionally not only higher species richness might be related to microclimate but also community composition and its stability over time. The temporal community replicates of Danum Valley were closely associated whereas in Sepilok Forest and the more disturbed forests of Deramakot the distance between communities was higher, although species number

was similar (see previous chapters). Therefore turn over might have been lower in the buffered forest of Danum Valley, where the litter layer was constantly wet and humid compared to the other forests.

10.4.4 Size of forest

In forest fragments, microclimate may have changed with an effect on animal communities. Additional factors influencing species richness and distribution are time since isolation, distance to other forests, size, shape and position in the landscape (Saunders *et al*., 1991). As total species number in the forest isolates was substantially lower than in the logged over forests, other factors apart from microclimate might play a role. The only measurement available in this study was the size of the forest fragments. Although only three forests are included in the analysis and a comparison is difficult as Danum Valley is connected to logged over forest, whereas Sepilok Forest and Kebun Cina stand isolated, I found a positive correlation of size with mean plot species number. The high r² value is interesting to note and might hint to another variable affecting ant species richness in forest isolates apart from microclimate and leaf litter volume.

Resources for specialist might be lacking in small forest isolates as e.g. prey for ants that specialise on certain arthropod groups like wood lice or termites or nest sites in special environmental conditions or of special structure. For rare species the size of a forest is also limiting the minimum viable population size leading to an extinction if the forest remnant is too small or too isolated from source pools. Certainly the size of a forest and not only its structure have an influence on the preservation of biodiversity and should be included as an important parameter in every conservation planning concept.

11   Leaf Litter - Shade Experiment

11.1   Introduction and experimental design

The forest floor of tropical primary rain forest is characterised by a thick layer of fine leaf litter and deep shade. In the logged over forest in contrast, the litter layer is reduced and the canopy is more open causing higher temperatures and lower humidity levels in the forest interior. The influence of leaf litter volume and the two components of microclimate, temperature and humidity on the number of litter ant species has been demonstrated in the previous chapter and other studies (Levings, 1983; Torres, 1984). The correlative evidence obtained did not allow me to untangle the possible interaction of the three components and therefore I conducted a field experiment with litter and shade as separate treatments.

The experiment was carried out in tree fall gaps in the primary forest of Danum Valley, where the largest potential ant species pool is present for the establishment of communities in four different treatments (two-way crossed design, similar to (Perfecto & Vandermeer, 1996)):

(1) shade & leaf litter

(2) shade & no leaf litter

(3) light & leaf litter

(4) light & no leaf litter

For the shade treatment a tent-like nursery shading (50% shade), which allowed precipitation to reach the ground was installed over the plots. The litter treatment was started in April 1998 with the input of 25 l of fine leaf litter collected during the general sampling in DVCA, which had been sun-dried for 5 days and was free of living arthropods. During the experiment, leaf litter collected monthly from the two shading roofs was divided equally between the two litter treatments. Great care was taken that no ants would be carried into the system. The area for each of the four treatments was 5 x 5 m, allowing an arrangement of all four treatments in one large gap. Distance to the forest and between treatments was 1-2 m (see sketch, Fig. 56).
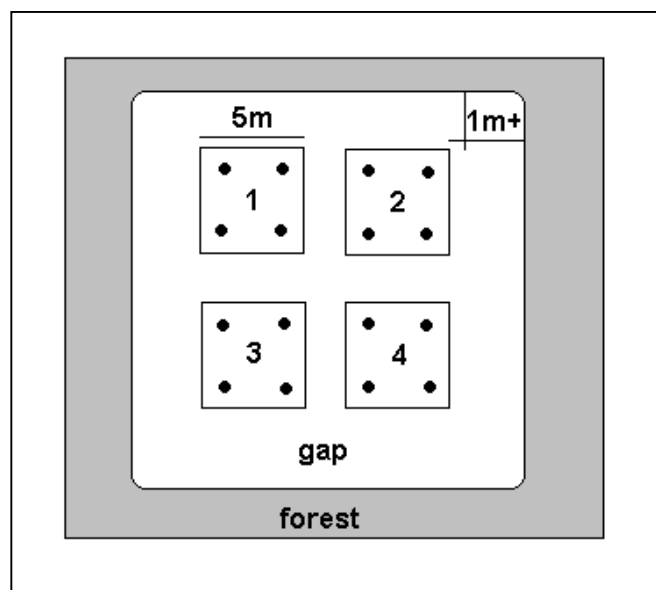
Fig. 56   Sketch of litter-shade experiment. Numbers refer to treatments. Tuna baits for sampling ●

In mid April 1998 the experiment was started in five large tree fall gaps not older than one year (see Fig. 57 and Fig. 58, Tab. 39). At the time these tree fall gaps were the only large ones within a radius of 2 km around the field station which represented the limiting factor for replication of the experiment.

Fig. 57   Installation of shading roofs in gap 1.
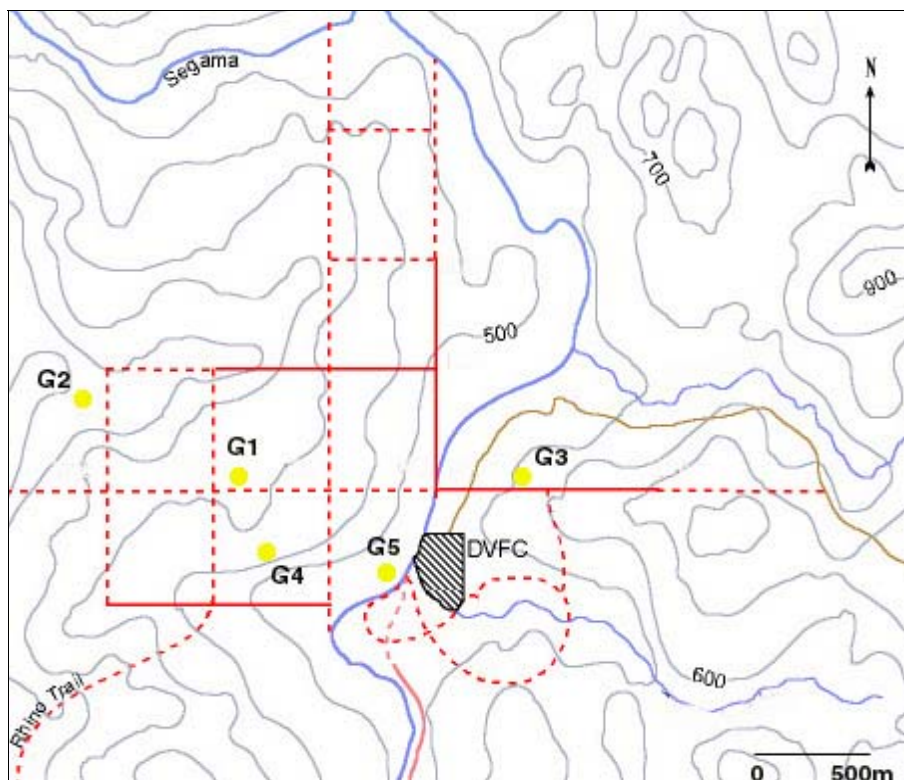
Fig. 58   Location of experimental gaps in DVCA (Heights in feet a.s.l.).

Tab. 39 Description of litter - shade experiment sites.					
Gap	Location	Age at start	GPS Position	Size	Description
1	West Trail, W9	1 year	N 4°57.918' E 117°47.699'	18 x 12 m	completely cleared
2	West Trail, 100 m west of W15, N 4	1 month	N 4°58.181' E 117°47.285'	25 x 20 m	vegetation and large tree trunk between treatments
3	East Trail, 20 m off E2	8 months	N 4°57.942' E 117°48.365'	15 x 12 m	vegetation between treatments, L shaped
4	Hydrology Trail ca. 300 m off W7	1 month	N 4°57.942' E 117°48.365'	25 x 20 m	large branches between treatments
5	Left bank of Segama River opposite camp site	2 weeks	N 4°57.815' E 117°48.056'	30 x 20 m	vegetation and large tree trunk between treatments

All gaps were cleared of small twigs and branches and within the treatments of all vegetation. At the start, Winkler samples of 2 m² were taken in each treatment to sample the already existing ant communities. Then the complete area in the gaps was lacking a deep leaf litter layer and was exposed to direct sunlight during the day. In April 1998 the ENSO event was still prevalent leading to extremely high temperatures and low humidity levels in the tree fall gaps. After half a year running time, new fine leaf litter was added in January 1999 to enhance the contrast in the litter treatments. Until April all treatment communities were sampled four times by using tuna baits. Baiting was used instead of litter sifting as the invasive litter sifting method would have had a high impact on the communities in the experiment by taking leaf litter and some colonies out of the system and damaging nests. Additionally after a few months there was not enough leaf litter present in treatments (2) and (4) for using the sifting method. Instead, four baits consisting of canned tuna were placed in each treatment in about one meter distance from the edges (Fig. 56) and every 30 minutes 5-10 workers of present ant species were collected for two hours. Sampling started again in January 2000 on a monthly turn and ended in April when 4 m² of treatment (1) were sampled by Winkler litter sifting in each gap. These end communities were only sampled in treatment (1) because only here a litter layer accumulated. The canopy openings in the tree fall gaps closed during the two years the experiment was running and the light treatment was less prevalent than at the start, although direct sunlight still reached the ground for a substantial period of time. In 2000 temperature in two gaps was recorded (gap 4: 16.3.-19.3.; gap 1: 18.4.-28.4.) with Celsi Pick[©] temperature loggers, which were placed directly on the ground. Two loggers were running in each treatment to avoid local temperature effects by sunflecks which were likely in the unroofed treatments. In the end recordings were pooled.

11.2 Results

11.2.1 Temperature

Mean, minimum and maximum ground temperatures of the pooled data were calculated in the different treatments in the two gaps (Tab. 40).

Tab. 40   Mean, minimum and maximum ground temperatures (in °C) recorded in the different treatments in gap 1 (10 d) and gap 4 (3 d).

Treatment	(1)	(2)	(3)	(4)
Gap 1				
Mean	24.10	24.11	24.68	24.88
Minimum	21.63	21.63	21.98	21.81
Maximum	28.23	28.77	32.11	36.96
Gap 4				
Mean	24.11	24.01	24.78	24.82
Minimum	22.51	22.33	22.68	22.51
Maximum	29.86	27.86	36.95	37.36

The temperatures recorded were similar in the two gaps. Treatment (1) and (2) showed about 0.5°C lower mean temperatures and also slightly lower minimum temperatures. The maxima recorded in treatments (3) and (4) were about 8°C higher than recorded in the shaded treatments (1) and (2). The differences of the shaded and non shaded treatments is also revealed in the daily mean temperatures (Fig. 59) with very similar temperature behaviour during the night but a sharp increase in treatment (4) reaching temperatures above 28°C around 11:00 h and rising further at noon. Temperatures in treatment (3) were rising more slowly and did not reach values as high as in treatment (4). The highest maximum value of ground temperature recorded by one logger in (4) was 38.4°C.
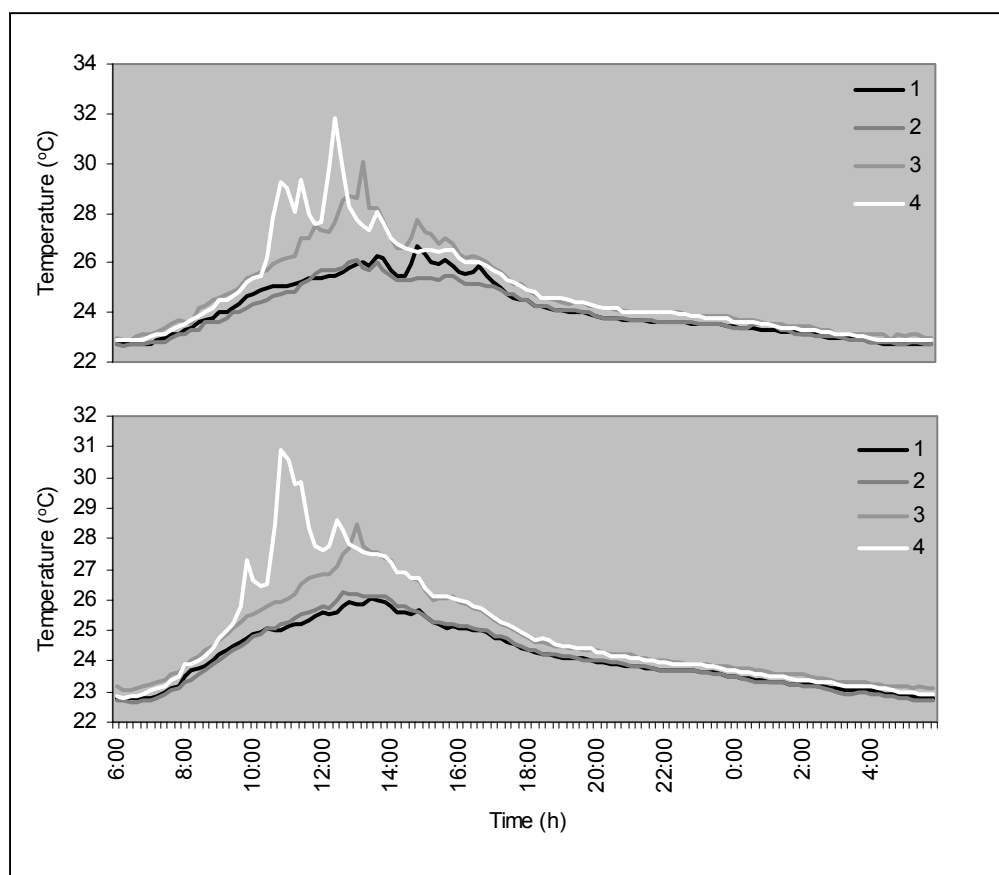

Fig. 59   Daily mean temperature in gap 1 (10 d) and gap 4 (3 d) in the different treatments (1: shade & litter, 2: shade & no litter, 3: light & litter, 4: light & no litter).

11.2.2 The ants in the treatments

Four different temporal images of the ant communities were received from my collections: At the beginning of the experiment in 1998 (termed start) I collected 2 m² of leaf litter in each treatment per gap and also used baits to collect the initial community. In 1999 and 2000 each treatment in each gap was sampled using tuna baits in four consecutive months adding up to 20 samples per year per treatment. In April 2000, leaf litter samples for Winkler litter extraction were collected in treatment (1) termed the end community. In total, 90 species of ants were collected in the experiment in the different plots and treatments during the two years. 25 species were only collected once, 12 species twice and eight species three times.

11.2.3 Characteristic species

For an analysis of treatment preference of species, I only included the samples of 1999 and 2000 and excluded the start and end communities with the following reasoning: at the start all gaps were very hot and dry and would more likely reflect treatments (3) and (4); the end community was only sampled in treatment (1). Moreover, these communities were sampled by litter sifting which collects different ant species than tuna baiting.

At the tuna baits, 67 species of leaf litter ants were collected in the eight sampling events of each treatment. 20 of the 67 species were only collected once, four species were collected twice and six species were collected three times. These species were neglected for an assignment to a specific treatment type. For the characterisation of a species the treatments themselves were used (type (1)-(4), see above) as well as the combinations shade ((1) and (2)), light ((3) and (4)), litter ((1) and (3)) and no litter ((2) and (4)). To be associated with one of these specific types a species had to be present in at least two different gaps in this treatment to avoid a local effect, as the ant colony might already have been established at this particular place for a long time. Ants were also not assigned to characteristic species if they occurred in other gaps in other treatments as this also indicates a local effect. If a species for example was collected in three gaps in treatment (1) but in the two others in treatment (4), it might be more reasonable to assume that the species had nests at the particular sites or was a generalist instead of assigning it to a specific type. If a species was collected in more than five samples and could not be assigned to any particular treatment, it was termed generalist.

Of the 36 species occurring in four and more samples, eight species were only found in a treatment in one or two gaps but found in a different treatment in another gap. They were therefore not included in any further analysis. Another five species were common in more than two treatments but occurred in less than five samples. They were also excluded from the assignment of characteristic species.

24 of the 67 species collected from 1999-2000 showed a particular distribution pattern and could be assigned to the described types (Tab. 41): four species were mostly found in the shade & litter treatments (1), one species was associated with shade & no litter (2) and seven species were found in either treatment (1) or (2), the shaded sites. One species was characteristic for treatment (4) with light & no litter and three species were confined to treatments (3) and (4) and therefore light. The remaining eight species were commonly found in the gaps, but could not be assigned to any special treatment and were therefore termed generalists. 14 of the 24 species were collected more than 10 times and displayed robust distribution patterns.

Tab. 41 Characteristic species for the different experimental treatments. Each species is present in at least two plots and the typical treatment (see text for detailed description). Species collected over 10 times in bold.

Species	Treatment type	1		2		3		4		Total
		99	00	99	00	99	00	99	00	
Pheidole aristotelis	**1**	**6**	**6**	**0**	**1**	**0**	**1**	**0**	**1**	**15**
Odontomachus rixosus	**1**	**5**	**6**	**0**	**1**	**1**	**0**	**1**	**0**	**14**
Tetramorium a	1	2	1	0	1	0	0	0	0	4
Pheidole annexus	1	3	0	0	0	1	0	0	0	4
Pheidole r	2	0	0	3	2	0	0	0	0	5
Pheidole lucioccipitalis	**shade**	**4**	**5**	**7**	**8**	**2**	**0**	**2**	**1**	**29**
Pheidole plagiaria	**shade**	**2**	**8**	**3**	**1**	**3**	**2**	**1**	**2**	**22**
Recurvidris kemneri	**shade**	**2**	**2**	**0**	**3**	**0**	**1**	**0**	**1**	**9**
Euprenolepis b	shade	2	1	1	0	0	0	0	0	4
Pheidologeton pygmaeus	shade	1	0	2	0	0	0	1	0	4
Pheidole poringensis	shade	1	2	0	1	0	0	0	0	4
Pheidole h	shade	1	1	1	1	0	0	0	0	4
Technomyrmex d	4	0	1	0	0	0	0	1	3	5
Lophomyrmex bedoti	**light**	**5**	**3**	**0**	**3**	**11**	**12**	**7**	**6**	**47**
Paratrechina g	**light**	**1**	**2**	**4**	**0**	**6**	**12**	**2**	**8**	**35**
Technomyrmex b	**light**	**1**	**3**	**0**	**0**	**2**	**2**	**3**	**3**	**14**
Pheidole cariniceps	**generalist**	**10**	**13**	**11**	**13**	**9**	**11**	**12**	**10**	**89**
Odontoponera transversa	**generalist**	**7**	**2**	**6**	**4**	**5**	**4**	**5**	**3**	**36**
Pheidole clypeocornis	**generalist**	**4**	**5**	**1**	**5**	**2**	**4**	**4**	**2**	**27**
Paratrechina a	**generalist**	**2**	**3**	**0**	**0**	**1**	**2**	**3**	**3**	**14**
Diacamma intricatum	**generalist**	**1**	**2**	**3**	**1**	**1**	**2**	**2**	**1**	**13**
Paratrechina h	**generalist**	**2**	**4**	**0**	**1**	**1**	**1**	**0**	**3**	**12**
Pheidologeton affinis	generalist	0	0	1	2	0	2	0	2	7
Pachycondyla b	generalist	0	2	0	1	0	2	0	1	6

11.2.4 Species number

The following number of ant species was recorded over all sampling events in the treatments in 1999: 36 (1), 27 (2), 22 (3), 22 (4) and in 2000: 30 (1), 27 (2), 26 (3), 28 (4). More species were collected in (1) and less in (3) and (4) although numbers increased in these two treatments during the time the experiment was running.

The change in species number during time dependent on treatment is even more obvious when the hot start community is compared with the end community of treatment (1). These two stages represent the two extremes in the experiment and were both sampled with litter sifting. Sample size was 8 m² per gap in the start communities and 4 m² in the end sampling in treatment (1). Although sample size was only 50% in the end community, 46 species were collected, whereas 11 species were present at the start of the experiment. All start species were still present at the end of the experiment, although in variable abundances. A strong change in abundance between start and end community was obvious in *Lophomyrmex bedoti,* decreasing from 13 samples in 1998 to two samples in 2000, and *Pheidole clypeocornis* and *Pheidologeton affinis* increasing from four to 10 and one to six respectively.

11.2.5 Community composition in the different treatments

To get a picture of the community composition of the different treatments, the bait samples of 1999 and 2000 were analysed. The start and end samples were not included for the already mentioned reasons. In total 67 species of leaf litter ants were recorded in the eight sampling events of each treatment. To obtain abundance data for the community analysis, I pooled the temporal samples of each treatment in the different gaps. Single temporal sampling events did not reveal enough resolution to separate the different treatment communities, because (a) they do not include enough species and (b) the bias of sampling a species e.g. typical of treatment (1) in treatment (3), which is sometimes the case as the distance between treatments is only around 2-3 m, has a huge effect on similarity calculations. The occasional collection of a species in an 'untypical' treatment has a much lower effect using higher total abundance data obtained after pooling. Species collected once, twice and three times were excluded from the community analysis as they do not show a typical pattern of treatment preference. They might have been collected in a treatment by pure chance representing foragers from nests in the surrounding forest. I also excluded eight ant species of the generalist type.

Finally 29 species of ants remained for the community analysis. As the data set consisted of pooled presence-absence data leading to species count data, the Steinhaus index was calculated after standardisation following the Faith protocol (Faith, Minchin & Belbin, 1987) and the resulting matrix was analysed with MDS (see General Methods). The positions of similar treatments in the two-dimensional scatter plot were connected with a line (Fig. 60).
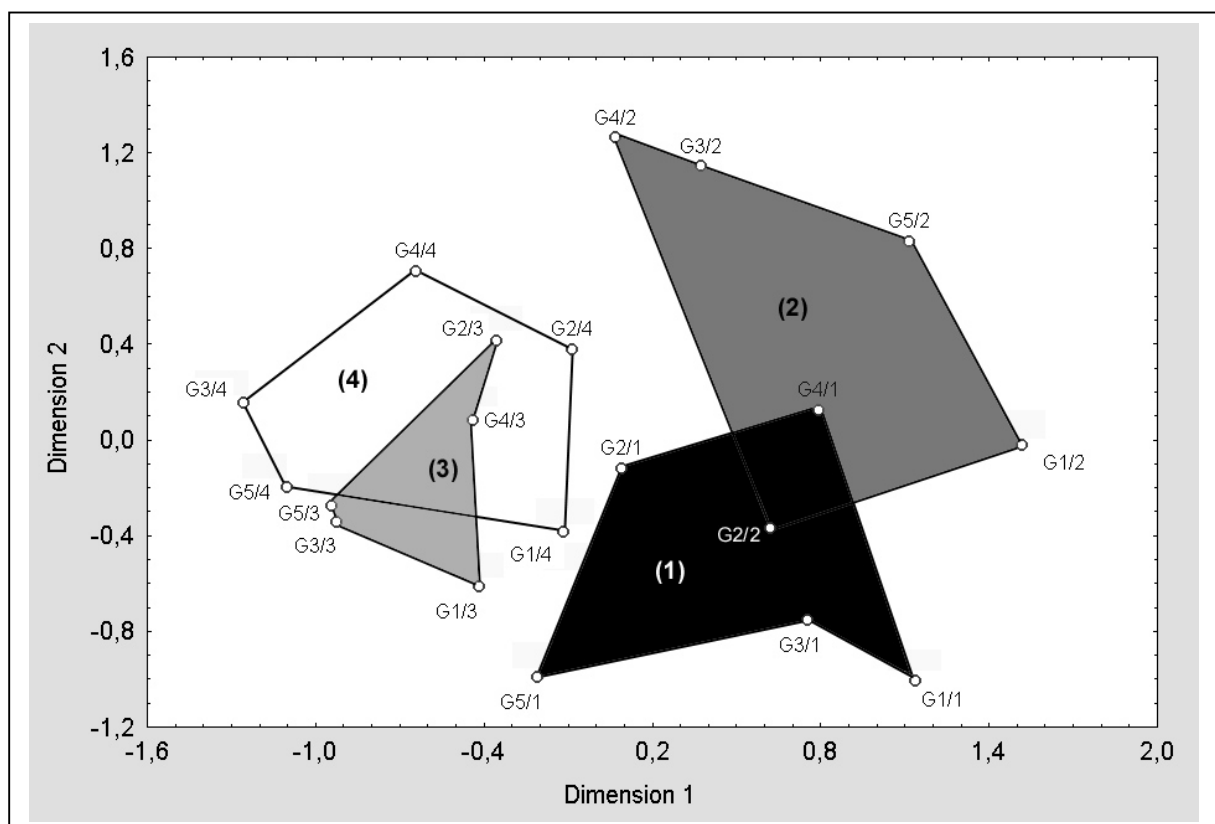
Fig. 60   MDS ordination of the ant community composition of the four treatments (two dimensions, stress = 0.222).

The two-dimensional MDS graph explained 77.8% of the variation in the data, dimension 1 accounted for 68.2% and dimension 2 for 9.6%. An ANOVA of the dimension 1 values showed significant differences between the four treatments (df = 3, F = 10.34 p < 0.001; dimension 2 n.s.). A Scheffe post-hoc test revealed significant differences between treatments (1) and (3)/(4) (p < 0.05) and (2) and (3)/(4) (p < 0.01) but not between treatment (1) and (2) or (3) and (4).

The distinction between light and shade treatments along axis 1 is significant with the shade treatments on the right and the light treatments on the left. The treatment litter only had a minor non-significant effect and separated the communities along axis 2 mostly noticeable in the shade & litter versus shade & non litter treatments.

The values of dimension 1 for the treatments of gap 1 and 4 obtained from MDS analysis were correlated with the mean temperature recorded in the different treatments in these gaps (Fig. 61). This relationship was highly significant ($r^2 = 0.76$, $p < 0.01$) and for these two gaps mean temperature is correlated with the species composition of the ant communities in the different treatments along dimension 1.

Fig. 61   Correlation of recorded mean temperatures in G1 and G4 with dimension 1 values of MDS (y = -1.43x + 35.39, r^2 = 0.764, p < 0.01). 95% confidence intervals are shown.

11.3 Discussion

11.3.1 Temperature

From both the daily temperature profiles and the different temperature values, the difference between the light and shade treatments became clear. The temperature profile of the light treatments resembled the profile for air temperature 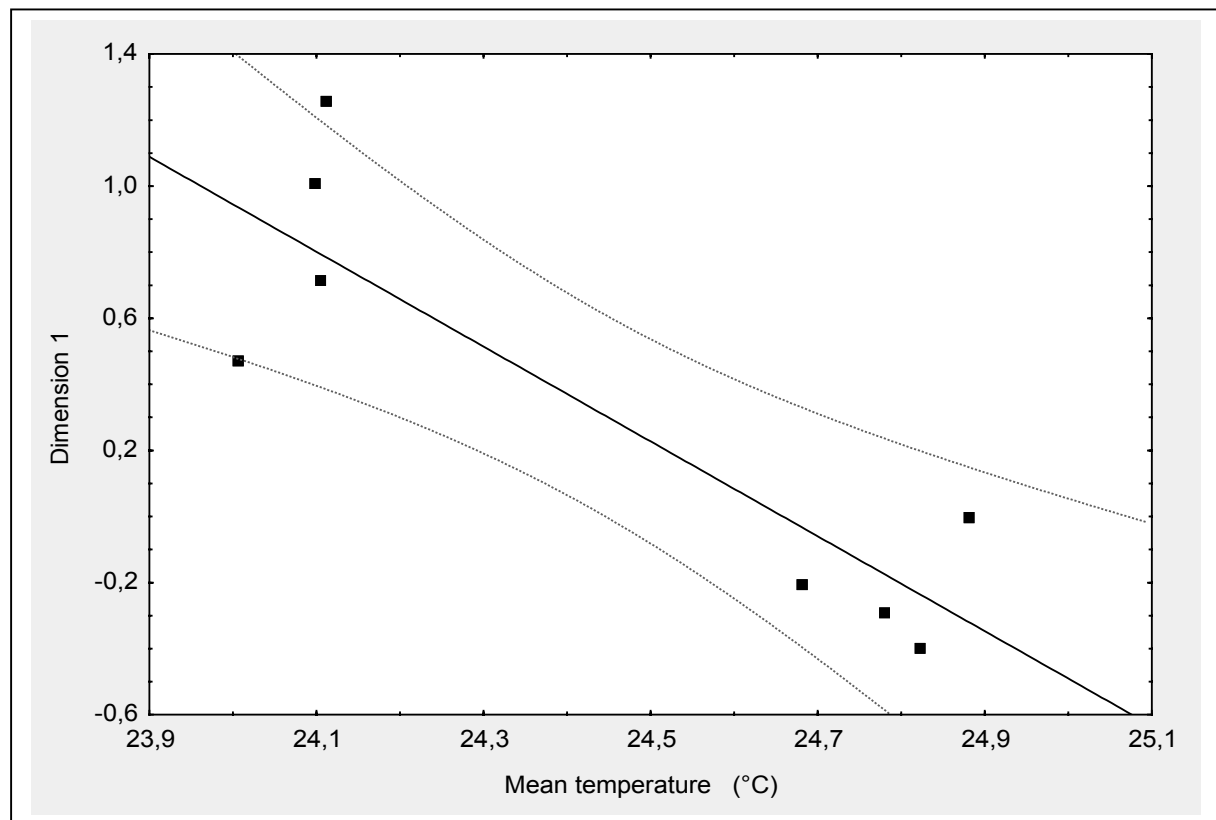in the logged over forest: the light treatment showed similar peaks at midday as the disturbed forest of Deramakot causing differences of over 8°C between the treatments. The highest recorded maximum of 38.4°C is approaching the maximum values of 40°C measured in leaf litter (Levings, 1983). Mean temperatures in light and shade treatments differed by around 0.7°C, which is lower than the difference detected between the logged over forest types (see Microclimate), possibly because the surrounding forest is buffering the temperature in the gaps. Temperature measurements were taken in 2000 and were then presumably lower in the light treatments than the years before as the canopy over the gaps was closing during the course of the experiment. Temperatures in the light and shade treatments were therefore mimicking the temperatures in the logged over forests, but the differences were not as pronounced.

11.3.2 The ants in the treatments

During the time the experiment was running, 90 species of litter dwelling ants were recorded in the different treatments by using tuna baits and Winkler litter sifting. This number is lower than the total species pool present in Danum Valley with 179 species collected in 180 m². This is explainable by the small number of litter samples collected by sifting and the baiting method which only attracts a certain set of leaf litter ant species. Practically no Dacetine ants were recorded at the baits making up a huge proportion of the cryptic litter ant species (see previous chapters). Instead large species of the genus *Diacamma, Odontoponera* and *Odontomachus* were included in the analysis as they were reliably collected with the tuna bait method. Although only a fraction of the ant community was sampled with baiting, this was done continually over months to account for variations in foraging activity.

11.3.3 Characteristic species

Seven of the characteristic species of the experiment were also among the most abundant species in the litter ant communities sampled with litter sifting along the disturbance and size gradient. *Tetramorium a* found in treatment (1) in the experiment was recognised a generalist in both of the other comparisons. *Pheidole annexus*, also a type (1) species was among the ten most abundant species in the Deramakot disturbed forest. *Pheidole plagiara*, a shade species, was found in high abundances in Kebun Cina and *Pheidole clypeocornis,* a generalist, in Danum Valley and Kebun Cina. *Lophomyrmex bedoti*, a light species, was typical for all logged over forests in Deramakot and the forest fragments of Sepilok and Kebun Cina. *Pachycondyla b* and *Paratrechina h,* generalists in the experiment, were recorded in all studied forests among the most common species.

Not all of the characteristic species found within a certain treatment were also recorded among the common species in the previous ant community comparisons. With a similar temperature profile and leaf litter layer, species in the shade & litter treatment were expected to be also present among the common species in the large primary forest and species of the

light & no leaf litter treatment among the common ones in the highly disturbed forests or small fragments. This was the case for *Lophomyrmex bedoti,* the light species, and the two generalists *Pachycondyla b* and *Paratrechina h. Pheidole annexus,* a shade species, is more a primary forest species, which can occasionally become abundant along forest edges and disturbed forests (Eguchi, K. pers comm.).

The other species in the experiment did not follow a distribution comparable to those noticed in the previous chapters. This might be caused by the lower sample size in the experiment and/or a different sampling method. Furthermore, the local species pool of the primary forest surrounding the experimental gaps is very different from the species pool in disturbed forests and includes many species for the colonisation of the treatments. However, the most influential factor for the dissimilarity of the communities of experiment and forests was probably the temperature in the gaps which showed less difference in mean temperature between light and shade treatment than measured in primary and logged over forests or forest fragments. Nevertheless, even at a smaller scale of a few square meters inside a gap and lower temperature differences as experienced along a natural disturbance gradient, characteristic species of the treatments could be identified.

11.3.4 Species number

The highest species number was recorded in treatment (1) in both years, followed by treatment (2). Treatment (3) and (4) increased in species number in 2000. This is explainable by a closing of the canopy during time and cooler and wetter conditions even in the open treatments compared to the previous year.

The need of shade and litter for many litter dwelling ants became clear in the increase of species number from the start to the end of the experiment from 11 to 46 species collected using litter sifting. The change in microclimate in the gaps is also reflected by a decrease of abundance of the 'light' species *Lophomyrmex bedoti* and the increase of *Pheidole clypeocornis* and *Pheidologeton affinis.*

11.3.5 Community composition in the different treatments

The MDS plot, based on a Steinhaus similarity matrix provided clear evidence of a separation of the light and shade treatments along dimension 1. The correlation of mean temperature and MDS positions of two gaps indicated, that community composition of light and shade treatments was evidently influenced by temperature represented by the installation of shading roofs in treatments (1) and (2). The treatment litter separated the communities along axis two especially in the shade treatments, although no quantitative data on leaf litter was collected in the treatments. At the end of the experiment a leaf litter layer only existed in treatments (1) and (3). Treatment (3) with its open gap conditions did however not contain much fine leaf litter. This pre-humus layer was only present in treatment (1) in all gaps.

I used the arrangement of a shading experiment conducted in coffee plantations in Costa Rica (Perfecto & Vandermeer, 1996) which was running for 31 days. Their experiment showed an increase in activity for forest species in shade treatments and an increase and dominance of *Solenopsis germinata* in the light treatments. In this agricultural system interactions between species were altered and lead to an indirect loss of biodiversity, although some of the forest species might have been limited directly by the absence of shade or leaf litter. In my experiment I did not record activity, but it is known of leaf litter ant communities in tropical

forests, that direct competition plays only a minor role in community composition (Byrne, 1994; Kaspari, 1996). In contrast to the Costa Rica experiment it is expected that most of the differences in community composition in Danum Valley were caused by direct effects of the treatments.

Species number of leaf litter ants was significantly correlated with leaf litter volume and temperature as well as humidity of the litter layer (see previous chapter). In the litter - shade experiment, temperature and leaf litter were even affecting the *community composition* in the different treatments. Temperature was recognised as a condition that allows access to resources like nest sites or food (Kaspari, 2000). This is even more evident in the experiment where in the shade treatments the lower temperatures allow foraging or nesting in the leaf litter for many species. Subsequently the effect of the treatment leaf litter becomes more important and separates the shade & litter and shade & no litter treatments from each other. Since in the light treatments temperatures were hotter, only a few species could forage or nest in the litter. This leads to a higher similarity of the two light communities obvious in the overlap along dimension 2 of the MDS plot.

In the previous chapter, it was difficult to determine, if temperature had a direct effect on the ants restricting foraging time or indirect effects leading together with lower humidity to lower food and nest site availability in the leaf litter. In the experimental arrangement, a treatment area of 5 x 5 m was subjected to different temperatures. The foraging distance of leaf litter ants is for most species below 1.5 m (Carvalho & Vasconcelos, 1998; Kaspari, 1993). In the experiment, baits were placed 1 m off the edge of the treatment, and therefore it is safe to assume that most of the species collected at the baits and assigned to the treatments were also nesting there. Since most of the litter dwelling ant species are nesting between leaves or in hollows in twigs in the leaf litter (Brown, 2000; Hölldobler & Wilson, 1990; Kaspari, 2000; Wilson, 1959) and temperature is crucial for the development of larvae and pupae of ants (Hölldobler & Wilson, 1990; Southerland, 1988), the interaction of the two factors is important.

The condition temperature most likely controls the access to the resource nest sites. In the shade & litter treatment the temperature is cool enough for many small-bodied leaf litter ant species to nest and the resource leaf litter is available (Kaspari, 1993; Torres, 1984). In the shade & no litter treatment the temperature is also within the preferred range, but nest sites in the leaf litter are scarce and more species might nest in the top soil layer. Therefore community composition is influenced by the factor leaf litter, which separates the shade communities from each other along dimension 2 in the MDS plot. Additionally, species number is slightly lower than in treatment (1). In the light treatment, the hotter temperature and probably especially the maxima recorded during midday may prevent many species from nesting in potentially present nest sites, at least in the light & litter treatment. Therefore leaf litter cannot be used as a nest resource and has a much lower effect on separating the two light treatments from each other. The condition temperature in this case may prevent access to the resource nest site. This not only leads to a different set of species present in the light treatments but also to a lower number of species as most litter dwelling species are not able to thrive in high temperatures (Kaspari, 1993; Torres, 1984). The closing of the canopy above the tree fall gaps in 2000 caused lower temperatures in the light treatment and the resource

litter was then useful to more ant species, resulting in an increase of species in the light treatments.

In summary, the experiment confirmed the influence of abiotic conditions on community composition and species number of leaf litter ants, although conducted on small scale and in a cooler environment than measured in logged over or fragmented forests. It has been suggested that the crucial factor for the distribution of ant species might be temperature which controls the availability of nest sites. Characteristic species of treatments were in most cases not recorded among the common species in comparable forests of the previous chapters (light treatment and disturbed forest or small fragment; shade treatment and large primary forest). This is most likely due to a different collecting method, the influence of the local species pool surrounding the gaps and the lower mean temperature differences between treatments in the gaps. However *Lophomyrmex bedoti* was recognised a species typical of the light treatments and also of disturbed forests and smaller fragments.

The interactions of temperature and leaf litter might be explained by the condition temperature allowing ants to use the resources in the leaf litter for nesting. In this context it would be most interesting to manipulate the other characteristic resource food and record the effect on the ant populations in the community.

12   Synthesis

In this study of leaf litter ant communities in tropical rain forests in Sabah it became obvious, that habitat changes due to logging and landscape conversion leading to isolation of forest remnants and total forest loss showed various effects.

In logged over forests, only 70% of the species of a primary forest were present even 25 years after the impact of timber extraction. The ant communities were thinned and could be described by a lower species density producing lower species numbers and a different community composition. A few species were positively associated with forest disturbance and increased in abundance in the logged over forests. The similarity in species number and community composition between logged over forests of different degrees of disturbance was explained by source-sink dynamics within the heterogeneous forest matrix in the Deramakot Forest Reserve: even within a heavily disturbed forest, consisting of almost pure stands of *Macaranga* pioneer trees over large areas, patches of primary forest stand structure were present which had escaped logging. These islands of favourable habitat in generally heavily disturbed forests lead to the accumulation of ants peaking in 41 species recorded in 1 m² of leaf litter. At a different spatial scale, large sized parts of forest logged with lower intensity were neighbouring highly disturbed areas.

Rain forest fragments displayed even higher reductions in species density, numbers and diversity due to a more pronounced thinning effect than recorded in logged over forests. Even forest isolates exceeding 4 000 ha in size did not support more than 50% of the species of the leaf litter ant community of a contiguous primary rain forest. Additionally, an increase in tramp species was recorded with decreasing size of the forest fragments, leading to a very different community composition. This increase in tramp species and species associated with the surrounding agricultural matrix resulted in similar species numbers in the primary forest fragments, even if size differed on an order of magnitude.

Regarding the leaf litter ant community, the remaining rain forest fragments of Sabah are effectively isolated by a barrier of oil palm plantation, now stretching all over the lowlands of the east coast. Only 13 species, which belonged to the forest ant community were collected in these plantations. These species were recognised to be associated with high disturbance levels in logged over forests. Some of the 10 other species of the highly reduced ground-dwelling ant community in the plantations are known as invasive tramp species, forming large exclusive territories. Especially *Anoplolepis gracilipes* was dominating the ant community in the oil palm plantations under study and was present at 70% of the bait sites. Most of the species only recorded in the plantations can be collected in every parking lot in the country.

Correlative evidence implied, that leaf litter humidity, volume and temperature affect the distribution of forest leaf litter ant species. The smaller primary forests and the most disturbed logged over forests in this study revealed higher temperatures and lower humidity levels and a reduction in leaf litter volume compared to a large primary forest or forests affected by a lower impact of timber harvesting.

An experiment clarified the interrelations between the three factors more specifically: it can be concluded that the abiotic conditions of humidity and temperature control the access to resources like nest sites in the leaf litter. In highly disturbed forests or small forest isolates, temperature becomes too high and the litter too dry, thus reducing the resource nest sites, although structurally present. Temperature is directly influenced by the impact of logging and the accompanied opening of the canopy and indirectly affected by large scale conversions of the landscape leading to an increase in minimum temperatures of the local climate surrounding forest fragments. Some species were identified as generalistic leaf litter ants present in high abundances in all forest types, and some thrived very well in higher temperature habitats. Especially one species was very common in disturbed forests, small forest fragments and light treatments in the experiment: *Lophomyrmex bedoti*.

The patterns recorded in leaf litter ant communities were confirmed by studies of ants of the lower vegetation and nymphalid butterflies in the same research sites. The effects of fragmentation were also studied on a molecular level in two ant species and showed a reduction in nucleotide diversity with smaller forest size. In contrast, stingless bees seemed to thrive especially well in the Sepilok forest fragment as there food resources are enhanced by the surrounding agricultural crops and fruit orchards.

The ants of the leaf litter proved to be a very promising taxon for the monitoring of biodiversity even along a disturbance gradient of a comparatively fine scale. With an appropriate sampling design and replication it was possible, to sample the existing ant communities to a high level of completeness and compare different aspects of their composition. Some plots were sampled in two climatically very different years, the El Niño in 1998 and the following La Niña in 1999, certainly the most extreme climatic circumstances to be encountered in the area in decades. Temporal replication revealed that the leaf litter ant communities are quite stable which is useful for biodiversity comparisons. It is therefore advisable to generally include this insect group into any monitoring scheme as it proved to be sensitive towards forest disturbance.

With the rapid and destructive conversion of one of the worlds oldest rain forest ecosystems and an acknowledged manifested biodiversity crisis, more studies on different animal groups in the remaining forest fragments in Sabah are urgently needed. If the pattern for leaf litter ants is confirmed for other taxa, the implications for any efficient management design aiming to preserve the majority of the biodiversity of the country are tremendous and current concepts need rethinking. Taking the results of this study into account, it seems to be reasonable for conservation efforts to focus on primary forest fragments within logged over forests and aim at connectivity between forest isolates. It seems most beneficial to include the size of a forest into management concepts and not only its condition. The establishment of new large scale oil palm plantations, leading to a loss of almost 95% of the forest leaf litter ant community, should be thoroughly considered, especially with the current low market price of the crop.

This and many other studies show that forest disturbance and fragmentation lead to an often severe loss of biodiversity. Another result of this study was a thinning of leaf litter ant communities and a decrease in species density per area. A next step should now aim at the question how this loss of diversity and thinning affects the ecosystem function of the group influencing soil processes like decomposition and nutrient cycling, which are crucial for the maintenance of soil fertility.

13 Zusammenfassung

In der vorliegenden Arbeit über die Ameisen der Laubstreu in tropischen Regenwäldern in Sabah wird deutlich, dass Habitatveränderungen, wie sie durch Holzeinschlag und eine Umgestaltung der Landschaft entstehen, die wiederum die Isolation von Waldresten und den Verlust von ganzen Wäldern zum Ergebnis hat, unterschiedlichste Auswirkungen nach sich ziehen.

In holzwirtschaftlich genutzten Wäldern waren selbst 25 Jahre nach vorhergegangenem selektivem Holzeinschlag nur noch 70% der Ameisenarten der Laubstreu eines Primärwaldes vorhanden. Die Ameisengemeinschaften waren ausgedünnt und zeichneten sich durch eine niedrige Artendichte pro Fläche aus, die wiederum insgesamt niedrige Artenzahlen und eine Verschiebung in der Zusammensetzung der Gemeinschaft zur Folge hatte. Einige Ameisenarten waren aber auch positiv mit der anthropogenen Störung assoziiert und zeigten eine Abundanzzunahme in genutzten Wäldern. Die Ähnlichkeit in der Anzahl der Arten und auch in der Zusammensetzung von Zönosen in verschieden stark eingeschlagene Wäldern, die immer noch eine sehr unterschiedlich Waldstruktur aufweisen, kann durch eine Source-sink-Dynamik innerhalb des heterogenen Waldbestandes im Deramakot Forest Reserve erklärt werden: sogar innerhalb der am stärksten gestörten Wälder, die über große Flächen fast ausschließlich aus *Macaranga* Pionierbäumen bestehen, waren kleinere Primärwaldflecken zu finden, die dem Holzeinschlag entgangen waren. Die günstigen Bedingungen in diesen Habitatinseln führten zu einer Akkumulation von Ameisen, die in 41 Arten in nur einem Quadratmeter Laubstreu ihr Maximum erreichte. Auf einer anderen räumlichen Skala waren für die Ähnlichkeiten der Ameisengemeinschaften auch die großflächige Anordnung von Waldstücken verantwortlich, in denen Wälder, die mit geringerer Intensität eingeschlagen worden waren, direkt benachbart zu stark gestörten Wäldern standen und so einen Austausch an Arten ermöglichten.

Isolierte Regenwaldfragmente zeigten eine noch stärkere Reduktion in Artendichte, -zahl und -diversität, die durch einen noch ausgeprägteren Ausdünnungseffekt als in eingeschlagenen Wäldern hervorgerufen wurden. Auch in Wäldern, die eine Größe von 4000 ha überschritten, konnten nicht mehr als 50% der Laubstreuameisenarten eines zusammenhängenden Primärwaldes nachgewiesen werden. Zusätzlich wurde eine Zunahme von invasiven Arten mit kleiner werdender Fragmentgröße verzeichnet, was zu einer Verschiebung in der Zusammensetzung der Gemeinschaft führte. Die Zunahme invasiver Arten und solcher, die mit der umgebenden, landwirtschaftlich genutzten Matrix assoziiert sind, hatten ähnliche Artenzahlen in den Primärwaldfragmenten zur Folge, auch wenn sie sich in bis zu zwei Größenordnungen unterschieden.

Die verbleibenden Regenwaldfragmente in Sabah sind für bodenbewohnende Waldameisen durch eine Barriere von Ölpalmenplantagen, die sich über das ganze Tiefland der Ostküste hinziehen, effektiv isoliert. Nur 13 Arten, die der Ameisengemeinschaft des Waldbodens zugerechnet werden, konnten in diesen Plantagen nachgewiesen werden. Dieses waren Arten, die alle vornehmlich in gestörten Wäldern zu finden sind. Einige der restlichen zehn Arten der

stark reduzierten Bodenameisengemeinschaft in den Plantagen sind invasive Arten die große, exklusive Territorien etablieren. Besonders *Anoplolepis gracilipes* dominierte die Ameisengemeinschaft in den untersuchten Ölpalmenplantagen und war an 70% aller Köderstellen präsent. Die meisten der Arten, die nur in den Ölpalmenplantagen nachgewiesen wurden, sind auf jedem Parkplatz im Land anzutreffen.

Korrelative Nachweise implizierten, dass Feuchte, Volumen und Temperatur der Laubstreu die Verteilung der bodenbewohnenden Ameisen beeinflussen. Die kleineren Primärwälder und die am stärksten gestörten, eingeschlagenen Wälder in dieser Untersuchung zeigten verglichen mit einem großen zusammenhängenden Primärwald oder Wäldern, die von einem weniger starken Holzeinschlag betroffen waren, höhere Temperaturen und eine Verringerung des Feuchtigkeitsniveaus und Laubstreuvolumens zusammen mit reduzierten Artenzahlen.

In einem Freilandexperiment konnte das Zusammenspiel der drei Faktoren noch weiter verdeutlicht werden: die abiotischen Faktoren Feuchtigkeit und Temperatur kontrollieren den Zugang zu Nistresourcen in der Laubstreu. Stark gestörte Wälder oder kleine Waldinseln weisen höhere Temperaturen und eine trockenere Streu auf, womit sich die Anzahl von geeigneten Nistplätzen reduziert, obwohl sie strukturell vorhanden wären. Die Temperatur innerhalb des Waldes wird direkt durch den Holzeinschlag und die damit verbundene Öffnung des Kronendachs beeinflusst und indirekt durch großflächige Veränderungen der Landschaft gesteuert, die zu einer Zunahme der Mindesttemperaturen in der Umgebung der verbleibenden Restwälder führt. Einige Ameisenarten konnten als Generalisten identifiziert werden, die in allen Wäldern in hohen Abundanzen vorhanden waren, andere hingegen waren in Habitaten mit höheren Temperaturen besonders häufig anzutreffen. Besonders eine Art war in den gestörten Wäldern, kleinen Waldfragmenten und auch im Experiment unter der Manipulation durch Licht sehr zahlreich: *Lophomyrmex bedoti*.

Die durch Störung und Fragmentation hervorgerufenen Muster in der Gemeinschaftsstruktur der Ameisen der Laubstreu wurden in den selben Untersuchungsflächen für die Ameisen der unteren Vegetation und einer Gruppe fruchtsaugender Tagfalter (Nymphalidae) bestätigt. Die Auswirkungen von Fragmentation wurden bei zwei ausgewählten Ameisenarten auch auf molekularem Niveau untersucht, welche eine Abnahme in der Nukleotiddiversität mit kleiner werdender Waldfläche aufzeigte. Im Unterschied dazu erging es stachellosen Bienen im Waldfragment von Sepilok besonders gut, da sich für diese durch die umgebenden landwirtschaftlichen Nutzpflanzen, Fruchtgärten und die angrenzende Mangrove die Nahrungsgrundlage wesentlich verbessert hatte.

Die Ameisen der Laubstreu erwiesen sich als eine sehr vielversprechende Zielgruppe für die Erfassung von Biodiversitätsmustern entlang eines Störungsgradienten auf einer vergleichbar feinen Skala. Mit einer adäquaten Besammlungsmethode und einer genügenden Anzahl von Replikaten war es möglich, die existierende Ameisengemeinschaft zu einem hohen Anteil zu erfassen und verschiedene Aspekte ihrer Zusammensetzung zu vergleichen. Zeitliche Replikate in zwei klimatisch sehr unterschiedlichen Jahren, die sicherlich die extremsten Umweltbedingungen darstellten, die in der Region zu erwarten sind (El Niño und das

anschließende La Niña Jahr), zeigten, dass die Ameisengemeinschaften der Laubstreu relativ stabil sind, was für Vergleiche von Biodiversitätsmuster besonders nützlich ist. Da sich diese Insektengruppe in ihrer Reaktion auf anthropogene Waldveränderung zudem sensibel zeigte, erscheint es empfehlenswert sie in jedes Biodiversitätserfassungsprogramm aufzunehmen.

Mit der schnell voranschreitenden und äußerst destruktiven Veränderung eines der ältesten Regenwälder der Erde und einer erkannten und eingestandenen Biodiversitätskrise sind weitere Studien in verschiedenen Tiergruppen in den verbleibenden Waldfragmenten Sabahs dringenst geboten. Falls das vorliegende Muster der Ameisen der Laubstreu auch in anderen Gruppen bestätigt wird, sind die Auswirkungen auf jedes bestehende Managementprogramm, das darauf hinarbeitet, den Großteil der Biodiversität des Landes zu erhalten, besorgniserregend und ein rasches Überdenken bisheriger Konzepte ist gefordert. Basierend auf den Ergebnissen dieser Untersuchung erscheint es für Naturschutzbemühungen vernünftig, sich auf Primärwaldfragmente in schon eingeschlagenen Wäldern zu konzentrieren und eine Verbindung von isolierten Waldinseln anzustreben. Es wäre sicher auch lohnend, die Größe eine Fragments in die Planung von Schutzmaßnahmen mit einzubeziehen, und nicht nur den strukturellen Zustand des Waldes. Die Etablierung neuer, großflächiger Ölpalmenplantagen, die einen Verlust von 95% der bodenbewohnenden Waldameisengemeinschaft zur Folge hätte, ist scharf zu überdenken, besonders aufgrund des zudem stark gefallenen Marktpreises für Palmöl.

Die vorliegende und viele andere Studien zeigen, dass anthropogene Störung und Fragmentation von tropischen Wäldern einen oft hohen Verlust der Artenvielfalt nach sich ziehen. Ein anderes Ergebnis dieser Arbeit ist die Ausdünnung der Ameisengemeinschaft und eine Verringerung der Artendichte. Es schließt sich die Frage an, inwieweit dieser Artenschwund und eine geringere Dichte die Funktion der gesamten Gruppe innerhalb des Ökosystems beeinflussen und dadurch Steuerungsprozesse innerhalb des Nährstoffkreislaufs verlangsamen und wichtige Abläufe für die Erhaltung der Bodenfruchtbarkeit stören.

14 Literature

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15   Appendix: Species Richness Estimators and Diversity Indices

Species richness estimators

Six different methods were used to calculate total species richness in the different forest plots. All formulae are from Colwell and Coddington (1994), where more details are given for the different estimators.

Tab. 42	**Definitions of variables of the species richness estimators (Colwell & Coddington, 1994).**

S_{est}	Estimated species richness, where <u>est</u> is replaced in the formula by the name of the estimator
S_{obs}	Total number of species observed in all samples pooled
S_{rare}	Number of rare species (each with 10 or fewer individuals) when all samples are pooled
S_{abund}	Number of abundant species (each with more than 10 individuals) when all samples are pooled
S_{infr}	Number of infrequent species (each found in 10 or fewer samples)
S_{freq}	Number of frequent species (each found in more than 10 samples)
m	Total number of samples
m_{infr}	Number of samples that have at least one infrequent species
F_i	Number of species that have exactly i individuals when all samples are pooled (F1 is the frequency of singletons, F2 the frequency of doubletons)
Q_j	Number of species that occur in exactly j samples (Q1 is the frequency of uniques, Q2 the frequency of duplicates)
p_k	Proportion of samples that contain species k
N_{rare}	Total number of individuals in rare species
N_{infr}	Total number of incidences (occurrences) of infrequent species
C_{ice}	Sample incidence coverage estimator
γ^2_{ice}	Estimated coefficient of variation of the Q_i's for infrequent species

1.   ICE:

Incidence-based Coverage Estimator of species richness. First note that

$$S_{obs} = S_{infr} + S_{freq} \; .$$

The sample coverage estimate based on incidence data is

$$C_{ice} = 1 - Q_1 / N_{infr} \; ,$$

where

$$N_{infr} = \sum_{j=1}^{10} j Q_j \; .$$

Thus, the sample coverage estimate is the proportion of all individuals in infrequent species that are not uniques. Then the ICE estimator of species richness is

$$S_{ice} = S_{freq} + \frac{S_{infr}}{C_{ice}} + \frac{Q_1}{C_{ice}} \gamma_{ice}^2 \; .$$

where γ_{ice}^2, which estimates the coefficient of variation of the Q_j's, is

$$\gamma_{ice}^2 = \max\left\{ \frac{S_{infr}}{C_{ice}} \frac{m_{infr}}{(m_{infr}-1)} \frac{\sum\limits_{j=1}^{10} j(j-1)Q_j}{(N_{infr})^2} -1, 0 \right\} \; .$$

2. Chao2:

An incidence-based estimator of species richness.

$$S_{Chao2} = S_{obs} + \frac{Q_1^2}{2Q_2} \; .$$

3. Jack1:

First-order jackknife estimator of species richness (incidence-based).

$$S_{jack1} = S_{obs} + Q_1\left(\frac{m-1}{m}\right) \; .$$

4. Jack2:

Second-order jackknife estimator of species richness (incidence-based).

$$S_{jack2} = S_{obs} + \left\lceil \frac{Q_1(2m-3)}{m} - \frac{Q_2(m-2)^2}{m(m-1)} \right\rceil \; .$$

5. Bootstrap:

Bootstrap estimator of species richness (incidence-based).

$$S_{boot} = S_{obs} + \sum_{k=1}^{S_{obs}} (1-p_k)^m \; .$$

6. Michaelis Menten Mean (MMMean):

Asymptotic model for species accumulation, estimating S_{max} and B from a set of values for S(n) as a function of n:

$$S(n) = \frac{S_{max}}{B+n} \; .$$

<u>Alpha-Diversity</u>

Three standard indices were used to express the α-diversity of the ant communities in the different plots (see General Methods). Calculations followed the description in Magurran (1988):

1. Fisher's α:

This parametric index presents the α log series parameter for each sample and assumes that species abundance follows the log series distribution. Therefore it is a prerequisite to test for log series distribution before this index can be used. The α log series parameter was calculated as:

$$S = \alpha \ln\left(1 + \frac{N}{\alpha}\right)$$

S = Number of species; N = Number of individuals; with

$$\alpha = \frac{N(1-x)}{x}$$

x estimated after:

$$\frac{S}{N} = \frac{1-x}{x}\left[-\ln(1-x)\right]$$

2. Shannon-Wiener index H'

H' presents the Shannon-Wiener (also known as Weaver) diversity index for each sample. The underlying function was devised to determine the amount of information in a code, and is defined as:

$$H = -\sum_{i=1}^{Sobs} p_i \log_e p$$

where p_i = the proportion of individuals in the ith species
        S_{obs}= observed species

3. Simpson index D

D is a diversity index to describe the probability that a second individual drawn from a population should be of the same species as the first. The statistic, C is given by:

$$C = \sum_{i}^{Sobs} p_i{}^2$$

but, for a finite population

$$p_i{}^2 = \frac{N_i(N_i - 1)}{N_T(N_T - 1)} -$$

where N_i is the number of individuals in the ith species and N_T the total individuals in the sample. The index calculated here is:

$$D = \frac{1}{C}$$

so the larger its value the greater the diversity.

4. Eveness J:

Equitability or eveness refers to the pattern of distribution of the individuals between the species. This measure of equitability compares the observed Shannon-Wiener index against the distribution of individuals between the observed species which would maximise diversity. If H is the observed Shannon-Wiener index, the maximum value this could take is log(S), where S is the total number of species in the habitat. Therefore the index is:

$$J = \frac{H}{\log(S)}$$

5. Renyi index:

Perhaps the most generally useful method for ordering and comparing diversities is the Renyi family which is based on the concept of entropy and is defined as (Legendre & Legendre, 1998):

$$H_\alpha = \frac{\left\{ \log \sum_{i=1}^{q} p_i^{\alpha} \right\}}{1 - \alpha}$$

where p_i is the proportional abundance of the ith species and log the logarithm to a base of choice (often e).

By varying α we may generate a range of diversity measures (0 = total species number, 1 = Shannon-Wiener, 2 = Simpsons's D). To test for non-comparability of communities H(α) is calculated for a range of values and the results presented graphically. If a community has always higher values of H(α) it can be considered to be more diverse. If two communities cross-over in H(α) they are non-comparable.

Beta-diversity

1. Steinhaus index:

The Steinhaus distance is a dissimilarity or complementarity (sensu Colwell & Coddington, 1994) index used for β-diversity calculations (between communities). The 1 - Steinhaus index is also known as the Bray Curtis index, a measurement of similarity that was used for cluster analysis.The Steinhaus coefficient compares two sites (x_1, x_2) in terms of the minimum abundance of each species:

$$S(x_1, x_2) = \frac{2W}{(A + B)}$$

where W is the sum of the minimum abundance of the various species, this minimum being defined as the abundance at the site where the species is rarest (Legendre & Legendre, 1998). As recommended by Faith and co-workers (1987) the data were standardised by dividing each value by the maximum abundance for that species in the data set before the calculation of the Steinhaus index.

16 Glossary

dbh.	diameter at breast height (measurement in forestry)
a.s.l.	above sea level
DVCA	Danum Valley Conservation Area
SFR	Sepilok Forest Reserve
KCFR	Kebun Cina Forest Reserve
DFR	Deramakot Forest Reserve
ICE	Incidence based Coverage Estimator
Chao2	Species richness estimator after Chao
Jack1	First-order jackknife species richness estimator
Jack2	Second-order jackknife species richness estimator
Bootstrap	Bootstrap species richness estimator
MMMean	Michaelis-Menten mean species richness estimator
UPGMA	Unweighted Pair – Group Method using arithmetic Averages cluster algorithm
SL	Single Linkage cluster algorithm
MDS	Multi Dimensional Scaling
FRC	Forest Research Center (Sandakan, Sabah)
DVFC	Danum Valley Field Center
BDFFP	Biological Dynamics Forest Fragments Project, Brazil
ENSO	El Niño Southern Oscillation

Study plots

Plot	Site	Forest type
A, B, C	Deramakot	good
D, E, F	Deramakot	regenerated
G, H, I	Deramakot	disturbed
K, K*	Sepilok	primary, fragment, large
L, M	Danum Valley	primary, contiguous
O	Kebun Cina	primary, fragment, small

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<div align="right">Wir hatten ein Haus in Borneo...</div>

Lebenslauf

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Erklärung

Hiermit erkläre ich ehrenwörtlich, dass ich die vorliegende Arbeit selbstständig angefertigt und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Ich habe diese Dissertation weder in gleicher noch in ähnlicher Weise in einem anderen Prüfungsverfahren vorgelegt.

Ich erkläre ferner, dass ich bisher noch keinen weiteren akademischen Grad erworben oder zu erwerben versucht habe.

Würzburg, den 11. Juni 2001