Distribution of woody debris and saproxylic insects in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia

Fordeling av død ved og saproxyliske insekter i brent og ubrent lavlands dipterokarp regnskog, øst Kalimantan, Indonesia



Anders Endrestøl Master thesis in Natural Resource Management



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Thesis outline

This thesis was conducted as a part of the G. Fredriksson¹ research project on Malayan sun bears, carried out in the Sungai Wain Protection Forest, East Kalimantan, Indonesia. Large areas of primary rainforest were devastated due to forest fires in South- East Asia, both in 1983- 84 and 1997-98 during prolonged droughts caused by strong El Niño Southern Oscillation (ENSO) events. The effects of these fires were an apparent destruction of habitat and food resources for the sun bear (*Helarctos malayanus*), an endangered species living in the lowland dipterocarp rainforests, of which the ecology is practically unknown.

The bears feed mainly on fruits, termites, ants, and other saproxylic insects², and change their diet dependent on what is available (G. Fredriksson, *unpubl. data*). The bears are known to feed daily on saproxylic insects (mainly beetle larva and cockroaches, apart from termites and ants) making this an important resource in the bears' diet (G. Fredriksson, *unpubl. data*). It is thus of interest to investigate the distribution of these insects and to determine to which extent the fires have changed their abundance and richness. Studies of the availability of other important foods for the sun bear have been presented earlier, fruits (Danielsen³ 2003), and termites (Mathisen⁴ 2003).

Since so little is known about the distributions of dead wood and saproxylic insects from the tropics, and how these are affected by forest fires, these topics were investigated separately. This thesis is divided into two parts. The first part concerns the distribution of dead wood (fine and coarse woody debris) and the second part discusses the distribution of saproxylic insects. The saproxylic insects investigated in this thesis are Coleoptera, Blattodea, Diptera, Lepidoptera, and Orthoptera, with emphasis on the two first orders. An overall abstract is presented along with abstracts presented at the start of each part.

Frontcover drawing: Passalidae (larvae), by Timbull. Last page drawing: Foreststream, by Timbull.

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 $^{^{2}}$ Saproxylic insects: Insects that in some part of their lifecycle are dependent upon dead wood. See citations in part two of this thesis.

³ Danielsen, L., 2003. The effects of the drought and fires after the 1997/98 El Niño on fruit availability for the sun bear (*Helarctos malayanus*) in East Kalimantan, Indonesia. Cand. Agric. Thesis, Agricultural University of Norway.

⁴ Mathisen, K. M., 2003. Effects of forest fires on termites (Isoptera) and availability of food for the sun bear (*Ursus malayanus*) in a dipterocarp forest of East Kalimantan, Indonesia. Cand. Scient Thesis, Agricultural University of Norway.

Overall abstract

Dead wood forms major structural features and represents important resources of nutrients and energy for the forest ecosystem. It plays an important role for biodiversity and is an important substrate for both animals and plants. The saproxylic insect fauna is dependent on woody debris (WD) during some part of their life cycle and would therefore be affected by changes in quantity and qualities of WD. Forest practices in temperate and boreal areas have resulted in a faunal and floral devastation, resulting in many of the saproxylic insects being regarded as threatened and found on "red-lists". Major deforestations have also occurred in the tropics due to human-induced fires, unsustainable logging practices, and conversion of forest areas to agricultural lands. Very little is known about the saproxylic fauna in general, and its response to such human-caused disturbances in the tropics. The objective of this study was to investigate the distribution of WD (fine woody debris, FWD, and coarse woody debris, CWD) and saproxylic insects (Coleoptera, Blattodea, Diptera, Lepidoptera, and Orthoptera) in burnt and unburnt lowland dipterocarp rainforest. The study area was located in the Sungai Wain Protection Forest, East Kalimantan, Indonesia. This area experienced two of the worst forest fires in recent history, in 1982-83 and 1997-98, during prolonged droughts caused by strong El Niño Southern Oscillation (ENSO) events. Seven paired sample plots (each with two plots of 0.2 ha, totalling 2.8 ha) were in 2001 investigated for WD in both burnt (1.4 ha) and unburnt (1.4 ha) forest. An area of 0.04 ha was selected in the middle of these plots and investigated for saproxylic insect by physically chopping up the wood using an axe or a machete. Environmental parameters along with qualities and quantities of WD were measured. A total of 1616 individual saproxylic insects were encountered, hand collected, and subsequently weighed and allocated to order, or to family/subfamily level for Coleoptera (28 families identified) and Blattodea (Panesthia sp. identified). Environmental parameters influencing composition and abundance of taxa were investigated using multivariate analyses (CCA).

This study reports some of the highest amounts of WD ever reported from the tropics, both for burnt and unburnt forest, with an average of 196.6 m³ ha⁻¹ in unburnt forest and 373.8 m³ ha⁻¹ in burnt forest. The occurrence of snags was on average 36.8% in unburnt forest and 45.1% in burnt forest of the WD volume encountered. There was a significantly different distribution of decay classes between burnt and unburnt forest, with relatively less decayed CWD in the burnt forest. Also, relatively more large sized snags were found in unburnt forest, even though there was significantly higher volume of snags in burnt plots. No differences in density of insects were found between burnt and unburnt forest areas, except for the Coleopteran family Eucnemidae, which were found in higher numbers per m³ WD in unburnt forest. Regarding biomass, only Blattodea (all individuals excluding Panesthia sp.), differed significantly between burnt and unburnt forest, with higher masses found in burnt areas. A close to significant difference of higher total biomass for both Panesthia sp. and Blattodea (total) in burnt forest were found. Several of the most frequent found taxa showed a significant preference for a certain degree of decay. Decay class of WD was also found to be the most important environmental parameter explaining the distribution of the saproxylic insects. Total sample abundance was positively correlated with WD decay class and WD volume. No differences in sample richness or total richness were found between burnt and unburnt forests, but total sample richness was positively correlated with WD decay class and volume. Richness was also positively correlated with WD connectivity.

The higher amounts of WD found in the burnt areas are largely explained by the occurrence of more small sized snags created by the fires. The overall high amount of WD found in unburnt forest was probably due to the severe drought during the prolonged ENSO events in both 1982-83 and 1997-98, but it could also partly be explained by low decay rate due to floristic domination of certain species and decreased water content of WD due to drought. The nature of the 1997-98 fires might have left some of the saproxylic fauna alive, which could still be reflected at the time of this study due to extended life cycles of xylophagous insects. The similarities could also be explained by a quick restoration of the saproxylic fauna, as saproxylic insects might still use the substrate in the burnt forest.

Future research is recommended to acquire knowledge about the saproxylic insects in the tropics and to further understand the effects of forest fires on the saproxylic fauna. Also, the high amount of WD present in both burnt and unburnt forest constitutes a large amount of fuel for future forest fires, which necessitates a high investment in fire prevention, including public information and changes in land-use policies.

Keyword: Kalimantan, saproxylic insects, forest fires, tropics, decay, woody debris

Abstrak

Penyembaran Kayu Lapuk dan serangga Saproxylic di daerah bekas terbakar dan tidak terbakar pada Hutan Hujan dataran rendah Dipterocarpaceae, Kalimantan Timur, Indonesia

Pohon mati merupakan ciri struktur utama yang mewakili sumber nutrisi dan energi penting bagi ekosistem hutan. Memainkan peran penting untuk keanekaragaman hayati dan substrat penting bagi binatang dan tumbuhan. Serangga saproxylic tergantung pada reruntuhan pohon selama putaran tertentu dalam hidupnya, hal ini mengakibatkan perubahan jumlah dan kualitas reruntuhan pohon. Praktek ke Hutan di daerah dingin dan boreal sepanjang abad 19 menunjukkan adanya pengrusakan atau penghancuran pada bunga dan binatang, sehingga keberadaan serangga saproxylic terancam dan masuk dalam daftar merah. Deforestrasi terutama terjadi di daerah tropis yang diakibatkan oleh kebakaran akibat ulah manusia, praktek logging yang terus berkelanjutan dan konversi hutan menjadi lahan pertanian. Umumnya hanya sedikit yang mengetahui tentang serangga saproxylic, di daerah tropis dianggap sebagai pengganggu. Objektif dari studi ini adalah investigasi penyebaran reruntuhan pohon (Reruntuhan Pohon halus dan reruntuhan pohon yang kasar) dan serangga saproxylic (Coleoptera, Blattodea, Diptera, Lepidoptera, dan Orthoptera) di daerah bekas terbakar dan tidak terbakar di Hutan Hujan Dipterocarpaceae. Penelitian dilakukan di Hutan Lindung Sungai Wain, Kaltim, Indonesia. Daerah ini mengalami dua kebakaran terburuk beberapa tahun terakhir ini, yaitu pada tahun 1982-83 dan 1997-98, selama musim kemarau akibat El Niño Southern Oscillation atau ENSO. Tujuh pasang sampel plot (masingmasing dengan dua plot sebesar 0.2 ha, total 2.8 ha) untuk mengamati reruntuhan pohon di Hutan bekas terbakar (1.4 ha) dan tidak terbakar (1.4 ha). Daerah seluas 0.04 ha dipilih di pertengahan plot untuk meneliti serangga saproxylic dengan cara memotong pohon dengan menggunakan kapak atau parang. Parameter lingkungan termasuk jumlah dan kualitas reruntuhan pohon juga diukur. Ditemukan sebanyak 1616 serangga saproxylic, dikumpulkan dengan tangan dan diurutkan berdasarkan berat atau diletakkan berdasarkan level famili/sub famili untuk Coleoptera (teridentifikasi 28 famili) dan Blattodea (teridentifikasi Panesthia sp). Parameter lingkungan mempengaruhi komposisi dan kelebihan taxa diteliti dengan menggunakan analisis multivariate (CCA).

Studi ini melaporkan jumlah pohon mati terbanyak yang pernah ada di daerah tropis untuk hutan bekas terbakar dan tidak, dengan nilai rata-rata 196.6 m³ ha⁻¹ di daerah tidak terbakar dan 373.8m³ ha⁻¹ di daerah bekas terbakar. Terdapat sobekan rata-rata 36.8% di daerah tidak terbakar dan 45.1% di daerah terbakar dari volume reruntuhan yang ditemui. Terdapat perbedaan yang signifikan terhadap penyebaran kelas kerusakan antara hutan bekas terbakar dengan yang tidak terbakar. Dengan kerusakan yang relative sedikit pada reruntuhan pohon yang kasar di daerah hutan bekas terbakar. Juga, ukuran sobekan relative lebih besar ditemukan di daerah tidak terbakar, walaupun secara signifikan lebih banyak sobekan di daerah bekas terbakar. Tidak ada perbedaan kerapatan serangga ditemukan diantara daerah hutan bekas terbakar dan tidak, kecuali untuk famili Eucnemidae Coleopteran, dimana ditemukan jumlah yang lebih besar per m³ reruntuhan pohon di daerah tidak terbakar. Menurut biomassa, hanya Blattodea (semua individu kecuali untuk Panesthia sp.), berbeda secara signifikan antara hutan bekas terbakar dan tidak, dengan massa yang lebih tinggi ditemukan di daerah terbakar. Tren mendekati signifikan dari total biomassa tertinggi untuk Panesthia sp. dan Blattodea (total) ditemukan di daerah hutan terbakar . Beberapa taxa yang sering ditemukan menunjukkan preferensi yang signifikan untuk derajat kerusakan tertentu. Kelas kerusakan dari reruntuhan pohon adalah parameter lingkungan terpenting yang dapat menjelaskan penyebaran serangga saproxylic. Jumlah sample berlebihan berkorelasi positip dengan kelas kerusakan dan volume reruntuhan pohon. Tidak ada perbedaan pada kesuburan sampel atau total kesuburan ditemukan pada hutan bekas terbakar dan tidak, tetapi total kesuburan sample berkorelasi positip dengan kelas kerusakan dan volume reruntuhan pohon. Kesuburan juga berkorelasi positip dengan konektivitas reruntuhan pohon.

Jumlah reruntuhan pohon tertinggi ditemukan di daerah terbakar menjelaskan bahwa api menciptakan sobeka yang lebih banyak. Keseluruhan jumlah reruntuhan pohon ditemukan di hutan bekas terbakar kemungkinan selama masa kemarau panjang akibat ENSO antara tahun 1982-83 dan 1997-98, tetapi sebagian juga bias dijelaskan sebagai tingkat kerusakan rencah dimana didominasi bunga spesies tertentu dan menurunkan kandungan air dari reruntuhan pohon selama kemarau. Kebakaran tahun 1997-98 mungkin masih meninggalkan beberapa serangga saproxylic yang masih hidup, yang bisa menggambarkan ketika studi ini dilakukan adlah perpanjangan putaran hidup serangga saproxylic. Persamaan juga bis dijelaskan dengan pemulihan diri yang cepat oleh binatang saproxylic, serangga saproxylic mungkin menggunakan substrat pada hutan terbakar.

Penelitian lanjutan dimasa yang akan datang disarankan untuk mendapatkan pengetahuan tentang serangga saproxylic di daerah tropis dan pemahaman mendalam dampak kebakaran hutan pada binatang saproxylic. Juga, jumlah besar dari reruntuhan pohon yang ada di hutan bekas terbakar dan tidak merupakan bahan baker untuk kebakaran hutan dimasa yang akan datang, dimana mengharuskan investasi tinggi untuk mencegah api, termasuk informasi public dan kebijakan perubahan penggunaan lahan.

Sammendrag

Fordeling av død ved og saproxyliske insekter i brent og ubrent lavlands dipterokarp regnskog, øst Kalimantan, Indonesia

Død ved er en svært viktig komponent i skogsøkosystemet, både som fysiske strukturer og som lagre av næringsstoffer og energi. Død ved spiller en nøkkelrolle for biodiversitet og er et viktig substrat for både planter og dyr. Den saproxyliske insektsfaunaen er avhenging av død ved og vil derfor bli påvirket av forandringer i mengder og kvaliteter av død ved. Skogskjøtselen i tempererte og boreale områder har i løpet av det siste århundre vært svært ødeleggende for både flora og fauna, hvilket har medført at mange av de saproxyliske insektene er "rød-listet". Store avskogninger som følge av skogbranner, tømmerhugst og nyetablering av jordbruksarealer har også foregått i tropene, men man vet generelt svært mye mindre om den saproxyliske insekts faunaen i tropene og hvordan den responderer på menneskeskapte forstyrrelser. Målet for denne studien var å undersøke fordelingen av død ved (fin og grov) og saproxyliske insekter (Coleoptera, Blattodea, Diptera, Lepidoptera og Orthoptera) i brent og ubrent lavlands dipterokarp regnskog. Studieområdet var lokalisert i skogsreservatet Sungai Wain i øst Kalimantan, Indonesia. I dette området herjet to av de verste skogbrannene i senere tid, både i 1982-83 og 1997-98, etter sterk tørke forårsaket av El Niño Southern Oscillation (ENSO) fenomener. Sju plott (hver på 0.2 ha, totalt 2.8 ha) ble i 2001 undersøkt for forekomsten av død ved i både brent (1.4 ha) og ubrent (1.4 ha) skog. Videre ble et område på 0.04 ha valgt i midten av disse plottene igjen, hvor veden ble fysisk undersøkt for forekomsten av saproxyliske insekter ved å bryte den opp med en øks eller machete. Totalt 1616 saproxyliske individer ble funnet, samlet inn og senere veid og identifisert til orden, foruten individer av Coleoptera (28 familier identifisert) og Blattodea (Panesthia sp. identifisert fra de andre). De ulike miljø parametrenes innvirkning på fordelingen og mengden av taxa ble undersøkt ved å benytte multivariat analyse (CCA).

Denne studien dokumenterer noen av de høyeste verdiene for død ved noensinne dokumentert i tropene, både for brent og ubrent regnskog, men et gjennomsnitt på 196.60 m³ ha⁻¹ i ubrent skog og 373.84 m³ ha⁻¹ i brent skog. Andelen av stående døde trær var gjennomsnittelig 36.8% i ubrent skog og 45.1% i brent skog av den totale andelen død ved. Det var en signifikant forskjellig fordeling av råttenhetsklasser mellom brent og ubrent skog, med relativt mer lite nedbrutt ved i ubrent skog. Det ble ikke funnet noen forskjeller i tettheter av saproxyliske insekter mellom brent og ubrent skog, foruten billefamilien Eucnemidae, som ble funnet i større mengder pr m³ død ved i ubrent skog. Av biomassefordelinger ble kun Blattodea (alle individer foruten *Panesthia* sp.) funnet i større mengder i brent skog. En nær-signifikant forskjell for høyere total biomasse i brent skog, ble funnet både for Blattodea (totalt) og *Panesthia* sp. Flere av de viktigste faktorene for fordelingen av saproxyliske insekter. Totalt antall insekter i den døde veden var også positivt korrelert med vedens råttenhet og volum. Det ble ikke funnet forskjeller i vedens råttenhet og volum. Rikhet var også positivt korrelert med økende tetthet av død ved.

Grunnen til at det ble funnet mer død ved i de brente områdene skyldes for en stor del all den stående døde veden (av relativ liten diameter) dannet av brann. De generelt høye verdiene funnet i ubrent skog antas å skyldes den sterke tørken i 1982-83 og 1997-98. De høye verdien funnet kan også forklares som følge av lav forråtnelseshastighet på grunn av floristisk dominans av enkelte arter, og redusert vanninnhold i veden på grunn av tørke. Noe av den saproxyliske faunaen kan ha overlevd skogbrannen i 1997-98, hvilket kan ha blitt reflektert under denne studien på grunn av en forlenget livssyklus hos de xylofage insektene. Likhetene som ble funnet mellom brent og ubrent skog kan også skyldes en rask restaurering av den saproxyliske faunaen, siden døde veden i den brente skogen fremdeles kan nyttiggjøres som substrat.

Det anbefales å gjøre flere studier for å øke kunnskapen om saproxyliske insekter i tropene og for å forstå effekten av menneskeskapte skogbranner på den saproxyliske faunaen. På bakgrunn av den store mengden død ved som er tilgjengelig både i brent og ubrent skog anbefales det å investere i brannforebyggende tiltak, inkludert informasjonsmateriell til befolkningen, samt å gjøre arealpolitiske forandringer.

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i var midt i de umåtelige urskoger som dekker Borneo og som bidrar til å holde atmosfæren kjølig og hindrer at luftstrømmer stiger opp i disse vindløse tropiske trakter. Vi var omtrent akkurat under ekvator, og omkring hundre meter over havet. I januar hadde det vært lite regn, og om dagen hadde det rådet en fuktig varme, men uten noen overdreven hete å tale om, forutsatt at ens antrekk passer for tropene [...]
Som regel var dagene lyse og varme med vakkert vær. De få dager da det var overskyet, kjentes det rent kjølig, så man stundet efter at solen skulde komme frem igjen [...]
En annen eiendommelig iaktagelse jeg gjorde ved Mahakamfloden var den virkning som tørrværet hadde på urskogen. På et sted hvor den dekker de høider som steg opp fra elvebredden, så ikke alene underskogen men også mange store trær helt døde ut. Efter hvad jeg senere hørte om skogbrandene i Sarawak, hvor usedvanlig tørt vær kan forårsake brand som varer i måndesvis, var dette utvilsomt også tilfellet her, men det er underlig at i et land så fuktig som Borneo kan været, skjønt riktignok meget variabelt, bli tørt nok til å ødelegge skogene på denne måten..."

-Carl Lumholtz*-



^{*} Carl Lumholtz: "Under tropenes himmel- to år blandt hodejegerne på Borneo", Gyldendal Norsk Forlag, Oslo, 1938.

Fuel For Future Forest Fires Distribution of woody debris in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia

Abstract

Dead wood (woody debris; WD) forms major structural features and represents important sources of nutrients and energy for the forest ecosystem. It plays an important role for biodiversity and is an important substrate for both animals and plants, yet still little is know about the distribution and amount of WD in the tropics compared to temperate regions. In this study, the distribution of fine woody debris ($5 \le FWD \le 10$ cm diameter) and coarse woody debris ($CWD \ge 10$ cm diameter) was investigated in 2001, both in burnt and unburnt lowland dipterocarp rainforest in the Sungai Wain Protection Forest near Balikpapan, East Kalimantan, Indonesia. This area experienced two of the worst forest fires in resent history, both in 1982-83 and 1997-98, during prolonged droughts caused by strong El Niño Southern Oscillation (ENSO) events. The objectives of this study were to investigate the amount of WD, stages of decomposition, and structural distribution (log/snag and sizeclasses) between burnt and unburnt forest. This study reports some of the highest amounts of WD ever reported from the tropics, both for burnt and unburnt forest, with an average of 196.6 m³ ha⁻¹ in unburnt forest and 373.8 m³ ha⁻¹ in burnt forest. The occurrence of snags was on average 36.8% in unburnt forest and 45.1% in burnt forest of the WD volume encountered. There was a significantly different distribution of decay classes between burnt and unburnt forest, with a relatively less decayed CWD in the burnt forest. The size class distribution was also significantly different, with more small-sized CWD (< 30 diameter) in the burnt forest. More WD was encountered in burnt forest towards the north in the study area, which is explained indirectly by fire intensity through differences in moisture conditions due to topographical differences. The higher amounts of WD found in the burnt areas are largely explained by more snags, created by the fires. The overall high amount of WD found in unburnt forest may be due to the severe drought during the prolonged ENSO events, both 1982-83 and 1997-98, causing elevated mortality rates. It could also partly be explained by low decay rates due to floristic domination of certain species, and decreased water content of WD due to drought. The WD present in both burnt and unburnt forest constitutes a large amount of fuel for future forest fires, which necessitates a high investment in fire prevention, including public information and change in land-use policies.

Keywords: woody debris; East Kalimantan; Indonesia; dipterocarp; forest fires; deforestation; El Niño

Introduction

The lowland dipterocarp rainforest (LDRF) of East Kalimantan, Indonesia, is one of the most speciesrich ecosystems in the world, both florally and faunally (Whitmore 1984 *in* Makihara *et al.* 2000; Primack & Hall 1992; MacKinnon *et al.* 1996; Schweithelm & Glover 1999). Historically, natural fires in this area have been rare and only occurred periodically, but due to human activities (e.g. logging, agriculture, plantation and settlement) the risk of fire has increased dramatically over the past decades (Schweithelm & Glover 1999; Dam *et al.* 2001). Large forest areas in East Kalimantan have been set on fire several times. The worst fires occurred in 1982-83 and 1997-98 during prolonged droughts caused by strong El Niño Southern Oscillation (ENSO) events (Harper 1995; Schweithelm & Glover 1999; Mori 2000). During the biggest fires in 1997-98, more than 5 million ha were affected in East Kalimantan alone, of which more than 2.5 million ha were forest (Ruitenbeek 1999; Siegert *et al.* 2001). The costs of the fires have been dramatic, both ecologically (Schweithelm & Glover 1999) and economically (Ruitenbeek 1999).

During the latter half of the last century, large-scale changes in forest ecosystems have mainly been caused by human activities such as logging, settlement (transmigration), pollution and human-caused forest fires (Bierregaard et al. 1992; Primack & Hall 1992; Fearnside 1997a; Phillips 1997; Nepstad et al. 1999; review in Laurance 1999; Fridman & Walheim 2000; Mori 2000; Pyne 2001; Groven et al. 2002). Thus, forest management practices along with natural disasters, like uprooting during storms, drought, or epidemic pests and diseases, can all be agents of increased tree mortality, and will largely affect the amount of woody debris (WD) in an area (review in Harmon et al. 1986; Franklin et al. 1987; Fridman & Walheim 2000; Gale 2000; Gerwing 2002). Different natural mortality agents also have a synergistic effect on mortality of individual trees (e.g. a tree weakened by fire can be killed by a secondary insect attack) or stands (e. g. trees surviving after a fire can experience greater exposure to winds and be killed by uprooting) (Harmon et al. 1986). There are also synergistic effects of human-induced mortality agents, e.g. prior logged or burnt forest is more susceptible to future fire (review in Laurance 1999; Siegert et al. 2001; Gerwing 2002). Burning may result in the removal of WD from the forest, but it can also be responsible for the creation of additional WD through fire- or bark beetlecaused mortality (Geiszler et al. 1980; Nieuwstadt 2002). Therefore, the overall amount of WD remaining after fire is likely to be site-specific and dependent on the amount of WD consumed by fire and the amount of WD created (directly or indirectly) by the fire (Niwa et al. 2001). Also, decomposition rates of WD vary widely among different forest types and stands, and as a result the amount of WD accumulated over time also varies among forest types and regions (Sollins 1982; review in Vogt et al. 1986; Idol et al. 2000; Carmona et al. 2002).

WD, both in the form of snags and logs, forms major structural features and represents important sources of nutrients and energy for the forest ecosystem, as well as for specialized organisms that have evolved to conduct the task of decomposition (Harmon *et al.* 1986; Speight 1989; Niwa *et al.* 2001). WD plays an important role for biodiversity and is an important source of substrate for vertebrates (e.g. birds, mammals, amphibians, and fish), invertebrates (e. g. snails, spiders, pseudoscorpions, insects, earthworms), bryophytes, fungi, lichens and higher plants (*review in* Harmon *et al.* 1986 and Samulesson *et al.* 1994). WD, varying with decay rates, is a pool for nutrients (N, P, S), and nutrients in freshly fallen WD can be unavailable for regenerating vegetation for several decades in temperate/boreal regions (Harmon *et al.* 1986; Franklin *et al.* 1987; Idol *et al.* 2000; Hughes *et al.* 2001). Generally, tropical forests have a greater N-retention in living biomass than on the forest floor (in fine and coarse debris), compared with temperate or boreal forests (*review in* Vogt *et al.* 1986). In a lowland rainforest, coarse woody debris (CWD \geq 10 cm diameter) can account for about one-third of the total organic matter accumulation (Yoda & Kira 1982). The functional importance of WD depends not only on the amount of WD, but also its distribution in terms of size, spatial arrangement, degree of decay, species, and position (e.g. snags versus logs) (e.g. Harmon *et al.* 1986; Tavakilian *et al.* 1997; Schiegg 2000; Jonsell & Weslien 2003; Endrestøl 2003, *in prep.*).

Although it is known that WD is an important factor in forest ecosystems, little is known about the distribution and amount of dead wood in the tropics compared to temperate regions (Harmon *et al.* 1995; Grove 2001; Waddell 2001; Clark *et al.* 2002; Nascimento & Laurance 2002). There is also general lack of knowledge on dead wood and its associated biodiversity in the tropical regions compared to temperate/boreal regions (Samuelsson *et al.* 1994; Grove 2000; Carmona *et al.* 2002).

The objective of this study was to document the amount of WD found in a LDRF, and determine to what extent forest fires have contributed to the distribution of FWD and CWD, both quantitative (volumes and size-class distributions) and qualitative (decay classes and log/snag distribution).

Materials and Methods

Study area

The study was carried out in the Sungai Wain Protection Forest, a water-catchment reserve of ca 100 km² near Balikpapan, East Kalimantan (116° 54' E and 1° 16' S), Indonesia (Fig. 1.1). Three-quarters of the reserve are covered with LDRF. The eastern quarter of the reserve has been encroached by illegal settlers, and is covered with agricultural land and shrub. The reserve borders low-intensity agricultural land (so-called alang-alang, *Imperata* sp. shrub lands) in the south and the east, a mosaic of logged forest and plantations in the north, and a mosaic of logged forest and mangrove forest in the west. The topography of the reserve consists of gentle to sometimes steep hills, and is intersected by several small rivers. There is a slight north-south gradient in altitude, which varies from 40 to 140 m.a.s.l. (Topographical classification and distribution is given in Table A1.1.1, Appendix 1.1). The soil consists mainly of alisols (MacKinnon *et al.* 1996). These are strongly weathered, very deep, infertile soils, which contain a high fraction of loam and clay.

The abundance of tree families in the Sungai Wain Protection Forest is typical for dipterocarp rainforest (Table A1.1.2 in Appendix 1.1). The most common families with stems above 10 cm diameter at breast height (dbh) are Euphorbiaceae, Dipterocarpaceae and Sapotaceae. The relative dominance of Dipterocarpaceae increases substantially in the larger size classes. No single tree species (stems > 10 cm dbh) dominates the vegetation (Table A1.1.3 in Appendix 1.1). Together, the 25 most common species form 40% of the total stem density. The dominance of Dipterocarpaceae in the larger size classes is due primarily to *Shorea laevis*. Above 50 cm dbh, *Shorea laevis* is by far the most abundant, whereas *Dipterocarpus confertus, Eusideroxylon zwageri, Koompassia malaccensis, Shorea smithiana, Dipterocarpus humeratus* and *Dipterocarpus cornutus* are also fairly abundant. Emergent trees of *Shorea laevis* form nearly monodominant stands on some of the ridges in the reserve (Nieuwstadt 2002).

Temperatures are relatively constant throughout the year, and are normally between 25°C and 35°C in lowland areas of Kalimantan (MacKinnon *et al.* 1996). All parts of Kalimantan lie within the everwet zone (MacKinnon *et al.* 1996) and average annual rainfall in the Sungai Wain Protection forest was 2968 \pm 510 (mm y⁻¹ \pm SD) from January 1998 to January 2002 (G. Fredriksson, *unpubl. data*). Rainfall patterns are not consistent on an annual basis, but a "wet" and a "dry" season can usually be distinguished, with the former starting in October-April and the latter starting in May-September (Fig. 1.2).



Figure 1.1. Map of the Sungai Wain Protection Forest and the permanent sample plots (PSPs). The enlargement shows the Sungai Wain forest indicating the unburnt area (dark grey), and the areas which burned once in (1998) (light grey) or twice (1983 and 1998) (white). East Kalimantan, Indonesia. (*Source*: Nieuwstadt 2002)





ENSO events have occurred throughout history, with the climatic effects varying from event to event (Harper 1995). Based on an inventory made by Leighton (1984, *in* Mori 2000), Nieuwstadt (2002) calculated that since 1887, severe droughts had occurred with intervals of 18 ± 8 years in East Kalimantan. Fires, associated with extended ENSO-related droughts, were described as early as 1914 for East Kalimantan but these were small in scale (Goldammer *et al.* 1996 *in* Siegert *et al.* 2001). East Kalimantan has also been exposed to several fires after prolonged droughts caused by strong ENSO events, both in 1983-84 and 1997-98 (Woods 1989; Schweithelm & Glover 1999; Mori 2000). The 1997-98 ENSO was the severest recorded in history, and a positive feedback between logging and occurrences of fire was found in this period (Siegert *et al.* 2001). The increase in forest fires in East Kalimantan from 1982 onwards can largely be explained by the expansion of forest exploitation (Mori 2000).

The 1982-83 fires occurred in the eastern part of the Sungai Wain Protection forest, but to which extent the reserve was affected is not known for sure (Nieuwstadt 2002, G. Fredriksson, *pers. com.*) (Fig. 1.1). The second fire occurred during the last part of the drought in March- April 1998, burning two-thirds of the reserve. A core area of one-third of the total area (24 km²) has never been affected by fire (Nieuwstadt 2002) (Fig. 1.1).

Permanent sample plots (PSPs)

In the Sungai Wain Forest 18 permanent sample plots (PSPs) of 20 x 200 m (0.4 ha) each have been established in unburnt primary forest and in forest that had burned once in March 1998 (Fig. 1.1). The PSPs cross one-metre wide man-made firebreaks, which were established during the fires. The firebreaks did not correspond to any topographical feature in the places where the PSPs were positioned, and so allowed for a random sampling scheme, with paired plots of unburnt and burnt forest at short distances from each other. The PSPs were laid out in nine pairs; each pair of PSPs adjacent to each other on either side of the firebreak in burnt and unburnt forest. Thus, each pair of PSPs formed one contiguous transect of 20 x 400 m, half in burnt and half in unburnt forest. The PSPs were nested into three groups- (located south, west and north in the study area) with three PSP pairs in each forest area, spread out over a total area of ~20 km². The distance between two pairs of PSPs was always more than 500 m (Nieuwstadt 2002). The northern PSPs were mainly situated on ridges and slopes, whereas the southern PSPs were located on slopes and swamps, whilst the western PSPs were intermediate, representing a more heterogeneous topography (A. Endrestøl, *unpubl. data*). This, combined with the south-north altitude gradient, permits a ranking of the PSP groups according to moisture conditions, with the northern area as the driest, the southern as the wettest, and the western PSPs of intermediate moisture.

Fourteen of the 18 PSPs were used in this study (two pairs of the southern and the northern plots, and three pairs of the western plots). To avoid some of the boundary effects, only the area >100 m from the firebreaks were used (20 x 100 m). The plots in burnt and unburnt forest were therefore 200 m apart on each side of the firebreaks. In this way seven plots (each with two plots of 0.2 ha, totalling 2.8 ha) were investigated in both burnt (1.4 ha) and unburnt (1.4 ha) LDRF. Each plot was subdivided into 20 subplots, each 10 x 10 m, to facilitate sampling efforts (Fig. 1.3). In some of the southern PSPs small-scale low-intensity illegal logging activities have taken place. The main tree species that has been harvested is ironwood (*Eusideroxylon zwageri*) (Fredriksson & de Kam 1999).



Figure 1.3. A diagram illustrating the structure of a permanent sample plot (PSP). Only the areas indicated by subplot numbers (totalling 0.2 ha on each side of the firebreak) were used for sampling woody debris in the present study.

Woody debris (WD) measurements

The fieldwork was conducted between February and April 2001. In each PSP, all coarse woody debris (CWD \geq 10 cm at the larger end) were counted and measured. For each fallen dead tree (log) we measured the length and diameter at both ends. For logs over 5 m in length a middle diameter was also measured. When logs were elevated from the forest floor, girth was measured instead of diameter because this is a more accurate measurement. If the girth or diameter measurements of the CWD would clearly over- or under estimate the volume (e.g. if the log was hollow or with big trunks), an estimated percentage (more or less than 100%) was added to the measurements and later used in the volume calculations. For standing dead trees (snags) we measured the girth at breast height and visually estimated the height. Because all snags had only one measurement for girth or diameter, a measurement for top diameter had to be estimated. To estimate a top diameter for snags, all logs over 10 m in length with more than one measurement of diameter were analysed for decrease in diameter m⁻¹. Maximum and minimum diameter values were used, and the difference was divided by the total length of the log. The calculation showed that logs in general declined 2.8% in diameter m⁻¹ of length. This number was used to estimate volumes of snags having just one measurement for girth. All CWD were also allocated to one of 5 decay classes according to the decomposition state (tested with a machete) accompanied with a visual factor (Table 1.1). No attempt was made to identify dead trees to species due to high species diversity (>180 species ha⁻¹; van Nieuwstadt 2002).

An area of 5 x 10 m inside subplot 9 or 11 (Fig. 1.3) was selected at random and all fine woody debris $(5 \le FWD < 10 \text{ cm diameter})$, were measured in the same manner as for CWD. The terms "log" and "snag" will not be used for FWD, but instead referred to as "downed" and "standing". The "downed" category of FWD consisted for a large part of branches and twigs.

Table 1.1. Decay classes for woody debris (WD) used in Sungai Wain Protection Forest, East Kalimantan, Indonesia (modified after Irmler *et al.* 1996).

Decay class	Description
1	Wood hard. The bark is firmly attached to the wood. Relatively newly fallen or standing dead tree.
2	Wood hard. Bark missing or loosely attached to the wood.
3	Wood hard. Ill- defined shape. Often just cores (heartwood). Mostly hardwood species. Heavily burned logs, which were still hard, also fall in to this category.
4	Outer layer of the wood soft, still with a hard core. Bark missing or loosely attached.
5	Wood rotten. Hard core missing. Shape variable. Bark can still be attached.

All statistical analyses were conducted in SigmaStat 1.0 with a level of significance set at 0.05. Standard deviation was used to reveal variations within the data. Parametric tests have been used, except for correlations including categorical data.

Results

Volume of coarse woody debris (CWD)

Five of 3717 CWD samples (logs and snags) lacked enough measurements to calculate the volume, and another four were removed because of extreme volume values (probably due to incorrect measurements). A total of 798.6 m³ CWD was measured in the 14- 0.2 ha plots, with 34% of CWD found in unburnt plots and 66% found in burnt plots. There was significantly more dead wood in burnt PSPs than in the unburnt PSPs, with on average 196.6 m³ ha⁻¹ CWD in unburnt PSPs, and 373.8 m³ ha⁻¹ in burnt PSPs, (t- test, t = 3.21, df = 12, p = 0.0075, Table 1.2).

Table 1.2. Average amount (m³ ha⁻¹ ± SD) of coarse woody debris (CWD \geq 10 cm diameter) as logs and snags in burnt and unburnt lowland dipterocarp rainforest (LDRF), East Kalimantan, Indonesia

	Unburnt LDRF	Burnt LDRF
Logs	123.8 ± 71.8	205.1 ± 45.9
Snags	72.4 ± 25.9	168.7 ± 115.9
Total CWD	196.6 ± 134.7	373.8 ± 56.9

When comparing the various PSPs separately, the average amount of CWD in the *unburnt* subplots was not significantly different among the three PSP locations (north, west, south) (ANOVA, F = 0.68, df = 2, p = 0.50), but differed significantly in *burnt* subplots (ANOVA, F = 3.32, df = 2, p = 0.043, Fig. 1.4). A Student-Newman-Keuls test revealed that there was a significant difference between the north and south PSPs. The amount of CWD in the burnt areas showed a gradient from south (wettest) to north (driest) (Spearman Rank Order Correlation, R = 0.31, p = 0.016, Fig. 1.4). No such gradient was found in the unburnt areas (Spearman Rank Order Correlation, R = -0.22, p = 0.092). No significant difference was found in the amount of CWD between burnt and unburnt subplots in the south (t- test, t = 0.27, df = 38, p = 0.79). In the west and the north however, there was significantly more CWD in the burnt plots (W; t- test, t = 2.85, df = 38, p = 0.007. N; t-test, t = 3.39, df = 38, p = 0.0016, Fig. 1.4).

Table 1.3. Size class distribution of coarse woody debris (CWD \geq 10 cm diameter) in burnt and unburnt lowland dipterocarp rainforest (LDRF), East Kalimantan, Indonesia.

	Size classes (d)	10-19.9	20- 29.9	30- 39.9	40- 49.9	50- 59.9	60- 69.9	70- 79.9	> 80 cm
Loge	Burnt LDRF	84.1%	10.5%	2.7%	1.2%	0.5%	0.3%	0.2%	0.6%
Logs	Unburnt LDRF	82.3%	10.4%	2.9%	2.0%	1.5%	0.2%	0.3%	0.4%
Spage	Burnt LDRF	69.6%	16.7%	5.6%	2.8%	1.9%	1.3%	0.6%	1.7%
Snags	Unburnt LDRF	53.3%	22.1%	8.3%	6.7%	2.9%	2.5%	1.3%	2.9%

Most CWD had large-end diameters ranging from 10-19.9 cm (Table 1.3). To investigate for differences in size distribution of CWD between burnt and unburnt forest, chi-square tests were applied to the frequency distribution in each size class, pooling the two last classes to increase the power of the test (Table 1.3). There was no difference in the size distribution of logs between burnt and unburnt forest areas, although a close to significant difference was found ($\chi^2 = 11.9$, df= 6, p= 0.065, Table 1.3). However, a significant difference was found in snag size distribution between burnt and unburnt forest areas ($\chi^2 = 22.9$, df = 6, p < 0.001, Table 1.3), with more large snags in the unburnt PSPs. There was a relatively more even distribution of CWD amongst the different size classes in unburnt forest, with ~10% more of the CWD found in the two first size classes in burnt compared with unburnt (Table 1.3).



Figure 1.4. Average volume $(m^3 ha^{-1})$ of coarse woody debris (CWD ≥ 10 cm diameter) in the different forest areas in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia.



Figure 1.5. Relative distribution of logs and snags in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia.

There was no significant difference in the volume of logs (205.1 m³ ha⁻¹ ± 45.9 SD, n = 7) compared to snags (168.7 m³ ha⁻¹ ± 115.9 SD, n = 7) in *burnt* PSPs (t-test, t = 1.21, df = 38, p = 0.24), but there was a significant difference in *unburnt* PSPs (logs; 123.8 m³ ha⁻¹ ± 71.8 SD, n = 7, snags; 72.4 m³ ha⁻¹ ± 25.9 SD, n = 7; t- test, t = 2.26, df = 38, p = 0.03, Fig. 1.5, Table 1.2), with a higher volume of logs than snags. The combined data showed that there were relatively more of both snags and logs (m³) in the burnt subplots than in the unburnt subplots (snags; t-test, t = 3.79, df = 38, p = 0.0005. logs; t-test, t = 2.95, df = 38, p = 0.005, Fig. 6-7, Table 1.2).

Though there was a significantly different volume of *logs* between burnt and unburnt forest, no differences could be detected between the different burnt and unburnt forest areas (south, west, north) (burnt; ANOVA, F = 0.3, df = 2, p = 0.75 - unburnt; ANOVA, F = 2.91, df = 2, p = 0.063. Fig. 1.7). The close to significant difference between volume of logs among unburnt forest areas (Fig. 1.7) is supported by a negative correlation between the PSPs, ranked according to moisture conditions and volume of logs (Spearman Rank Order Correlation, R = -0.32, p = 0.013). No such correlation was found among the burnt forest areas (Spearman Rank Order Correlation, R = 0.166, p = 0.20).

For *snags*, no significant differences were found among the different unburnt forest areas (ANOVA; F = 0.88, df = 2, p = 0.42), but there were significant differences among the burnt PSP locations (ANOVA, F = 5.50, df = 2, p = 0.008, Fig. 1.6). In the post hoc pairwise comparison (Student-Newman-Keuls Method), the only areas not differing were the south compared to the west. More snags were found in the north compared to both west and south. In addition, a positive correlation between the different *burnt* forest areas ranked according to moisture and the volume (m³) of snags was found (Spearman Rank Order Correlation, R = 0.27, p = 0.037, Fig. 1.6). No such correlation was found for unburnt forest areas (Spearman Rank Order Correlation, R = -0.012, p = 0.93).



Figure 1.6. Average volume $(m^3 ha^{-1})$ of snags in the different forest areas of a lowland dipterocarp rainforest, East Kalimantan, Indonesia.



Figure 1.7. Average volume $(m^3 ha^{-1})$ of logs in the different forest areas of a lowland dipterocarp rainforest, East Kalimantan, Indonesia.

Volume of coarse woody debris (CWD) in different decay classes

I calculated the relative volume of each decay class within each PSP, conducted an arcsine root transformation and applied a Two-Way-ANOVA on the distributions, with burnt/unburnt and decay class as controlling factors. There was a statistically significant interaction between the distribution of decay classes and whether the area was burnt or unburnt (F = 9.685, df = 69, p < 0.0001, Fig. 1.8).



Figure 1.8. The relative proportion of the volume of different decay classes for total of coarse woody debris (CWD ≥ 10 cm diameter) in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia.



Figure 1.9. Average volume (m³ ha⁻¹ \pm SD) of different decay classes of coarse woody debris (CWD \geq 10 cm diameter) in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia.

The average volume (m³) of each decay class displayed high variation within the PSPs, both in burnt and unburnt plots (Fig. 1.9). This was caused by one or two toppled big trees in one plot, which account for much of the volume, especially in decay class 1 and 2. There was a significant difference in the distribution of the volume (m³) of CWD among the decay classes in both unburnt and burnt PSPs (unburnt; ANOVA, F = 13.9, df = 4, p < 0.0001, burnt; ANOVA, F = 19.7, df = 4, p < 0.0001, Fig. 1.9). In the multiple pairwise comparisons, all decay classes differed significantly in unburnt forest, except decay class 3 compared with decay class 5 and 1 (Student-Newman-Keuls Method). In the pairwise comparisons between decay classes in burnt forest, all decay classes differed significantly from decay class 2, and decay class 1 differed significantly from decay class 5.

There was significantly more volume of CWD in decay class 2 in burnt forest (t-test, t = 3.33, df = 12, p = 0.006, Fig. 1.9) compared with the unburnt, and significantly more CWD of decay class 3 in unburnt forest (t-test, t = 2.75, df = 12, p = 0.018, Fig. 9) compared with burnt forest. There were no significant differences for the other decay classes (1; t-test, t = 2.12, df = 12, p = 0.056. 4; t-test, t = 1.03, df = 12, p = 0.32. 5; t-test, t = 1.31, df = 12, p = 0.21), even though there was a close to significant difference of more decay class 1 in burnt forest.

Volume of fine woody debris (FWD)

Because of small plots size used for sampling fine woody debris (FWD), volumes were calculated per plot (50 m²) (Fig. 10-11, Table 4). Extrapolations to m³ ha⁻¹ in Table 1.4 (in brackets) are given for comparative purposes only. One of 285 samples lacked enough measurements to calculate volume. A total of 1.26 m³ FWD was measured in the 14- 50 m² plots, with 27% of FWD found in unburnt plots and 73% found in burnt plots (Table 1.4). There was significantly more FWD debris (pooled standing and downed) in burnt than in unburnt plots (t-test, t = 3.01, df = 12, p = 0.011, Table 1.4).

Table 1.4. Average volume of fine woody debris (m³ 50m⁻² FWD \pm SD (m³ ha⁻¹ FWD \pm SD)) shown for downed, standing, and total in burnt and unburnt lowland dipterocarp rainforest (LDRF), East Kalimantan, Indonesia.

	Unburn	t LDRF	Burnt LDRF			
	$m^3 50 m^{-2} \pm SD$	$(m^3 ha^{-1} \pm SD)$	$m^3 50 m^{-2} \pm SD$	$(m^3 ha^{-1} \pm SD)$		
Downed	0.0471 ± 0.030	(9.412 ± 5.974)	0.1080 ± 0.058	(21.607 ± 11.558)		
Standing	0.0017 ± 0.003	(0.296 ± 0.627)	0.0226 ± 0.026	(4.517 ± 5.133)		
Total FWD	0.049 ± 0.03	(9.708 ± 6.282)	0.13 ± 0.06	(26.124 ± 12.966)		



Figure 1.10. Relative proportion of standing and downed fine woody debris $(m^3 50m^{-2})$ in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia.



Figure 1.11. Average volume of fine woody debris $(m^3 50m^{-2})$ in the different forest areas of burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia.

Differences between burnt and unburnt forest for downed FWD were also significant (t-test, t = 2.48, p = 0.029, Fig. 1.10), with more in burnt plots. A close to significant difference was found for standing FWD (t-test, t = 2.16, df = 12, p = 0.051. Fig. 1.10). There was also a significant positive correlation between the volume of CWD and FWD found in unburnt plots (Pearson Product Moment Correlation, R = 0.81, p= 0.0258). No such correlation was found for burnt areas (Pearson Product Moment Correlation, R = 0.13, p = 0.78) (using just the middle 4 subplots of the PSPs for CWD (400m²) to increase the comparability).

It was not possible to analyse for differences of FWD distributions among the different PSP locations within burnt and unburnt forest separately, due to insufficient replications. Even so, there seemed to be a higher amount of FWD in all the burnt forest areas compared with the unburnt (Fig. 11). The decay classes of the FWD were not analysed due to small plot and sample sizes.

Discussion

I documented some of the highest volumes of coarse woody debris (CWD) per hectare ever reported from the tropics, with an average of 196.6 m³ ha⁻¹ in unburnt forest, and 373.8 m³ ha⁻¹ in burnt forest. Gale (2000) compared the amount of CWD in four tropical rainforest sites, with three sites located in north Borneo (Belalong, Andalau, Danum), and one in western Ecuador (Hoja Blanca). He found that dead tree volumes ranged from 97 to 154 m³ ha⁻¹, and that Andalau had the highest volume in Borneo (151.1 m³ ha⁻¹). He also found the proportions of CWD present as snags to be two to three times higher in the Bornean sites compared with Hoja Blanca. A study conducted in an old-growth tropical lowland rainforest in Australia showed that the average amount of CWD was 35.7 m³ ha⁻¹ of logs, and 10.7 m³ ha⁻¹ of snags (total CWD of 46.4 m³ ha⁻¹) (Grove 2001). Clark et al. (2002) found an average of 108.6 m³ ha⁻¹ for logs and 14.5 m³ ha⁻¹ for snags (total CWD of 123.1 m³ ha⁻¹) in an old-growth wet tropical rainforest in Costa Rica. In general, the values reported for tropical forests tend to be slightly higher than those for temperate deciduous forest, but much less than those for temperate or boreal evergreen/coniferous forest (review in Harmon et al. 1986; Grove 2001). A recent study from a temperate forest in Chiloé Island, Chile (representative for evergreen, broad-leaved forests of the North Patagonian type), reported a very high volume of CWD (~1100 m³ ha⁻¹) (Carmona et al. 2002). One should think that the amount of CWD would be higher in a burnt forest area compared with an unburnt area, but in the study from Chiloé, the amounts of CWD in an early-successional site (recently burnt) were equal to the amounts of CWD found in an old-growth site, and that snags represented about 90% of all CWD found in both sites (Carmona et al. 2002).

In my study there was twice as much CWD in burnt forest areas compared to unburnt, with an average distribution of 36.8% snags in unburnt forest and 45.1% snags in burnt forest. When the distribution of the CWD was investigated in more detail, I found a gradient in the burnt areas from the south to the north, ranking them according to moisture condition, with significantly more dead wood in the north (dry) compared to the south (wet). No such gradient, or differences, were found for the unburnt areas. In the south there was no significant difference in the amount of dead wood in the burnt and the unburnt PSPs. Since swamp is a highly represented typological type in the south, this could be due to differences in fire intensity as a result of moisture conditions in the area. Both the western and the northern PSPs had more CWD in the burnt areas than the unburnt.

I found no difference in the total volume of snags and logs in the burnt PSPs, but there was a significantly lower volume of snags in the unburnt areas compared to logs. There was also a significantly higher amount of snags in the northern (drier) PSPs, compared to the other burnt forest plots in the west and south. This was supported by a correlation between relative moisture in forest areas and the amount of snags for burnt areas, with a higher volume of snags towards the drier north. A correlation was also found in the unburnt areas for logs, with lower volume of logs towards the north compared with other unburnt areas.

Although there was overall a higher volume of logs in the burnt forest than in the unburnt, most of the additional dead wood created by the fires (and drought) were snags, and proportionally more snags were created by the fires (and drought) towards the northern PSPs. Gale (2000) explained the higher amount of snags in Borneo compared to Hoja Blanca with differences in prevailing mode of tree death, with much uprooting in Hoja Blanca, whilst mortality due to drought was more prevalent in Borneo. Harmon *et al.*

(1995) found similar results, as 98% of the CWD in their burnt forest site were snags, compared with only 26% snags in their hurricane-damaged forest site. My results also show a significant difference in size-class distribution of snags between burnt and unburnt forest areas, but no such difference for logs.

There could be several reasons why such a high amount of CWD was found in my study. It could be due to either a higher input (tree mortality) of CWD, or it could be due to a lower output (decay) of CWD compared with other sites. Because there are overlapping factors controlling input and output of CWD in burnt and unburnt areas and comparative sites, they will be discussed together.

The high amount of CWD found in the burnt areas could largely be explained by fire mortality (Nieuwstadt 2002), but different mortality agents could also contribute to killing an individual tree (e.g. a tree weakened by fire subsequently killed by a secondary insect attack) or stands (e. g. survivors after a fire experiencing greater exposure to winds and being killed by uprooting) (Harmon *et al.* 1986). The burnt forest areas within the Sungai Wain Protection Forest were still, during my fieldwork 34 months after the fire, experiencing elevated mortality rates compared to the unburnt area (21- 36 months after the fires; unburnt 4% \pm 3% SD, burnt 16% \pm 7% SD), which could be explained by these synergistic mortality agents (Danielsen 2003). The fact that fire mortality increases with decreasing dbh (Woods 1989; Mori 2000; Nieuwstadt 2002) supports my finding of more snags in the lower size classes in the burnt areas. This increase of small-sized snags in burnt forest could also be explained by an increased competition for light, space, soil nutrients, and moisture (Greif & Archibold 2000).

A high increase in mortality rates in tropical forests due to extreme drought has been documented after strong ENSO events (Woods 1989; Mori 2000; Nieuwstadt 2002). In Sungai Wain, mortality was 20-26% amongst trees > 10 cm dbh two years after the drought, and species-specific mortality among trees > 30 cm dbh varied ten-fold. For trees larger than 10 cm dbh, the mortality (caused by fire and drought) was 74% 21 months after the fire. Of the total mortality among trees > 10 cm dbh (burnt and unburnt areas) 21 months after the fire, almost 40% was caused by the drought (Nieuwstadt 2002, Table A1.1.4 in Appendix 1.1). Although fire mortality increases with decreasing dbh, large trees were most vulnerable to drought, and species mortality after drought was negatively related with wood density (Nieuwstadt 2002). This combined effect of drought and fire could explain the increasing amount of snags towards the north, as the northern area probably was the most affected by the droughts due to topography and moisture conditions. The higher input of CWD into this area, mainly created by fire and drought, was encountered both in burnt and unburnt areas. Differences in amounts of CWD, size class distributions, and distribution of logs and snags among the forest areas, can largely be explained by differences in topographical features controlling moisture condition and thus the exposure to drought and subsequently fire intensity. Conversely, the high amount of CWD and its distribution could also be explained by low output of CWD (decay rate), compared with other forest ecosystems.

The residence time (output) of woody debris varies between forest ecosystems and partly explains the different accumulations of CWD encountered (*review in* Harmon *et al.* 1986). As most dominant tree species in LDRF have high wood densities, one could expect the CWD to have a slow decay rate. Wood density is the factor contributing most to differences in decay rates, besides temperature and humidity (Chamber *et al.* 2000; Mackensen *et al.* 2003). Concentration of lignin has also been shown to correlate well with decay rates in the tropics (Vogt *et al.* 1986). Many of the dominant species at this study site have wood

densities > 0.7 g cm⁻³, with *Madhuca kingiana* (Sapotaceae) being the most dominant species > 9.9 cm dbh (27.2%, D = 0.79 g cm⁻³), whereas *Shorea laevis* (Dipterocarpaceae) being the most dominant species > 29.9 cm dbh (D = 0.93 g cm⁻³) (Table A1.1.4 in Appendix 1.1). The explanation of low decay rates linked to high wood densities are also supported by Gale (2000), who suspected that one of the reasons for the high amount of CWD found on the ridges in a LDRF could be floristic dominance of certain taxa, e.g., *Shorea*, which have high wood densities. In comparison, average wood density in tropical forest of the Brazilian Amazon is 0.69 g m⁻³ (Fearnside 1997b).

Yoda & Kira (1982) estimated that the 95% disappearance time for CWD (≥ 10 cm diameter) amounts to 15-16 years (in peninsular Malaysia). This disappearance time might be greatly underestimated, since they used a decay rate constant (k, percent mass loss year⁻¹) = 0.19 year⁻¹. However, Harmon *et al.* (1995) found that there were substantial differences in decomposition rates among species (Yucatan Peninsula, Mexico) and that several species decomposed at rates slower than 0.1 yr⁻¹. They also found that many of the examined species did not decompose linearly with time, and estimated the disappearance time to range from 30- 150 years, depending on species composition. Mackensen *et al.* (2003) reviewed available literature and calculated 184 values for lifetime of CWD (most from temperate forest regions). In 57% of all the cases, the calculated lifetime ($t_{0.95}$) was longer than 40 years (median = 49 yr, mean = 92 yr) (*for details on decay rates and the decay rate constant see reviews in* Harmon *et al.* 1986 and Mackensen *et al.* 2003).

Drought will additionally lead to lower water content of CWD, because of high leaf shedding and increased sunlight penetration to the forest floor, which in turn causes decreased decomposition rates of the CWD (Harmon *et al.* 1986; Mori 2000; Mackensen *et al.* 2003). The same effect is also seen in burnt areas, where there soil temperature was found to be higher, partly due to increased sunlight (higher canopy openness) in burnt areas (also correlated with forest area and topographical types) (Endrestøl 2003, *in prep.*). In the burnt areas, higher substrate temperatures may also lead to a reduced decay rate because many saproxylic organisms might have a lower temperature tolerance (e.g. most wood- decaying fungi cannot grow above 40°C) (*review in* Harmon *et al.* 1986). Even though decay rates often increase with moisture content, it could also be retarded in saturated wood (Rayner & Boddy 1988 *in* Mackensen *et al.* 2003; Progar *et al.* 2000). This could be an explanation for the higher amount of WD found in unburnt areas toward the south, as the southern areas consisted of more swamps and were wetter than the other areas. Thus, high input rate, created by fires and drought (accompanied with secondary mortality factors), and low decay rates due to drought (reduced humidity) and high wood densities, could largely explain the high volume and distribution of CWD found in Sungai Wain.

The large number of dead standing trees (snags) in the burnt areas, explains why significantly more wood in decay class 2, and nearly significant (p = 0.056) more wood of decay class 1, was encountered in the burnt forest. There also was as a significant difference in the relative distribution of decay classes between burnt and unburnt forest, with relatively more CWD of lower decay classes in the burnt forest. No differences were found in the volume of CWD in the higher decay classes (4 and 5) between burnt and unburnt PSPs. There was significantly higher volume of decay class 3 in the unburnt PSPs, which is somewhat unexpected, as charred logs were also allocated to this category. It is possible that this decay class might not have been defined appropriately. Decay class 3 also included logs and stumps that were heavily decayed, but still contained a very hard inner core (often just heartwood), and usually had an ill-defined shape. Heartwood is

known to have a large degree of decay resistance (Harmon *et al.* 1995), which explains why so much of decay class 3 was found in unburnt forest. Overall, the burnt area had a decay distribution skewed toward less decayed wood than unburnt areas. Therefore, it can be argued that very little of the CWD of the highest decay classes was consumed by the fire.

In many ecosystems, intermediate decay classes or states tend to make up the largest portion of CWD biomass, and the highest and lowest decay classes comprise the smallest portion (review in Harmon et al. 1986). This was also found in my study for unburnt forest. However, disturbance, along with other factors, will cause a deviation from the expected steady-state decay class pattern (Harmon et al. 1986). This was also found in my study, as there was a shift towards less decayed CWD in the burnt forest. This comparison among sites within the same study is quite straight forward, but less so among studies. The distribution of the decay classes depends on the definitions used, and the transition times used for the different decay classes. Due to the fact that there are no widely agreed upon definitions (yet) for categorizing CWD into the various decay classes, comparisons with other studies are somewhat difficult. I have used my own decay classes (modified after Irmler et al. 1996), whilst other studies have used their own, or modified a formally used, system, ranging from a few classes up to eight different categories (Yoda & Kira 1982; review in Harmon et al. 1986; Araya 1993; review in Samuelsson et al. 1994; Irmler et al. 1996; Økland et al. 1996; Jonsell et al. 1998; Pyle & Brown 1999; Fridman & Walheim 2000; Grove 2000; Sverdrup-Thygeson 2001; Clark et al. 2002; Groven et al. 2002; Nascimento & Laurance 2002; Similä et al. 2003). Several studies have used, or recommend using, the five-class system described by Sollins (1982) (see Idol et al. 2000; Carmona et al. 2002; Waddell 2002), which was developed for coniferous forests (manly Douglas-fir (Pseudotsuga menziesii), Sitka spruce (Picea sitchènsis)) (Sollins 1982). These decay classes have been found to correlate well with structural, biochemical, and ecological characteristics of dead wood (Sollins 1982; Idol et al. 2000).

On the other hand, allocating CWD into a certain decay class might be a bit misleading, because a log of a given decay class is likely to provide a greater heterogeneity of habitat conditions than might be suggested by its decay class definition, due to within-log decay heterogeneity (Pyle & Brown 1999). It is also possible that logs, placed in the middle of a decay sequence, have the highest heterogeneity (Pyle & Brown 1999). This might have been true for my decay classes 2 and 4, excluding decay class 3 (because of reasons described earlier). Also, the nutrient content of CWD in the different decay classes may be overlapping, which is why Idol *et al.* (2000) suggested that class 2 and 3 should be combined into a single class, to better reflect substrate quality (decay classes after Sollins 1982).

I also found a significant difference in fine woody debris (FWD) between burnt and unburnt forest areas, although it was difficult to compare the results with other studies. Again, this is due to differences in defining this category. FWD has not been investigated as much as CWD, and is often included in "forest floor litter", or a broader definition than I used (see methods), is applied (Yoda & Kira 1982; Takyu *et al.* 2002). The size classes I used for FWD are occasionally incorporated into CWD definitions (Harmon *et al.* 1986; Carmona *et al.* 2002) or treated as one fraction, dead wood (Martikainen *et al.* 1999). Both drought and fire, as discussed above for CWD, could be the reason for the higher amount of FWD found in burnt forest. CWD will produce more FWD, in the form of broken branches and twigs. I found a positive correlation between the amount of CWD and FWD in unburnt areas, but not so for the burnt areas. This could be explained by a higher variation of FWD found in the burnt areas regardless of the amount of CWD found. This variation

could be caused both by the consumption of FWD during the fire (Fearnside *et al.* 1999), or by and production of additional FWD after the fire in burnt forest (e.g. indirectly through the production of more CWD, and increased amount of standing FWD due to fire-mortality (*see above*)). Harmon *et al.* (1995) found that the amount of FWD was low after a fire due to consumption, with highest amount found in undisturbed or hurricane-damaged forest.

The cumulative damaging effects of forest clearing by fire, and extreme drought caused by interannual climate variability such as ENSO events, interact to destroy tropical forests (Goldammer 1999, *review in* Laurance 1999). Nepstad *et al.* (1999) demonstrated that fire (together with logging) increases the vulnerability of tropical forests to future burning (Gerwing 2002). There is also likely to be an increase in the frequency and severity of ENSO events as a consequence of increasing greenhouse gas concentrations (Timmermann *et al.* 1999), through e.g. future logging and forest fires (Fearnside *et al.* 1999; Nepstad *et al.* 1999; Hughes *et al.* 2000). Increased fuel loads may also affect future fire intensity. Extensive build up of fuel, due to fire-mortality, extensive droughts, or logging activities, could make intense fires possible in environments previously not prone to fire (Scott 2000).

Conclusion

My study shows that there are very high amounts of woody debris (WD) present in the Sungai Wain Protection Forest, both in burnt (373.8 m³ ha⁻¹) and in unburnt (196.6 m³ ha⁻¹) forest areas. The WD in the burnt areas is skewed towards bigger and less decayed WD, with a relative higher fraction of snags. The total amount of WD found in burnt areas in Sungai Wain increased towards north (driest areas), with an increasing amount of snags. Not mutually exclusive, the high amounts of WD found are explained either by high input of WD through increased mortality by fire and drought, or as a low output due to decreased decay rates because of high wood densities and drought.

Though the amount of CWD may not be the same in the rest of East Kalimantan, a high amount of WD is likely to be present in similar LDRF areas, which have also been affected by the same environmental and anthropogenic conditions. Prolonged droughts, linked to ENSO events, is likely to increase in the future, increasing the residence time for the WD, due to increased tree mortality and the subsequent rise in sunlight penetration to the forest floor.

The scenario can be summed as follows;

- 1. Increasing frequency of ENSO events with increasing frequency of prolonged droughts.
- 2. Increasing frequency of forest fires due to logging and other human activity.
- 3. Increased fire intensity due to large stores of combustibles (WD).

This scenario, given the economic and ecological cost of previous forest fires, strongly argues for implementation of precautionary principles in management practices. This includes monitoring systems that can detect future ENSO events, and prevention of future forest fires (*see* Harger *et al.* 1993 and Mori 2000,), by providing public information, and implementing changes in land-use policies (*see* Primack & Hall 1992; Fearnside 1997; Schweithelm *et al.* 1999).

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Appendix 1.1: Tree composition, wood density and mortality rates in Sungai Wain Protection Forest, East Kalimantan, Indonesia.

Table A1.1.1. Distribution of topographical types used within the Sungai Wain Protection Forest (relative occurrence \pm SD). East Kalimantan, Indonesia.

	North	South
Swamp	5,9 ± 4,6 %	$16,2 \pm 7,7 \%$
Alluvial	17,3 ± 4 %	$23,7 \pm 9,1 \%$
High-flat	24,8 ± 9,3 %	$28,6 \pm 11,6 \%$
Slope	45,3 ± 9,1 %	$28{,}3\pm6{,}3~\%$
Ridge	$6,7 \pm 2,7 \%$	$3,2 \pm 2,1 \%$

(Source: G. Fredriksson, unpubl. data)

Table A1.1.2. Stem density (stems ha⁻¹) of most common tree families in the unburnt forest areas of Sungai Wain Protection Forest eight months after the 1997-98 drought (average \pm SD of 9 permanent sample plots (PSPs)). East Kalimantan, Indonesia.

Data are presented for all trees (excl. Palmae (Arecaceae)) above the indicated minimum size limit. Percentages indicate the relative contribution of each family to the total stem density.

	>9.9 c	em dbh		>29.9 cm dbh >49.9 cm				em db	h
Family	Average	SD	%	Average	SD	%	Average	SD	%
Euporbiaceae	69.2	16.2	14	3.2	1.9	4	0.3	0.5	1
Dipterocarpaceae	57.5	22.8	12	19.1	6.9	26	10.6	5.9	48
Sapotaceae	55.6	23.8	11	3.7	2.0	5	0.2	0.3	1
Myrtaceae	35.6	26.0	7	3.9	1.7	5	0.5	0.6	2
Myristicaceae	27.5	18.1	6	1.5	1.1	2	0.0	0.0	0
Lauraceae	25.0	11.6	5	4.2	4.3	6	1.2	2.0	6
Burseraceae	19.2	8.7	4	2.4	1.3	3	0.6	0.5	3
Ulmaceae	16.9	6.5	3	1.2	1.1	2	0.1	0.2	0
Bombacaceae	15.3	10.9	3	1.3	1.5	2	0.1	0.2	1
Caesalpinioidae	15.0	9.9	3	4.3	1.7	6	1.4	0.9	6
Moraceae	12.5	7.1	3	1.4	1.2	2	0.1	0.4	1
Ana cardiace a e	10.6	5.1	2	1.9	1.1	3	0.6	0.6	2
Annonaceae	9.4	6.7	2	0.6	0.5	1	0.1	0.2	1
Melastomataceae	8.6	3.8	2	0.1	0.2	0	0.0	0.0	0
Olacaceae	8.1	5.1	2	0.9	0.9	1	0.0	0.0	0
Fagaceae	7.5	2.5	2	0.7	0.9	1	0.2	0.3	1
Rubiaceae	7.5	5.6	2	0.4	0.5	1	0.1	0.2	0
Ebenaceae	7.2	5.1	1	0.4	0.5	1	0.0	0.0	0
Lecythidaceae	6.7	4.8	1	0.4	0.5	1	0.1	0.2	0
Sterculiaceae	6.4	4.2	1	0.4	0.4	1	0.2	0.3	1
Meliaceae	5.8	4.0	1	0.5	0.3	1	0.1	0.2	1
Guttiferae	5.3	2.3	1	0.4	0.5	1	0.1	0.2	0
Mimosoidae	4.7	3.2	1	1.0	0.8	1	0.2	0.4	1
Polygalaceae	4.7	4.6	1	1.4	1.0	2	0.2	0.3	1
Sapindaceae	4.7	5.2	1	0.2	0.3	0	0.0	0.0	0
Other	42.2	18.0	9	18.6	7.1	25	5.3	5.1	24

(Source: Nieuwstadt 2002)

Table A1.1.3. Stem density (stems ha⁻¹) of most common species in the unburnt forest areas of Sungai Wain Protection Forest eight months after the 1997-98 drought (average \pm SD of 9 permanent sample plots (PSPs)). East Kalimantan, Indonesia. Data are presented for all trees above the indicated minimal size limit. Percentages indicate the relative contribution of each species to the total stem density. * For Borassodendron (Palmae), no dbh was measured. All individuals were < 29.9 cm dbh. ** These species were included in the table because they are relatively common in the size class > 49.9 cm dbh.

	> 9.9 cm dbh			> 29.9	cm d	bh	>49.9 cm dbh		
Species	Aver.	SD	%	Aver.	Aver. SD %			SD	%
Madhuca kingiana (Brace) H.J.Lam	27.2	35.6	6	1.2	0.9	2			
Gironniera nervosa Planch	14.7	6.2	3	1.2	1.1	2	0.1	0.2	0
Macaranga lowii King ex Hook.f.	12.2	6.5	3						
Borassodendron cf. borneensis*	11.1	13.0	2						
Shorea laevis Ridl.	10.3	7.6	2	7.7	4.6	13	5.2	3.6	29
Eugenia tawahense	10.3	13.2	2	0.7	0.9	1			
Payena lucida (G.Don) DC.	10.0	9.0	2	1.1	1.5	2			
Koompassia malaccensis Maing. Ex Benth.	9.2	9.3	2	2.3	1.5	4	0.7	0.8	4
Durio acutifolius (Mast.) Kosterm.	8.9	8.0	2	0.1	0.2	0			
Eusideroxylon zwageri Teijsm. & Binn.	7.2	9.4	2	2.7	3.9	4	1.0	2.0	5
Drypetes kikir Airy Shaw	6.9	7.7	1	0.9	0.9	1	0.1	0.2	0
Shorea ovalis (Korth.) Blume	6.4	5.6	1	1.1	0.8	2	0.3	0.4	2
Dipterocarpus confertus Sloot.	5.8	5.7	1	2.3	1.7	4	1.1	0.9	6
Vatica umbonata (Hook.f.) Burck	5.3	4.4	1	0.2	0.4	0			
Gymnacranthera farguhariana (Hook.f. &	4.7	8.5	1	0.2	0.4	0			
Thomson) Warb.									
Shorea parvifolia Dyer	4.7	3.4	1	0.9	0.9	1	0.2	0.3	1
Dipterocarpus tempehes Slooten	4.7	10.0	1	0.2	0.4	0	0.1	0.2	1
Dacryodes rostrata (Blume) H.J.Lam	4.4	5.1	1						
Chaetocarpus castanocarpus (Roxb.) Thwaites	4.2	6.1	1	1.2	1.0	2	0.2	0.3	1
Dipterocarpus cornutus Dyer	3.9	5.3	1	0.9	1.2	1	0.5	0.7	3
Ochanostachys amentacea Mast.	3.6	2.2	1	0.5	0.5	1			
Diospyros borneensis Hiern	3.6	3.6	1						
Aporosa dioica (Roxb.) Mull.Arg.	3.6	5.9	1						
Barringtonia macrostachya Jack	3.6	4.7	1	0.3	0.4	1			
Madhuca pierrei Van der Assem	3.6	5.3	1	0.4	0.9	1	0.1	0.2	0
Gonystylus affinis Radlk	3.3	5.9	1	0.1	0.2	0			
Shorea smithiana Sym **	2.2	1.5	0	1.0	0.6	2	0.7	0.7	4
Dipterocarpus humeratus Slooten **	0.6	1.1	0	0.8	2.4	1	0.7	2.0	4
Other	278.3	49.7	59	32.0		53	7.3		40

(Source: Nieuwstadt 2002)

Table A1.1.4. Species-specific mortality after the 1997-98 drought and fire of trees above 30 cm dbh in Sungai Wain Protection Forest (21 months after the end of the fire and drought). East Kalimantan, Indonesia.

The percentage dead trees after "drought" and "drought x fire" are given as the average percentage dead trees per permanent sample plot (PSP) (n = 6). To calculate the mortality exclusively caused by fire, the mortality after drought per PSP is subtracted pairwise from the mortality after "fire x drought" for each pair of adjacent PSPs.

]	Percent	age dead t	rees					
	Wood density		Drought							
Species	$(g \text{ cm}^{-3})$	Drought	sd	x fire	sd	Fire	sd			
Arto anis	0.718	20	27	92	17	67	24			
Dipt conf	0.803	15	18	8	10	-14	19			
Dipt corn	0.843	14	13	29	6	15	18			
Dryp kiki	0.999	13	14	31	30	27	18			
Eusi zwag	1.066	5	6	39	5	30	10			
Giro nerv	0.603	30	23	59	39	29	39			
Koom mala	0.934	64	24	92	12	29	24			
Madh king	0.79	17	19	59	38	42	38			
Shor laev	0.933	23	18	44	14	29	21			
Shor oval	0.537	28	22	20	27	-5	33			

(Source: Nieuwstadt 2002)

P we ter en dump dunking som bæres som en skjebnesklokkes klemt gjennom bruset av jungelens stemmer. Sikadenes intense, gjennomtrengende gnisling, sangfuglenes jubel, apenes skrik og neshornfuglens dystre latter formår ikke å overdøve dunkingen. Det er som om jungelen forstår dette varsel. En kan faktisk fornemme hvordan den forsøker å drukne og kvele det i sin mørke og grønne fuktighet. Og gråapene og papegøyene stemmer også opp med energiske protester. Det hjelper ikke. Dunkingen fortsetter. Det er øksehugg..."

- Eric Lundquist *-



^{*} Eric Lundquist: "I jungelens vold"

Gyldendal Norsk Forlag, Oslo, 1954

Burnt Bole, Burnt Bug? Distribution of saproxylic insects in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia

Abstract

The saproxylic fauna form a large part of the terrestrial biodiversity and is an important resource for forest ecosystems, e.g. as decomposers of woody debris (WD) and as a food source for other animals. Forest practices in temperate and boreal areas during the 19th and 20th centuries have resulted in a faunal and floral devastation, resulting in many of the saproxylic insects currently being listed as threatened. Major deforestation has also occurred in the tropics, due to agricultural development, human-caused fires, and extensive logging practices, but still very little is known of the saproxylic fauna in general, and its responses to such human-caused disturbances. This study investigated the distribution of saproxylic fauna (Coleoptera, Blattodea, Diptera, Lepidoptera, and Orthoptera) in 14-0.04 ha sampling plots, within the Sungai Wain Protection Forest, a lowland dipterocarp rainforest reserve in East Kalimantan, Indonesia. The main focus of this study was to compare primary rainforest areas with forest areas that were affected by fires in 1998, coinciding with a prolonged drought caused by an El Niño Southern Oscillation (ENSO). Fine woody debris (5 cm \leq FWD < 10 cm diameter) and coarse woody debris (CWD \ge 10 cm diameter) were investigated by physically chopping up the wood, using an axe or a machete. All 1616 insect individuals encountered and hand collected, were weighed and allocated to order, except for individuals of Coleoptera (28 families identified) and Blattodea (Panesthia sp. identified). Environmental parameters influencing on distribution of saproxylic insects were investigated using multivariate analyses (CCA). Decay class of WD was the most explanatory environmental parameter, even though a low species-score distribution was found. No differences in saproxylic insect density were found between burnt and unburnt forest areas, except for the Coleopteran family Eucnemidae, which were found in higher densities in unburnt forest areas. No differences in sample richness or total richness were found between burnt and unburnt forest area. Total abundance and richness was positively correlated with WD volume and decay class. Richness was also positively correlated with WD connectivity. When looking at biomass, only Blattodea (all individuals excluding Panesthia sp.) differed significantly between burnt and unburnt forest areas, with higher biomasses encountered in burnt areas. Both Panesthia sp. and Blattodea (total) displayed a close to significant difference indicating higher biomasses per hectare in burnt forest. Several of the most frequently found taxa showed a significant preference for certain decay classes. The nature of the 1997-98 fires, at this primary rainforest site, might have left some of the saproxylic fauna alive, which could still be reflected at the time of this study due to the extended life cycles of xylophagous insects. The similarities could also be explained by a quick restoration of the saproxylic fauna, as saproxylic insects still use the substrate in the burnt forest. Future research is recommended to acquire knowledge about the saproxylic insects in the tropics and to further understand the effects of human disturbances on the saproxylic fauna.

Keywords: Saproxylic insects; Kalimantan; Dipterocarp; Forest fire; Decay

Introduction

The lowland dipterocarp rainforests (LDRF) of East Kalimantan, Indonesia, is one of the most species-rich ecosystems in the world, both florally and faunally (Whitmore 1984 *in* Makihara *et al.* 2000; Primack & Hall 1992; MacKinnon *et al.* 1996, Schweithelm & Glover 1999). Historically, natural fires in this area have been rare, but due to human activities (e.g. logging, agriculture, plantation and settlement) the risk

of fire has increased dramatically over the past decades (Schweithelm & Glover 1999; Dam *et al.* 2001). Large forest areas in East Kalimantan have been set on fire several times. The worst fires occurred in 1982-83 and 1997-98, during prolonged droughts caused by strong El Niño Southern Oscillation (ENSO) events (Harper 1995; Schweithelm & Glover 1999; Mori 2000). During the biggest fire disaster in East Kalimantan in 1997-98, more than 5 million ha were affected by the fires, of which more than 2.5 million ha were forest (Ruitenbeek 1999; Siegert *et al.* 2001). The costs of the fires have been dramatic, both ecologically (Schweithelm & Glover 1999) as well as economically (Ruitenbeek 1999).

Habitat destruction, alteration, and fragmentation of large habitats into small patches are often described as the largest threats to biodiversity worldwide (Meffe et al. 1997; Phillips 1997), and the vast majority of the threatened species are insects (Meffe et al. 1997). In a forest ecosystem, fragmentation occurs due to natural phenomena such as uprooting, occasional fires, drought, or epidemic pests (Geiszler et al. 1980; review in Harmon et al. 1986; Franklin et al. 1987; Waring 1987; Scott 2000; Lindbladh et al. 2003). These fragmentations belonging to a natural regime are not necessarily harmful (Phillips 1997), but can be crucial to maintain habitat for threatened species (Muona & Rutanen 1994; Wikars 1997; Jonsell et al. 1998; Niklasson & Drakenberg 2001; Lindbladh et al. 2003). Even so, forest fragmentation due to large-scale deforestation seen during the latter half of the previous century is mainly caused by human activities such as logging, settlement (transmigration), plantations and human-caused forest fires (Speight 1989; Bierregaard et al. 1992; Primack & Hall 1992; Fearnside 1997; Phillips 1997; Laurance 1999; Nepstad et al. 1999; Fridman & Walheim et al. 2000; Mori 2000; Pyne 2001; Groven et al. 2002). Synergistic effects of deforestation are also likely to occur (Phillips 1997), e.g. as a positive feedback between logging and fire occurrences (review in Laurance 1999; Siegert et al. 2001; Gerwing 2002). These events will alter the amount of dead wood found within a forest ecosystem and its continuity (Franklin et al. 1989; Fridman & Walheim 2000; Gale 2000; Endrestøl 2003, in prep.).

Dead wood is a resource representing an important supply and storage of nutrients and energy in a forest ecosystem, as well as a habitat for specialized organisms that decompose it (review in Harmon et al. 1986; Speight 1989; Niwa et al. 2001; Grove 2002). Animals and plants that live in and on dead wood (termed saproxylic, Speight 1989; Key 1993; Grove 2000) assist in breaking down the woody material, in recycling nutrients back into the forest ecosystem (review in Harmon et al. 1986: Speight 1989: MacKinnon et al. 1996), and serve as important sources of food for other species (Niwa et al. 2001). A major group of the saproxylics are the insects (Niwa et al. 2001), mainly beetles (Coleoptera) and flies (Diptera) (Key 1993). A change in the amount of woody debris (WD) could change the species richness and the abundance of the saproxylic insects (McLean & Speight 1993). The distribution and richness of saproxylic insects are shown to be sensitive to many WD characteristics, such as amount of dead wood, decay stage, dead wood diversity, or dead wood connectivity (Irmler et al. 1996; Økland et al. 1996; Jonsell et al. 1998; Martikainen et al. 2000; Schiegg 2000; Sverdrup-Thygeson 2001; Grove 2002; Similä et al. 2003). The mode of tree death also influences the amount and distribution of saproxylics, because trees that die standing upright provide different habitats from downed logs (Franklin et al. 1989; Jonsell & Weslien 2003). Still, studies on saproxylic insects and their responses to habitat destruction and disturbance often provide mixed or inconclusive results (Niwa et al. 2001).

Forest practices in temperate and boreal areas during the 19th and 20th centuries have resulted in a faunal and floral devastation, resulting in many of the saproxylic insects regarded as threatened and on the "red lists" (Muona & Rutanen 1994; Økland *et al.* 1996; Jonsell *et al.* 1998; Lindbladh *et al.* 2003; Similä *et al.* 2003). Speight (1989) reports that 40% or more of the saproxylic species are under threat of extinction on the European continent. Despite a growing body of literature on saproxylic insects and WD, knowledge about biodiversity linked to WD is still poor (Samuelsson *et al.* 1994; Grove 2000; Carmona *et al.* 2002). This applies especially to the tropics, where studies of saproxylic insects are almost absent from the literature (Grove & Stork 1999, 2000; *review in* Grove 2002), and virtually nothing is known about the effects of human-induced disturbance on these insects (Grove & Stork 1999). How much is left to investigate can be exemplified by a plant-host survey made in the Sinnamary River Basin of French Guiana in 1991- 93, where 334 species of one saproxylic beetle family (Cerambycidae) were collected, of which one-quarter had not yet been described (Tavakilian *et al.* 1997).

The objective of this study was to describe the distribution of saproxylic insects (Coleoptera, Blattodea, Diptera, Lepidoptera, and Orthoptera) in both burnt and unburnt LDRF. The study also examines which environmental parameters contribute most to their distribution and to what extent previous fires and droughts have influenced on their numbers.

Materials and Methods

Study area

The study was carried out in the Sungai Wain Protection Forest, a water-catchment reserve of ca 100 km² near Balikpapan, East Kalimantan (1° 16' S and 116° 54' E), Indonesia (Fig. 2.1). Three-quarters of the reserve is covered with LRDF. The eastern quarter of the reserve has been encroached upon by illegal settlers and is covered with agricultural land and shrub. The reserve borders low-intensity agricultural land (so-called alang-alang, *Imperata* sp. shrub lands) to the south and the east, a mosaic of logged forest and plantations in the north, and a mosaic of logged forest and mangrove forest in the west. The topography of the reserve consists of gentle to sometimes steep hills, and is intersected by several small rivers.

There is a gentle north-south gradient in altitude, which varies from 40 to 140 m.a.s.l. The soil consists mainly of alisols (MacKinnon *et al.* 1996). These are strongly weathered, very deep, infertile soils, which contain a high fraction of loam and clay. For more information on vegetation, fire events, and distribution of fine woody debris ($5 \text{ cm} \le \text{FWD} < 10 \text{ cm}$ diameter) and coarse woody debris ($CWD \ge 10 \text{ cm}$ diameter) in the study area, see the previous manuscript (A. Endrestøl 2003, *in prep.*). The abundance and distribution of tree families in the Sungai Wain Protection Forest is typical for a LDRF (Nieuwstadt 2002).

Permanent sample plots (PSPs)

In the Sungai Wain Forest 18 permanent sample plots (PSPs) of 20 x 200 m (0.4 ha) each, have been established in unburnt primary forest and in forest that had burned once in March 1998 (Fig. 2.1). The PSPs cross one-metre wide man-made firebreaks, which were made during the fires (Fig. 2.2). The firebreaks did not correspond to any topographical feature in the places were the PSPs were positioned, which allowed for a random sampling scheme, with paired plots of unburnt and burnt forest at a short distance from each other.
The PSPs were laid out in nine pairs; each pair of PSPs adjacent to each other on either side of the firebreak in burnt and unburnt forest. Thus, each pair of PSPs formed one contiguous transect of 20 x 400 m, half in burnt and half in unburnt forest. The PSPs were nested into three groups (located in the south, west and north of the reserve) with three PSP pairs in each location, spread over a total area of ~20 km² (Fig. 2.1). The distance between two pairs of PSPs was always more than 500 m (Nieuwstadt 2002). There was significantly more dead wood in burnt PSPs than in the unburnt PSPs, on average 196.6 m³ ha⁻¹ CWD in unburnt PSPs and 373.8 m³ ha⁻¹ in burnt PSPs (A. Endrestøl 2003, *in prep.*).

Fourteen of the 18 PSPs were used in this study (two pairs of the southern and the northern plots, and three pairs of the western plots). To avoid some of the boundary effects, the sampling plots (20 x 20 m) were located > 140 m from the firebreak (Fig 2.2). The paired plots in burnt and unburnt forest were therefore 280 m apart on either side of the firebreak. In this way seven paired plots (each with two plots of 0.04 ha, totalling 0.28 ha) were investigated in both burnt (0.14 ha) and unburnt (0.14 ha) LDRF. Each plot was subdivided into 4 subplots, each 10 x 10 m, to facilitate sampling efforts. Even though there was a higher average amount of CWD in the burnt sample plots (14.15 m³ ± 3.14 SE) compared to the unburnt sample plots (7.82 m³ ± 1.80 SE), this was not overall significant because of high variation (Mann-Whitney, T = 64.0, p = 0.17) (A. Endrestøl, *unpubl. data*).



Figure 2.1. Map of the Sungai Wain Protection Forest and the permanent sample plots (PSPs). The enlargement shows the Sungai Wain Protection Forest indicating the unburnt area (dark grey), and the areas which burned once in (1998) (light grey) or twice (1983 and 1998) (white). East Kalimantan, Indonesia (*Source*: Nieuwstadt 2002).



Figure 2.2. A diagram illustrating the structure of a permanent sample plot (PSP) with the area used for sampling saproxylic insects (20 x 20 m).

Environmental measurements

The fieldwork was conducted between February and April 2001, three years after the 1997-98 fire events. Environmental measurements were made at the common corner of the four subplots (Fig. 2.2). Soil temperature was measured with a Beaverton soil thermometer (*UEI/NSF*, -58 - 300 F). Canopy openness was estimated with a spherical densiometer for forest overstory density (Lemmon 1957).

Table 2.1. Distribution of topographical types (relative occurrence \pm SD) within the Sungai Wain Protection Forest, East Kalimantan, Indonesia.

	North	South
Swamp	$5.9\pm4.6~\%$	$16.2 \pm 7.7 \ \%$
Alluvial	$17,3 \pm 4.0 \%$	$23.7\pm9.1~\%$
High-flat	$24.8\pm9.3~\%$	28.6 ± 11.6 %
Slope	$45.3\pm9.1~\%$	$28.3 \pm 6.3 \%$
Ridge	$6.7\pm2.7~\%$	$3.2 \pm 2.1 \%$

(Source: G. Fredriksson, unpubl. data)

Five different topographical types had earlier been classified in the forest: swamp, alluvial, slope, high-flat, and ridge (G. Fredriksson, *unpubl. data*, Fig. 2.1). Transects (18.5 km), laid out in an east-west and north-south direction, were walked and topographical type was recorded every 25 m. "Swamp" type was given when the area showed signs of regular inundation (pneumatophore roots) or was inundated, and had a high density of rattans, high density of small trees and saplings, and a large numbers of climbers. "Alluvial" type was given to flat non-inundated areas close to rivers characterized by large trees. "High-flat" type was give to flat areas at higher elevated sites away from rivers, usually with large trees. "Slope" type was given when the area had a relatively steep inclination (> 5 m difference in elevation between two recording points). "Ridge" type was given to narrow tops with steep sides of hills, or crests of longer hill chains. Each plot was allocated to one of the five topographical types.

Table 2.2. Environmental parameters measured or estimated, including parameters of woody debris.

All parameters were included in the Canonical Correspondence Analysis (CCA), except for those strongly intercorrelated with volume**.

Environmental parameters	In CCA	Level of	Unity
		measurement*	
Topographical type	Alluvial, HighFlat, Slope, Ridge, Swamp	Nominal	0 or 1
Forest area	S (South), W (West), N (North)	Nominal	0 or 1
Burnt/unburnt	B.U	Nominal	0 or 1
WD volume	Volume	Ratio	m ³
WD length	Length**	Ratio	cm
Log/snag	0/1	Nominal	0 or 1
WD decay class	DECAY	Ordinal	From 1 to 5
WD average diameter	AvDM**	Ratio	cm
WD average area	AvAREA**	Ratio	cm ²
Termites (Isoptera) in WD	Iso	Nominal	0 or 1
Ants (Formicidae) in WD	Form	Nominal	0 or 1
Canopy openness (densiometer)	CanCov50	Absolute	%
Soil temperature	EaTemp50	Ratio	°C

* Stevens (1946 in Chrisman 2002) levels of measurement with additions by Chrisman (2002).

Insect sampling

In all 0.04 ha plots (subplots 9, 10, 11, and 12 in each PSP, Fig. 2.2), all the coarse woody debris (CWD \geq 10 cm diameter) was examined for its content of saproxylic insects. Saproxylic denotes a functional group of insects that in some part of their life cycle are dependent upon dead or dying wood or other saproxylic organisms (Speight 1989; Key 1993; Grove 2000). The occurrence of saproxylic insects in fine woody debris (5 cm \leq FWD < 10 cm diameter) was investigated in areas of 50 m² (0.005 ha, chosen random in either subplot 9 or 11, Fig. 2.2). All WD samples, both FWD and CWD, were given a number so that contents could be matched with the different qualities of the WD samples and the environmental properties of the plot.

The content of the WD was examined by chopping up the wood using an axe or a machete. Chopping methods varied according to size and hardness of the WD. For big hard logs, bark was peeled off and only the boreholes were examined in greater detail. For very rotten logs, the whole log was chopped up and examined in detail. For snags, the bark was peeled off and boreholes examined up to two meters in height. No attempt was made to identify dead trees to species due to high species diversity (>180 species ha⁻¹; Nieuwstadt 2002). For methods on measurements of qualities and quantities of WD, see the previous manuscript (Endrestøl 2003, *in prep*.).

All insects encountered were counted, collected, and preserved in 70% ethanol for subsequent identification. In the following, analyses of all beetles (Coleoptera), cockroaches (Blattodea), flies (Diptera), moths (Lepidoptera), and crickets (Orthoptera) are considered. All Lepidoptera and Diptera investigated are of larvae stage (caterpillars and maggots). Because of higher taxonomic resolution and larger sample sizes, most attention will be given to Coleoptera and Blattodea.

The analyses for this thesis will make use of two different data sets. The first data set contains all insect samples that were collected in the field and subsequently identified with highest possible taxonomic resolution (data set I) (*see* Insect identification) whereas the second data set contains subfamilies/genera and life stages lumped to family or order level (data set II). Taxa in data set I were divided into life stages, because larvae and nymphs might have different ecological niches than imagos and adults (Grove 2000). A lumping of life stages and taxa (data set II) was used to increase the number of individuals in each taxon so that more information could be included in the multivariate analyses (*see* Statistics and Mathematics).

Insect identification

All identifications were made by the author, except for the cockroach belonging to the genus *Panesthia* (family Blaberidae, a morpho-species later referred to as *Panesthia* sp.), which was identified by Wijnand R.B. Heitmans (Expert Centre for Taxonomic Identification, University of Amsterdam). Other cockroaches were not identified further than order level (later referred to as Blattodea sfm (subfamilies)). All beetles (imagos and larvae) were identified to family or subfamily/genus level using INTKEY 3.04 Beetle Larvae of the World (Lawrence *et al.* 1993) and INTKEY 5.09 Beetles of the World 1.0 (Lawrence *et al.* 1999). Other collected insects (Diptera, Lepidoptera, and Orthoptera,) were not identified further than order. All pupae found were treated as one group regardless of taxonomical order. The taxonomic identification of those is very difficult, and they are used for biomass and density comparisons only.

All identified insects (data set I) were weighed to compare relative biomass between different WD samples, and environments. The weights are of individuals stored in 70% ethanol, and dried *lightly* on a piece of paper, to remove most of the surface alcohol. The weights are therefore overestimates of the true wet weights, and this error will increase with smaller individuals. If there was more than one individual of the same taxon in a sample, the weight given is the number of individuals multiplied by weight of one selected individual (middle size in that sample). Total biomass within a taxon is the number of individuals multiplied by the average weight of all samples. Because the biomass estimates are based upon sampled individuals, masses of Orthoptera and Blattodea would probably be underestimated, both because many individuals of those taxa escaped collection, and because of their relatively high individual weight compared to larvae of other taxa.

Estimates of diversity require clear taxonomic classifications, with all individuals assigned to a particular class assumed to be identical (Krebs 1999). The taxonomic levels used in this thesis are not consistent at one level, but depend on the possibilities of the identification program/key. Nevertheless, all individuals encountered in the different plots have been identified using the same key and been placed in the same taxonomic level. "Species" is sometimes used as a term (e.g. "species richness"), even though "taxon" would be a proper term, since no individuals were identified to species in this study. No attempt was made to distinguish between "obligate" and "facultative" saproxylic insects or to group the insects into guilds (Grove 2000)

As the material has not been checked by others, some errors might occur in the identification. This is especially true for the beetle larvae, and in particular for the following taxa: genera of Cerambycidae and Elateridae (*Cerambycidae: Lamiinae, Cerambycidae: Cerambycinae, Cerambycidae: Prioninae, Elateridae: Cardiophorinae, Elateridae: Denticollinae, Elateridae: Elaterinae, Elateridae: Negastriinae*), and the families: Anthribidae, Brentidae, Mordellidae, Curculionidae, and also rare taxa that occurred in just one sample with few individuals. Within the order of Diptera identification of larvae is very difficult. I suspect that many of the Dipterans belong to Mycetophilidae.

Statistics and Mathematics

I calculated densities of different saproxylic taxa, both as individuals per m³ WD and hectare LDRF, and biomass per m³ WD and hectare LDRF. When calculating number of insects and biomass per m³ WD, all individuals found within a plot, lumping insects found in CWD and FWD, were used. All WD samples within a plot were lumped, regardless of the structural distribution. Because different plot sizes were used when investigating CWD and FWD, insects found within FWD were excluded when calculating densities per hectare. Because of overall few samples/individuals per taxa per plot, an extrapolation of individuals found within the FWD plot would highly affect the densities and the statistics. Even so, densities measurements, either as m³ or hectare, do not represent "true" densities, but merely trends among treatments, bearing in mind the methods used for insect collection (*see* Insect sampling).

Environmental parameters influencing distribution of taxa were investigated using multivariate analyses. Ordination techniques are often used in community ecology, as they allow simultaneous investigation of the effects of multiple environmental factors. Ordination is used to describe relationships between taxonomical composition patterns and the underlying environmental gradients influencing these patterns, and to summarise and arrange the data in an ordination diagram. To investigate for linearity rather than unimodality (Gaussian response), taxa-abundance matrixes were subjected to a detrended correspondence analysis (DCA). The output of the DCA includes information on the lengths of the axis gradients measured as standard deviations. If those lengths are 4.0 or more, then an ordination technique sensitive to unimodal responses would be appropriate (I used 4.0 as a level, though there are different opinions; both 2 (Grove 2000) and 3 (ter Braak & Prentice 1988) have been recommended). As the axis gradient lengths of my detrended taxa-abundance matrixes were between 4.1 and 6.4 in data set I and between 3.8 and 4.8 in data set II, I used canonical correspondence analyses (CCA), a direct gradient technique based on environmental parameters sensitive to unimodal responses. The technique selects the linear combination of environmental parameters that maximize the dispersion of the taxa score (seen as the first ordination axis in the ordination diagram). The other axes also select linear combinations of environmental parameters that maximize the dispersion of the taxa score, but being uncorrelated with previous CCA axes (correlation matrixes given in Table A2.2.5, Appendix 2.2). The eigenvalues of the ordination axes are equal to the (maximised) dispersion of the taxa score on the ordination axis, and are thus a measure of importance of the ordination axis. The eigenvalues of a CCA always lies between 0 and 1. Values over 0.5 often denote a good separation of the taxa along the axis (ter Braak 1995). For analyses of mobile organisms, eigenvalues tend to be smaller, and eigenvalues higher than 0.3 are regarded as very good (K. Thunes, pers. com.).

Forward selection was applied to rank environmental parameters in importance for determining the taxonomical distribution found in the data. In automatic selection, as used in these analyses, the K best parameters are selected sequentially on the basis of maximum extra fit (ter Braak & Smilauer 1997). The variable that would have the smallest p value if it were the only predictor in ordination is selected first. Each subsequent step adds the variable that has the smallest p value in the presence of the predictors already in the equation. Parameters are added as long as their p values are small enough, typically less than 0.05 or 0.10, and as long the variable adds extra fit to the model.

Because the distribution of the taxa showed a skewed distribution, they were log transformed. This was done to prevent a few high abundance values from unduly influencing the analyses (ter Braak, 1986). To avoid overemphasis of the role of single samples with highly divergent taxon composition (so called "outliers"), the option of "down weighting of rare species" was used. To test for significance of the first ordination axis, overall ordination significance and significance of single parameters in the forward selection, Monte-Carlo permutation tests were used (199 permutations, as default by the program).

Two data sets were used, one where all defined taxa was used (data set I), and one where different subfamilies/genera and stages were lumped to the family or order level (data set II) when possible. Samples that could not be related to environmental parameters (because of lacking sub-sample numbers or lack of measurements) were removed from the analysis. In both data sets this represented 74 insect individuals (4.6 % of the total number of individuals encountered) and 5.86 m³ WD (3.8 % of the total WD, where three samples lacked volume measurement). In both data sets, all taxa constituting less than 8 individuals were taken out of the analysis (taxa that represented less than 0.45% out of the total number of individuals identified).

In the CCA analysis of data set I, 1469 individuals (out of 1616 identified) distributed among 22 taxa (of 54 defined including separation of life stages), were used. In the CCA analysis of data set II, 1518 individuals (out of 1626 identified) distributed among 18 taxa (out of 34 defined), were used. Data set II

included ten individuals more than data set I because they could only be placed into a higher taxonomic level. CCA was conducted using Canoco 4.0 (ter Braak & Smilauer 1997) with diagrams constructed in CanoDraw 3.1 (Smilauer 1997) and CanoPost 1.0 (Smilauer 1996).

Differences in taxon richness between burnt and unburnt forest, and for the different decay classes were computed using EstimateS 5 (Colwell 1997). This software computes randomised species accumulation curves, statistical estimators of true species richness, and a statistical estimator of the true number of species shared between pairs of samples, based on species-by-sample (or sample-by-species) incidence or abundance matrices. The number of randomisation runs was set to 500. Otherwise program defaults were used. Only WD samples with complete measurements were used. Individuals of the same taxon separated into different stages in data set I, were lumped. For this analysis, 40 taxa were defined. Accumulation curves are regarded as significantly different if SD does not overlap between them. Accumulation curves are shown with a few SD values only, to increase the visual aspect.

To investigate WD decay preferences in families of Coleoptera and subtaxa of Blattodea, Kruskal-Wallis ANOVA on rank tests were applied. If significant differences were found among decay classes, a Dunn's Method of pairwise comparison was used to compare for significance between decay classes. If the Dunn's Method could not detect any significance among the decay classes, a *post hoc* Mann-Whitney with a Bonferroni correction was applied ($\alpha < 0.00102$) between classes with the highest differences in rank. This was done to predict the direction of the preference found by the ANOVA.

All other statistical analyses were conducted in SigmaStat 1.0, with a level of significance set at 0.05. Standard error (SE) was used to reveal variation within the data, except for species richness accumulation curves, were standard deviation (SD) was used. This was because EstimateS does not produce SE of the different estimators. Non-parametric tests were applied, because number of individuals varied widely among taxa and normal distribution could not be assumed for all samples.

Results

Abundances and densities

All identified taxa and respective numbers of individuals encountered in FWD and CWD, are listed in Appendix 2.1 (Data set I: Table A2.1.1; Data set II: Table A2.1.2). Based on data set II (taxa with more than 8 individuals found), the number of individuals and density (per hectare and m^3 WD) within the families of Coleoptera were compared between burnt and unburnt plots (Figs. 2.3- 2.4). There were no significant differences in the number of individuals per hectare LDRF of the selected Coleoptera families (Fig 2.3, *Statistical results*; Table A2.2.1 in Appendix 2.2) and only Eucnemidae had significantly more individuals per m^3 WD in unburnt plots (Mann- Whitney, T = 68.5, p = 0.038, Fig 2.4, *Statistical results*; Table A2.2.2 in Appendix 2.2). The reason for the large average number of individuals per m^3 and the large standard error for this family were because one sample in unburnt forest that had a big cluster of individuals. Even so, reducing this sample to just one individual reveals the same result.

There were no significant differences within Blattodea densities, either per ha or m³ WD between burnt and unburnt forest areas (Figs 2.5- 2.6, *Statistical results;* Appendix 2.2, Tables A2.2.1- A2.2.2). No attempt was made to calculate within taxon differences (life-stages) between burnt and unburnt sampling plots.



Figure 2.3. Average density of saproxylic individuals (no ha⁻¹ \pm SE) of selected families of Coleoptera found in coarse woody debris (CWD \geq 10 cm diameter) in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia. Area was extrapolated from 400 m² up to one hectare.



Figure 2.4. Average density of saproxylic individuals (no $m^{-3} \pm SE$) of selected families of Coleoptera found in fine and coarse woody debris (5 cm \leq FWD < 10 cm diameter, CWD \geq 10 cm diameter) in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia.



Figure 2.5. Density (no $ha^{-1} \pm SE$) of *Panesthia* sp. (Blaberidae) and Blattodea (sfm.) found in coarse woody debris (CWD ≥ 10 cm diameter) in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia. Area was extrapolated from 400 m² up to one hectare.



Figure 2.6. Density (no $m^{-3} \pm SE$) of *Panesthia* sp. (Blaberidae) and Blattodea (sfm) found in fine and coarse woody debris (5 cm \leq FWD < 10 cm diameter, CWD \geq 10 cm diameter) in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia.

I also investigated to what extent other environmental parameters affected total abundance of saproxylic insects (lumping all taxa) using Spearman Rank Order Correlation and Kruskal- Wallis ANOVA. Total sample abundance was positively correlated with WD sample volume (Spearman Rank Order Correlation, R = 0.39, n =346, p < 0.001). Sample density of saproxylic insects (number of ind m⁻³) was also found to correlate positively with WD sample decay class (Spearman Rank Order Correlation, R = 0.22, n = 346, p < 0.001). I also used Spearman Rank Order Correlation to investigate for correlation between the total abundance of saproxylic insects found within a sample plots and the number of WD samples encountered. Since the sample plots were of the same size, this could be used to interpret the correlation between number of insects found and the connectivity of WD samples. No such correlation was found (Spearman Rank Order Correlation, R = 0.31, n =14, p = 0.28). Number of WD samples encountered in each plot did not intercorrelate with total volume of the WD samples within each plot (Spearman Rank Order Correlation, R = 0.46, n = 14, p = 0.09), but more WD samples were encountered in burnt forest plots (Mann- Whitney, T = 29.5, p = 0.001). There were no significant differences in sample abundance among the different forest area ranking these according to moisture conditions (Spearman Rank Order Correlation, R = 0.04, n = 346, p = 0.42). No significant correlations were found between insect sample density and soil temperature (Spearman Rank Order Correlation, R = 0.05, n = 346, p = 0.37) or canopy openness (Spearman Rank Order Correlation, R = -0.01, n = 346, p = 0.8). I could also not detect any significant difference in total sample abundance among the different topographical types (Kruskal- Wallis ANOVA, H = 1.26, df = 2, p = 0.53). I did not investigate total abundance differences between snags and logs because of biased methodology (see Methods). Other WD measurements were not tested since they were strongly intercorrelated with volume.

Biomass distribution

The biomass of the saproxylic insects in WD at the study site consisted mainly of Coleoptera (Fig. 2.7), lumping burnt and unburnt forest areas. This order made up 66% of the total biomass, whereas Blattodea comprised 31%. Orthoptera comprised 2% of the biomass. Diptera and Lepidoptera accounted for a very small proportion of the biomass (1% and 0.003% respectively) of the saproxylic insects.

In data set II, the saproxylic insects were dominated by: *Panesthia* sp., Lucanidae, and Tenebrionidae (66%, Fig. 2.8, Table 2.3). *Panesthia* sp. is a big cockroach (Blattodea), with adults that can weigh up to 4 grams. Lucanidae is a beetle (Coleoptera) family, that usually has very big larvae, but some samples also consisted of clusters of small larvae (*pers. obs.*). Tenebrionidae (Coleoptera) generally has small larval stages, but occurred in large numbers in many samples. This taxon was also the most frequent occurring (Table 2.3). Cerambycidae (Coleoptera) also frequently occurred with small larvae. Scarabaeidae and Callirhipidae have in general big larvae, but were rarely found (Table 2.3).



Figure 2.7. Relative biomass of saproxylic insect orders found in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia.

Table 2.3. Total numbers, average individual mass (g), total mass (g) and mass per m^{-3} woody debris of selected saproxylic taxa (> 1% of total biomass) found in fine and coarse woody debris (5 cm \leq FWD < 10 cm diameter, CWD \geq 10 cm diameter), in burnt and unburnt (lumped) lowland dipterocarp rainforest, East Kalimantan, Indonesia. Numbers in brackets denotes column rank.

Taxa		No ind. (rank)		Av. ind. mass (g)		Total mass (g)		Av. g m ⁻³ \pm SE
	Callirhipidae	15	(11)	0.847	(2)	12.714	(7)	0.142 ± 0.123
	Cerambycidae	154	(3)	0.116	(7)	17.912	(4)	0.108 ± 0.028
	Elateridae	50	(8)	0.059	(10)	2.960	(11)	0.029 ± 0.011
Coleoptera	Lucanidae	159	(2)	0.301	(4)	47.876	(2)	0.274 ± 0.110
	Passalidae	82	(4)	0.107	(8)	8.790	(9)	0.072 ± 0.040
	Scarabaeidae	25	(9)	0.615	(3)	15.395	(6)	0.101 ± 0.058
	Tenebrionidae	464	(1)	0.100	(9)	46.442	(3)	0.312 ± 0.079
Plattadaa	Panesthia sp.	68	(6)	1.337	(1)	90.924	(1)	0.452 ± 0.118
Blattodea	Blattodea sfm.	58	(7)	0.170	(6)	9.875	(8)	0.058 ± 0.036
Other	Orthoptera	17	(10)	0.220	(5)	3.745	(10)	0.032 ± 0.028
Other	Pupae (all taxa)	77	(5)	0.220	(5)	16.951	(5)	0.122 ± 0.034



Figure 2.8. Relative biomass of the most important taxa (> 1% of total biomass) found in fine and coarse woody debris (5 cm \leq FWD < 10 cm diameter, CWD \geq 10 cm diameter) in burnt and unburnt (lumped) lowland dipterocarp rainforest, East Kalimantan, Indonesia.

There were no significant differences in the biomass distribution per ha per taxon between burnt and unburnt areas (*Statistical results*, Table A2.2.3 in Appendix 2.2), except for Blattodea (sfm.), which had greater biomass in burnt areas (Mann- Whitney, T = 35.0, p = 0.026). Close to significant differences indicating higher biomasses of both *Panesthia* sp. (Mann- Whitney, T = 37.5, p = 0.053) and Blattodea (total) (Mann- Whitney, T = 37.0, p = 0.053) in burnt areas were found. There was no significant difference in total biomass between burnt and unburnt plots per ha (*Statistical results*, Table A2.2.3 in Appendix 2.2). When comparing biomass of the different taxa per m³ per taxon between burnt and unburnt areas, only Blattodea (sfm.) differed significantly (Mann- Whitney, T = 34.0, p = 0.018), with higher biomass in the burnt areas. A close to significant difference indicating higher biomasses of Eucnemidae per m³ in unburnt areas was found (Mann- Whitney, T = 67.5, p = 0.053). There were also no significant differences in total biomass per m³ found between burnt and unburnt plots (*Statistical results*, Table A2.2.4 in Appendix 2.2).

Ordination analysis

Canonical correspondence analyses (CCA) provide an integrated description of species- environment relationships by assuming a response model that is similar to all species (unimodal), and the existence of a single set of underlying environmental gradients to which all the species respond. In the resulting ordination diagram, points represent species and arrows represent environmental parameters (Figs. 2.9-2.10) (ter Braak 1986). The length of the arrow is equal to the multiple correlation coefficient, R, of an environmental parameter with the ordination axes (ter Braak 1994). These diagrams show the main pattern of variation in community composition as accounted for by the environmental parameters, and also the distribution of the species along each environmental parameter (ter Braak 1986). Correlation matrixes between the ordination axis and the different environmental parameters are given in Table A2.2.5, Appendix 2.2.



Figure 2.9. Canonical Correspondence analysis (CCA)- biplot 1, data set I: Saproxylic insect taxa with > 8 individuals (1469 individuals total, identified to 22 taxa). Arrows represent environmental parameters (for abbreviations and explanations of the environmental parameters, *see* Table 2.2) and dots represents taxa (for taxa abbreviations, *see* Table A2.1.1, Appendix 2.1). All specimens were found in fine and coarse woody debris (5 cm \leq FWD < 10 cm diameter, CWD \geq 10 cm diameter) in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia.



Figure 2.10. Canonical Correspondence analysis (CCA)- biplot 2, data set II: Saproxylic insect taxa lumped from data set I with > 8 individuals (1518 individuals total, identified to 18 taxa). Arrows represent environmental parameters (for abbreviations and explanations of the environmental parameters, *see* Table 2.2) and dots represents taxa (for taxa abbreviations, *see* Table A2.1.2, Appendix 2.1). All specimens were found in fine and coarse woody debris ($5 \text{ cm} \le \text{FWD} < 10 \text{ cm}$ diameter, CWD $\ge 10 \text{ cm}$ diameter) in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia.

The explanatory value of the different parameters (fit λ_j) found through forward selection seems to be almost the same in the two data sets, though there is some difference in which parameters are significant (Table 2.4). "Decay" was the variable that best explained the variation among the taxa (9 % in data set I, 8 % in data II). In data set II, "log/snag" explained 4 %. Whether the plot was "slope" explained 4 % of the variation in both data sets. "Burnt/unburnt" also explained 4 % in data set II, and "south" location of the sampling site explained 4 % in data set I. Even though the explained values were low, the axes of the ordination were significant.

Table 2.4. Proportion of variance (eigenvalues) of saproxylic insects and significant level explained with the addition of each environmental variable during forward selection. λ_j = eigenvalue (fit) with variable j; p = significance level of effect, as obtained with a Monte Carlo permutation test with 199 random permutations. * denotes significant ($\alpha < 0.05$). ** denotes highly significant ($\alpha < 0.01$).

	Data set			
Environmental parameters		Ι		II
	F	$\lambda_{i}(p)$	F	λ_{j} (p)
Decay class WD	3.51	0.09 (0.005)**	3.74	0.08 (0.005)**
Log/snag	1.45	0.04 (0.075)	1.69	0.04 (0.035)*
Soil temp.	1.41	0.04 (0.11)	1.51	0.03 (0.085)
Slope	1.66	0.04 (0.035)*	1.90	0.04 (0.03)*
Burnt/unburnt	1.49	0.04 (0.085)	2.10	0.04 (0.01)**
South	1.72	0.04 (0.045)*	1.55	0.03 (0.075)
Canopy	1.36	0.03 (0.1)	1.52	0.03 (0.08)
North	1.02	0.03 (0.425)	1.16	0.02 (0.28)
Ants in WD	0.9	0.02 (0.57)	0.64	0.01 (0.86)
Volume WD	1.04	0.03 (0.345)	0.71	0.01 (0.525)
Termites in WD	0.89	0.02 (0.56)	0.86	0.02 (0.6)
High-flat	0.68	0.02 (0.785)	0.90	0.02 (0.565)
Sum		0.44		0.38

Table 2.5. Eigenvalues and significance of ordination axes of data set I and II. Significances of first axes are given in brackets.

	Eigenvalues						
Data set		Axis 1	Axis 2	Axis 3	Axis 4	signif	icance
	F	EV (p)	EV	EV	EV	F	р
Ι	4.439	0.117 (0.02)	0.072	0.057	0.047	1.433	0.01
II	5.098	0.111 (0.025)	0.062	0.054	0.05	1.528	0.005

My data shows small eigenvalues, but they are significant overall (Table 2.5). This means that the dispersion of the species scores was relatively small, and that environmental parameters explained relatively little of the variation seen in the species data, although still a significant amount of the variation was explained. Some of the parameters were more or less intercorrelated, especially "diameter" (AvDm), "length", "area" (AvArea), and "volume". Subsequently all parameters, except "volume", were taken out of the analyses. The correlation matrix of all the environmental parameters is given in Table A2.2.6, Appendix 2.2. The best correlations were found between "soil temperature" (EaTemp; R = 0.7) and "canopy openness" (CanCov50; R = 0.79), and "burnt/unburnt".

Species richness

I calculated different estimators for species richness, based on data set I. Richness was analysed graphically by plotting the estimator and the observed species richness as a function of the cumulative volume of wood. The volume of wood was pooled regardless of character (decay, volume, and log/snag) of the different wood samples. Burnt/unburnt and decay classes were analysed specifically.

Coleman curves (Figs. 2.11- 2.12) estimate *sample species richness* from the pooled total species richness, based on all species actually discovered (Coleman 1981). There was no difference in sample species richness in burnt and unburnt plots, as the two curves had overlapping standard deviations (Fig. 2.11). Coleman richness expectation in the different decay class showed that there was significantly higher sample species richness in decay class 5 (Fig. 2.12).



Figure 2.11. Coleman richness expectations (\pm SD) of saproxylic insects in cumulative volume of woody debris (log m³ WD) in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia.



Figure 2.12. Colemans richness expectations (\pm SD) of saproxylic insects in cumulative volume of woody debris (log m³ WD) of different decay classes in a lowland dipterocarp rainforest, East Kalimantan, Indonesia.

Richness curves based on rarefaction (Figs. 2.13-2.14), computed from Estimate S, showed the expected number of taxa in cumulative amounts of WD (either in burnt and unburnt, or in different decay classes). The difference between Coleman curves and Incidence-based coverage Estimator (ICE) is that ICE estimates total species richness from samples, including species not discovered in any sample, while Coleman curves estimate sample richness from the pooled total richness, based on species actually discovered (Colwell 1997).

In data with a skewed distribution, in which some classes are very common and others very rare, all the useful information about undiscovered classes lies in the rarely discovered classes. The Incidence-based Coverage Estimator (ICE) is based on species found in 10 or fewer sampling units (Lee and Chao 1994, *in EsimateS User's Guide*). The ICE estimator showed that no difference could be detected between burnt and unburnt plots (Fig. 2.13), but that a higher richness was found in decay class 5, with overlapping SD among the others (Fig. 2.14).



Figure 2.13. Incidence-based Coverage Estimator (ICE \pm SD) of saproxylic insects in cumulative volume of woody debris (log m³ WD) in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia.



Figure 2.14. Incidence-based Coverage Estimators (ICE) of saproxylic insects in cumulative volume of woody debris (log m³ WD) of different decay classes in a lowland dipterocarp rainforest, East Kalimantan, Indonesia.

I also investigated how other environmental parameters affected total richness of saproxylic insects using Spearman Rank Order Correlation and Kruskal- Wallis ANOVA on rank. Total sample richness was positively correlated with sample volume of WD (Spearman Rank Order Correlation, R = 0.37, n = 346, p < 0.001), but total plot richness did not correlate with total plot WD volume (Spearman Rank Order Correlation, R = 0.31, n = 14, p = 0.27). Taxa densities (number of taxa m^{-3}) were also positively correlated with sample decay class (Spearman Rank Order Correlation, R = 0.23, n = 346, p < 0.001, see Colemans richness expectations, Fig. 2.11). I also used Spearman Rank Order Correlation to investigate for correlation between the richness of saproxylic insects found within a sample plot and the respective number of WD samples investigated. Since the sample plots were of the same size, this could be used to interpret the correlation between number of insects found and the connectivity of WD samples. A positive correlation was found between number of taxa and number of WD sample within each plot (Spearman Rank Order Correlation, R = 0.54, n = 14, p = 0.04). There were no significant differences in sample richness among the different forest area ranking these according to moisture conditions (Spearman Rank Order Correlation, R = 0.00, n = 346, p = 0.93). No significant correlations were found between insect sample density and soil temperature (Spearman Rank Order Correlation, R = 0.06, n = 346, p = 0.23) or canopy openness (Spearman Rank Order Correlation, R = -0.01, n = 346, p = 0.8). I could also not detect any significant difference in total sample richness among the different topographical types (Kruskal- Wallis ANOVA, H = 1.93, df = 2, p = 0.38). I did not investigate total richness differences between snags and logs because of biased methology (see Methods). Other WD measurements were not tested since they were strongly intercorrelated with volume.

Preference for degree of decay

To investigate WD decay preferences in families of Coleoptera and subtaxa of Blattodea, Kruskal-Wallis ANOVA on rank tests were applied on number of individuals found per m³ WD between different decay classes in each plot, with a *post hoc* pairwise comparison (Dunn's Method or Mann- Whitney Rank Sum test, *see* Statistics and Mathematics). The significant outputs from the *post hoc* analysis are interpreted as a preference, even though the investigated taxa could have higher total densities found in another decay class (Fig 2.15). This was due to high variation, which leads to reduced differences in rank and reduced power of the test. Because less WD was found in decay class 5, and because of a negative correlation between decay class samples of WD and WD volume (Spearman Rank Order Correlation, R = -0.27, n = 1089, p < 0.001,), density variation is likely to be higher in decay class 5.

Table 2.6. Decay preferences of selected saproxylic insect taxa found in fine and coarse woody debris (5 cm \leq FWD < 10 cm diameter, CWD \geq 10 cm diameter) in a lowland dipterocarp rainforest, East Kalimantan, Indonesia. Significantly different decay classes are given with compared decay class in brackets.

	e	1	2		
Taxa	n	Н	df	p value	Preferred decay (sign. from)
Brentidae	30	8.34	4	0.0799	
Cerambycidae	148	26.7	4	<0.0001**	2 (1, 3, 4, 5)
Elateridae	48	22.3	4	0.0002**	4 (1, 3, 5)
Eucnemidae	79	25.0	4	<0.0001**	2 (5, 3, 1)
Lucanidae	158	14.9	4	0.0050**	$4(1:0.0198^{MW})$
Passalidae	74	16.9	4	0.0020**	2 (5, 3)
Scarabaeidae	25	12.3	4	0.0151*	4 (3)
Tenebrionidae	440	15.7	4	0.0035**	4 (1)
Σ Coleoptera	1002	8.68	4	0.0697	
Panesthia sp.	60	21.9	4	0.0002**	4 (1, 5, 3), 2 (1)
Blattodea sfm.	51	13.6	4	0.0086**	2 (3)
Σ Blattodea	111	16.8	4	0.0021**	4 (1, 3, 5)
Diptera	213	22.1	4	0.0002**	4 (1, 3, 5)
Lepidoptera	56	11.8	4	0.0192*	4 (3: 0.0789 ^{MW})
Orthoptera	17	16.7	4	0.0022**	2 (1, 3, 4, 5)
Pupae	72	19.4	4	0.0007**	2 (5), 4 (5)
Total	1518	7.22	4	0.125	

^{MW} denotes *post hoc* Mann-Whitney ($\alpha < 0.00102$).

* denotes significant ($\alpha < 0.05$).

** denotes highly significant ($\alpha < 0.001$).

Coleoptera showed no overall decay preference (Table 2.6, Fig. 2.15). Lepidoptera had a significant difference in distribution among decay classes, but *post-hoc* tests failed to reveal a preference. Diptera were found to prefer decay class 2 (Table 2.6, Fig. 2.15). This has to be interpreted with caution because of low sample number (Table A2.1.2, Appendix 2.1). Pupae showed preference for decay class 2 and 4, but since this probably represents a wide variety of taxa the findings should not be generalised (Table 2.6).

From the Coleoptera, only the family Brentidae showed no preference for decay (Table 2.6, Fig. 2.16). Tenebrionidae and Lucanidae were one of the most common taxa per m^3 WD, and their numbers increased with higher decay class (Fig. 2.16), even though the *post-hoc* tests failed to reveal any differences for Lucanidae (Table 2.6). Elateridae, Scarabaeidae, *Panesthia* sp., and Diptera also showed preference for higher decay classes (4). Cerambycidae had a clear preference towards hard wood. Blattodea (sfm.), Eucnemidae, and Passalidae also had a significant preference for less decayed WD (Table 2.6, Fig. 2.16). I found no overall preference for decay class, when all insects were lumped, in either burnt or unburnt forest (ANOVA; unburnt: H= 7. 21, df= 4, p= 0.12; burnt: H= 6.36, df= 4, p= 0.17).





Figure 2.15. Overall density of saproxylic insect orders found in woody debris (no m^{-3} WD) of different decay classes (burnt and unburnt forest pooled) in a lowland dipterocarp rainforest, East Kalimantan, Indonesia. The taxa included in the orders are based on data set II, and only taxa with more than 25 individuals are used.

Figure 2.16. Overall density of selected saproxylic Coleoptera families found in woody debris (no m^{-3} WD) of different decay classes (burnt and unburnt forest pooled) in a lowland dipterocarp rainforest, East Kalimantan, Indonesia. The taxa included are based on data set II, and only taxa with more than 25 individuals are shown.

Discussion

Effects of fire on density and abundance

The substrate and habitat changes due to a fire could largely influence the species composition and diversity of both vertebrate and invertebrate fauna (Fredericksen & Fredericksen 2002), including wood-living insects (Wikars 1997). The responses of the habitat disturbance on the insect fauna will vary from taxon to taxon, and contradictory affects have been observed between classes (Fredericksen & Fredericksen 2002), orders (Hansen 1986), families (Makihara *et al.* 2000), and species (Didham *et al.* 1998). The dispersal capabilities of species or guilds will affect the degree to which these organisms and their function are affected, and the amount of time necessary for re-colonisation and recovery (Niwa *et al.* 2001). Therefore, studies on saproxylic insects and their responses to habitat destruction and disturbance often provide mixed or inconclusive results (*see* Niwa *et al.* 2001).

A distinction can be made between the change of habitat and the change of substrate due to burning. One of the major habitat changes within burnt forest areas is the highly increased canopy openness. Canopy openness should be a measurement of the light conditions at the site, though some evaluations have found such measurements (with a densiometer) to be weakly correlated with light conditions (Engelbrecht & Herz 2001). Nevertheless, the positive correlation found between canopy openness, soil temperature, and burnt forest indicates that a higher substrate (WD) temperature could be found in burnt areas. Even though this habitat change also affects the substrate (Mori 2000), the habitat change itself is apparently more important than substrate change. The charring of the substrate will vary according to differences in burning intensity, but also among different tree species due to differences in relative content of lignin and cellulose (*review in* Scott 2000). Michaels & Bornemissza (1999) found that burnt logs did not render them useless as a habitat for all invertebrates, but that it depended on the intensity of charring. Even so, the higher soil temperatures (and thus also higher WD temperature) found in the burned areas might increase to a level not tolerated by many saproxylic organisms (*review in* Harmon *et al.* 1986). The elevated temperatures might also lead to lower water content of the WD (Mori 2000) and thereby change the distribution of the saproxylic organisms (*review in* Harmon *et al.* 1986).

The time-gap between the fire and the time of the study is also crucial for the interpretation of the results. Several studies have shown that fire influences beetle diversity and abundance shortly after a fire (e.g. Hansen 1986; Wikars 1997; Madoffe *et al.* 2000; Makihara *et al.* 2000; Blanche *et al.* 2001; Orgeas & Andersen 2001). Preliminary studies of emerging saproxylic insects from burnt and unburnt logs in Sweden concluded that the burning changed abundance, but not the taxa present (Wikars 1997). Wikars (1992, 1997) suggested that fires alter the abundance of common, dominant species and so create less competition for pioneers and pyrophilous species. This is supported by Didham *et al.* (1998), who found that common beetle species were significantly more likely to disappear from forest fragments (pastures created and maintained by fire), than rare species. Didham *et al.* (1998) also found no total species- richness differences of leaf-litter beetles between different fragmentation regimes, and explained this by high species replacement rates, presumably of species from disturbed habitats. During a fire, trees will be weakened or die, and many predators (e.g. spiders; Niwa & Peck *unpubl. data, in* Niwa *et al.* 2001) will die, which could lead to an increased number of wood-boring insects (Makihara *et al.* 2000) and grass-layer beetles (Orgeas & Andersen 2001). Spiders are also known to be one of

the most important predators of cockroaches, particularly in tropical habitats (Schal *et al.* 1984), and reduced numbers of spiders and possibly other predators could explain the increase in cockroaches (biomass) that I found in burnt forest. Contrary to these findings, Muona & Rutanen (1994) found an increase in predators (beetles) under bark shortly after a fire in boreal Finland. Hansen (1986) also found an increase in predaceous and parasitic hymenopterans (despite few flowers and potential hosts/prey- e.g. spiders, aphids, beetles, and bees), but a total absence of parasitic dipterans (despite abundant potential hosts (Homoptera)).

I found no significant evidence that there were any differences in saproxylic insect abundance or richness between burnt and unburnt forest areas, except for the beetle family Eucnemidae (*see below*). The densities of individuals per volume WD in burnt and unburnt forest could be a result of low sampling efforts, but also due to decreased competition by common species, and immigration of pyrophilous species, or species adapted to habitats similar to burnt forest, as described by Wikars (1997) and Didham *et al.* (1998). Historically, fires in East Kalimantan have occurred rarely (Schweithelm & Glover 1999; Dam *et al.* 2001), and fires are in general more frequent in temperate and boreal areas than in the humid tropics (*review in* Scott 2000). Supporting Wikars (1997), Madoffe *et al.* (2000) also found an overall similarity in abundance and diversity between burnt and unburnt forest areas in Tanzania, but they concluded that the reason was a quick restoration of vegetation to pre-fire levels. Orgeas & Andersen (2001) also found a strong resilience to fire for grass-layer beetles in an Australian tropical savannah, and explained that with a long history of association with frequent fires. Since those areas have annual fires and fire is regarded as a major factor for structuring the particular ecosystem, the same conclusions do not apply to the LDRF ecosystem, which historically have had a different fire regime (Schweithelm & Glover 1999; Dam *et al.* 2001).

Another reason could be that the study was carried out three years after the fires, and that the saproxylic fauna had been restored to pre-fire levels in the burnt areas. Makihara et al. (2000) studied how different beetle families recovered after a fire in East Kalimantan, and found that, of the families surveyed, the Bostrychidae, which can attack dry wood, was the least affected by the burning and had recovered within 6 months after the fire. The next most tolerant family was the Cerambycidae, which recovered to about half the level observed before the fires. In contrast, the fires seriously affected the Carabidae, Platypodidae, and Scolytidae and their numbers had still not recovered six months after the fires. Still, they concluded that wood-boring beetle populations were capable of early recovery in tall tree stands after a ground fire. Hanula et al. (2002) hypothesised a build up of bark beetles in burnt areas after a fire, but actually found that phloem-feeding bark beetles in general were less abundant in burnt forest stands (with some Scolytidae more abundant or unaffected). Hansen (1986) found an increase of specimens collected in Malaise traps soon after a fire in Utah, e.g. mosquitoes (Diptera) and phytophagous species of lygaeid bugs (Hemiptera: Lygaeidae), leafhoppers (Orthoptera), and moths (Lepidoptera), but that the number of species between burnt and unburnt sites were about equal a month after the fire. Fredericksen & Fredericksen (2002) also found an increase of Orthoptera and Lepidoptera (caterpillars) after a fire disturbance in a tropical rainforest of eastern Bolivia. The species investigated were mainly herbivores, so the increase found could be explained by an increase in food availability (Hansen 1986; Fredericksen & Frederiksen 2002). I found no differences in the densities of either saproxylic Lepidoptera (caterpillars) or saproxylic Orthoptera between burnt and unburnt forest. There might still be a difference in the herbivorous guild of the same orders, because an enormous number of Lepidoptera are associated with trees, but only a few taxa having wood-boring larvae, and thus being saproxylic (Harmon et al.

1986). Also, no differences were found in abundance and diversity of wood-dwelling termites between burnt and unburnt forest in the same study area (Mathisen 2003).

As described by Rugg & Rose (1990; 1989), all xylophagous cockroaches develop slowly due to low nutrient substrate (see below). This might also be true for other xylophagous invertebrates (review in Harmon et al. 1986). Yet another adaptation to growing in wood is an extended life cycle (Gullan & Cranston 1998). While most insects complete one to many generation cycles in a year, species feeding on wood use several years to complete their life cycles (Harmon et al. 1986). E.g. several species of Lucanidae can take 4 years or more for their larvae development (Wood et al. 1996; Harde 2000), with some Cerambycidae taking up to 10 years (Harde 2000). The opposite also occurs, with some bark beetles that can have six or more generations per year in the Southern United States (genus Ips, family Scolytidae) (Hanula et al. 2002), and some that might even exceed 10 generations per year in Belize (Dendroctonus sp. nova) (F. Midtgaard, pers. com.). These species attack weakened or recently dead trees and feed on their phloem (Hanula et al. 2002), which is more nutritious than the xylem (review in Harmon et al. 1986). As discussed below, the method used in this study would probably bias the feeding guilds within the saproxylics towards the xylophagous taxa. The similarity found between burnt and unburnt could therefore also partly be explained by survival of larval individuals within the WD during the fires (as described by Wikars (1997) and Makihara et al. (2000)), and a quick restoration of the saproxylic insect fauna, mainly of xylophagous taxa (Makihara et al. 2000). This is supported by the nature of the 1997-98 fire, which mainly was a surface-fire, hardly affecting the trunks and crowns directly (Mori 2000). Irmler et al. (1996) found that the distribution of mycophagous species (fungi- feeding) seemed to be controlled by both decay and water contents of the WD. Even though no guild distinction was made in my study, the mycophagous taxa could be more severely affected by the fires, as discussed below for the taxon Eucnemidae.

There were also no differences found in densities per ha between burnt and unburnt forest area. One should think that there would be, since almost twice as much CWD had been found in burnt PSPs compared with unburnt PSPs (A. Endrestøl 2003, *in prep.*). This difference could not be detected within the sampling plots even though the average volume of CWD was twice as high in the burnt sampling plots. The reason for this similarity per ha could be explained by high variation of CWD amounts. Within Coleoptera, three taxa dominated in total density per ha, namely Tenebrionidae, Lucanidae and Cerambycidae. Even though Tenebrionidae had almost three times more individuals per ha than the Lucanidae, their total biomass per ha was almost equal. No difference in total biomass or taxa biomass per volume WD or hectare could be detected between burnt and unburnt forest, except for Blattodea (sfm.) that had a higher biomass in burnt forest (*see below*).

One family of Coleoptera, Eucnemidae, showed a significant difference, being found in greater numbers per m³ in the unburnt forest, with a close to significant difference indicating higher biomasses in unburnt forest. As all eucnemids breed in wood infested by fungi (Muona 1993), there is a good possibility that the fungus itself is the actual source of nutrition and limitation. There are indications that the larvae are not, at least directly, xylophagous (Muona 1993). The sclerotized body, the serrate head and the spiny patches characteristic of most eucnemids (*Fornax*- type Macraulacinae genera) could possibly be viewed as adaptations for life in soft, moist conditions (Muona 1993). I found most of my eucnemid larvae in white-rot infested wood with a fibrous consistency (pers. obs.). Because many of these eucnemid larvae where found in big clusters (thus only sub-sampled), and due to their small size in connection with fungi (thus difficult to spot), their numbers are probably underestimated. Because the eucnemids are strongly connected with fungi, one could speculate that the reason

why they were not so abundant in the burnt forest is because there was less fungus there, as a result of the drier and hotter environment. This explanation is likely, since most wood- decaying fungi cannot grow above 40° C (Harmon *et al.* 1986), and that the burnt forest areas in my study areas could experience such temperatures.

I found that cockroaches make up a major part of the saproxylic insect community in this LDRF, comprising about one-third of the biomass. Blattodea (sfm). had higher biomass densities both per volume WD and hectare in burnt forest, with Panesthia sp. and Blattodea (total) showing close to significant differences towards higher biomasses per hectare in burnt forest. Xylophagy (wood-feeding) is not common in cockroaches, with only two well-known examples: Cryptocerus spp. and species from the subfamily Panesthiinae (Schal et al. 1984). Panesthia is the largest of the seven genera within Panesthiinae, with over 50 species (Rugg & Rose 1990). I found that individuals from the genus Panesthia (one morpho- species) made up 32% of the total biomass. This is due to the larger average size of the individuals compared with beetle larvae. Even so, the rest of the cockroaches (Blattodea sfm.) made up only 4% of the total biomass found. Because individuals of Blattodea (sfm.) were not identified to genus, some of them might belong to the genus Panesthia. However, it is more likely many of them they are not true xylophagous cockroaches, but just found in connection with WD (and might still classify as saproxylic!). There have been few studies of xylophagous cockroaches, and new examples of xylophagy in cockroaches have recently been discovered (Pellens et al. 2002), with probably many more to be discovered in the future. All xylophagous cockroach species are similar in that they develop slowly, a trait supposedly related to a low quality wood diet (Rugg & Rose 1989, 1990). A species within the genus Panesthia (P. cribrata) has been shown to have a nymphal development taking between 4 and 6 years, and with an adult longevity exceeding 4 years (Rugg & Rose 1990). This same species has in general one brood a year (Rugg & Rose 1989). Species of the genus Panesthia have also been shown to exhibit a subsocial behaviour, with nymphs of different broods living together with one or a pair of adults (Matsumoto 1988).

Many species of cockroaches have been collected under loose bark of live trees, snags and logs (Schal *et al.* 1984; *pers. obs.*). As stated before, this might not classify them as xylophagous, though they might be saproxylic (and would be in this study). There are examples of species where the nymphs are found under loose bark of trees, whereas the adults are found in the foliage. Also, time is known to be a major niche axis among the cockroaches, as many species rest diurnally in aboveground refugia, such as rolled dead leaves and loose bark (Schal *et al.* 1984). This could therefore bias the stadium of individuals collected, and overestimate the amount of saproxylic cockroaches. Since no difference in abundance between burnt and unburnt forest of Blattodea was found, one could assume that the individuals found in burnt forest were larger. This could either be due to a different species composition or a bias in life stage distribution, with more adult, and thus larger individuals, in the burnt forest. The first explanation is most likely, since the biplot from the CCA analysis of data set I arrange the life stage of all Blattodea relatively close together. Also, since an average biomass was used within each sample, variation and difference in rank could be quite different than using number of individuals.

Environmental parameters affecting densities and abundances

Canonical correspondence analysis (CCA) was used to investigate which of the environmental parameters contributed most to the distribution of saproxylic insects. Ordination techniques are often used in community ecology, as they give the opportunity to investigate the effects of multiple environmental factors on numbers of species simultaneously. The results showed that the environmental parameters measured explained little of the distribution seen in the taxonomical distribution data. Because of this, the taxa seen in the ordination diagrams tended to centre in the middle of the ordination diagram and the influence of the different vectors on each taxon was difficult to interpret. Even so, during forward selection, "decay", "slope", and "south" was found to explained some of the distribution data set I, while "decay", "slope", "burnt/unburnt" was found to explained some of the distribution found in data set II.

I found saproxylic insect abundance to positively correlate with both volume of WD and its decay class. Correlation like these must however be interpreted with caution because many environmental parameters often are intercorrelated (Økland et al. 1996, Martikainen et al. 2000). The increased abundance of saproxylic insect found in higher decay classes can be explained by the increased amount of taxa found in that substrate (see Species richness). The findings of increasing abundance with increasing volume of WD are somewhat contradictory to increased abundance with increases decay, because decay and volume are negatively correlated, and also because of methology (see Methods). Grove (2002) stated in his review on saproxylic insects that nearly all published studies on saproxylic insects suggest a positive relationship between diameter and species richness, incidence or abundance, and that very few suggest no relationship at all (e.g. Økland et al. 1996; Schiegg 2000). My findings also suggest that there are obvious decay preferences in different beetle families. Others have also found different decay preferences within beetle families (e.g. Araya 1992). According to Harmon et al. (1986), a number of beetles are found in very decayed wood, including representatives of Scarabaeidae, Lucanidae, and Passalidae. My finding supports the preferences of the two first families, though I found a clear preference in the Passalidae towards very hard, recently dead wood. WD in the form of logs and snags (position) explains some of the distribution of the saproxylics insects. This is mainly because snags provide a different habitat than logs (Franklin et al. 1989; Jonsell & Weslien 2003), with different physical qualities (review in Harmon et al. 1986). As moisture content of sound wood is negatively correlated with wood density, a decreasing wood density through decomposition would increase the moisture of the WD (review in Mackensen et al. 2003). Again, others have found the water content of WD to affect the distribution of saproxylic insects (e.g. Irmler et al. 1996; Jonsell and Weslien 2003). This is supported by the findings of decay preferences among the most important taxa. As the snags consist of a more uniform decay range than do logs, they would probably therefore harbour other taxa than logs in general. Water content could explain why slope affected the saproxylic fauna, as the moisture content of WD would depend on log position and degree of shading (review in Mackensen et al. 2003).

WD was not identified to species. This parameter might explain some of the variation in the taxonomical distribution data. In boreal forests there is a relationship between the richness of the saproxylic fauna and whether the WD is of coniferous or deciduous origin (e.g. Økland *et al.* 1996; Jonsell *et al.* 1998; Martikainen *et al.* 2000). Even so, Irmler *et al.* (1996) found tree species to be of minor importance influencing the distribution of saproxylic insects, when comparing Alder (*Alnus* sp.), Beech (*Betula* sp.) and Spruce (*Picea* sp.). Because of a high diversity of tree species, tree-host specificity might be a less reliable strategy in the tropics compared to boreal forests (Tavakilian *et al.* 1997). Host specificity, more narrowly defined as

monophagy, could actually be regarded as an uncommon strategy in the tropics (Berkov & Tavakilian 1999) even though host specificity at a higher taxonomic level (plant family) might still exist (Tavakilian *et al.* 1997). The inclusion of xylophagous taxa (e.g. Cerambycidae, Buprestidae, and Curculionidae) into the herbivorous guild was suggested to be one of the serious errors of Erwin's estimate on the number of arthropods in the world (~30 mill) by Basset *et al.* (1996). Because Erwin's estimate was based on host specificity, they argued that this inclusion would lead to an overestimate of the true number, since xylophagous taxa are less host-specific than herbivorous ones in the tropics. This is also one of the reasons that they scaled down the estimate of Erwin by a factor of 4.6, giving an estimate of 6.6 million arthropods in the world (*see* Basset *et al.* 1996 *for details*). Thus, tree species may not be a dominant environmental parameter for many saproxylic species in the tropics. This might especially be true in a LDRF, where no single tree species dominates the vegetation (Nieuwstadt 2002).

Species richness

Species that are found to be rare when collected by one method, or at a particular site, or season, may be abundantly collected by another method, or at a different site, or season (Frith & Frith 1985; Gaston & McArdle 1994; Siitonen 1994, Schiegg 2000). Therefore, a species accumulation curve is specific to an area, time, and the collection techniques employed (Fisher 1999).

Many of the non-parametric richness estimators are based on the rare taxa found. This could either be singletons (species represented by a single individual) and doubletons (species represented by exactly two individuals) (Chao 1), or uniques (species found in only one sample) and duplicates (species found in exactly two samples) (Jackknife, Chao 2) (Chazdon *et al.* 1998). Lee & Chao (1994) have developed a new class of estimators based on the statistical concept of "sample coverage" (*see* Chazdon *et al.* 1998 *for explanation*). The Incidence-based Coverage Estimator (ICE) is based on species found in ≤ 10 sampling units. This makes it more stable than estimates based on numbers of singletons and doubletons, if the species are patchily distributed (Chazdon *et al.* 1998). Longino *et al.* (2002) tested the ICE estimator using different methods for data collection and the pooled data, and found that the ICE estimator behaved differently for the different data sets. Longino *et al.* (2002) recommended that the ICE estimator should be viewed as yielding minimum estimates of true richness. Chazdon *et al.* (1998) found the ICE estimator to best satisfy the criteria established for an ideal species-richness estimator, and to be the least sensitive to sampling density and to patchiness (comparing; Chao 1, Chao 2, Jackknife 1, Jackknife 2, Bootstrap, Michaelis-Menten and ACE).

When using the ICE estimator on my data, most of the curves never reached a stable value. More dead wood was examined in the burnt areas (because more dead wood was found), but to obtain stable values from this estimator, the sampling effort should have been higher, or more efficient. This would probably be impossible even with much more resources, as accumulation curves involving tropical insect samples seldom stabilise (Grove 2000). Also, the amounts of wood sampled in the different groups should have been of the same volume, and other characteristics, and not in area, as it was done, although this might be difficult in practice. ICE (true richness), as with Colemans richness estimator (sample richness), showed higher richness in decay class 5. It is a bit difficult to interpret the richness in burnt and unburnt areas, because the estimator does not stabilise, but the overlapping SD implies that no difference exist.

Araya (1992) reported that there had been no detailed study on the occurrence of xylophagous insects in relation to decay types. Since then, and supporting my findings, decay stage of WD has been found to be correlated positively with species richness (Økland et al. 1996; Sverdrup-Thygeson 2001), and WD in late decay stages are considered to be one of the most important factors contributing to the conservation of saproxylic species richness (Irmler et al. 1996; Martikainen et al. 2000). Even so, contradictory results exists (e.g. Grove 2000), with higher richness found in mid-decay stages of WD (S. J. Grove, pers. com.) The increased number of taxa found in highly decayed WD could be a result of an increased heterogeneity of substrate, which would include species more associated with the litter and soil (including non-saproxylic taxa). Irmler et al. (1996) observed immigration from the adjacent litter layer into WD, and found the wood-dwelling fauna to become more similar to the litter-dwelling fauna as the age of the decaying wood increased. Even recognising tree-host specificity, as described above, this seems to decrease as the WD decay increases (Harmon et al. 1986; Wood et al. 1996; Jonsell et al. 1998). I also found a positive correlation between richness and WD volume. The same results have been reported by others (Grove 2000; Martikainen et al. 2000; Similä et al. 2003), and support ecological theory on habitat size and population fluctuations (Hanski & Gilpin 1991; Meffe et al. 1997). Midtgaard (1996) found that the probability of Bolitophagus reticulatus (inhabiting the fruiting bodies of tinder fungus (Fomes fomentarius)), being present on a large diameter tree was eight times the probalility for a small diameter tree. An increasing patch size (here WD sample) could therefore increase the probability for a species to colonize it, and thus increase its richness.

Without measuring the distances between the WD in each plot, I assumed that the numbers found in each plot would be an indirectly measurement of the connectivity between the WD samples because of identical plot sizes. The number of WD found in each plot was positively correlated with total plot richness. An added sample of WD to a plot will also add to the total volume of the same plot as well as to the connectivity (Schiegg 2000). Even so, a plot can consist of many small WD samples and thereby high connectivity, or a few large ones with less connectivity and still have the same total volume (since the ratio of volume to surface is not linear). Also, I did not find any correlation between total plot volumes of WD and plot richness, and number of WD sample within a plot was not correlated with total plot WD volume. Supporting this, Schiegg (2000) found connectivity to correlate well with species richness of saproxylic insects in Switzerland, and that species richness seemed to depend more on the spatial arrangement of WD rather than the total volume. Schiegg (2000) also found that species composition depended on connectivity of WD, and concluded that most saproxylic insects would not be able to recolonize forests from which they have become extinct. Isolation on small scale level (treedistances) have been found to highly affect the possibility of beetle (Bolitophagus reticulatus) presence on tinder fungus (Fomes fomentarius) in forest fragments in south-eastern Norway (Midtgaard 1996). Connectivity and isolation is now recognised as a very important element of landscape structure and ecology, because it incorporate movement as a critical feature of population survival (Taylor et al. 1993; Meffe et al. 1997), and would therefore affect population extinction rates (Hanski & Gilpin 1991). This is especially true for many saproxylic insects, which have low powers of dispersal and populations governed by metapopulation dynamics operating among habitat patches measured in cubic meters (Grove 2002).

Even though I only analysed for richness, without considering the composition of the taxa found (though incorporated in the CCA), one might expect to find a different species composition in burnt and unburnt forest. This is expected because the distribution of different habitats and structure has changed, and the

disturbance itself will cause a shift towards fugitive or stress-resistant species (Hansen 1986). The fires have also strongly affected WD characteristics in my study area. The total volume found in burnt area is more than twice the amount found in unburnt forest, and more WD samples are encountered (A. Endrestøl 2003, in prep.). WD characteristics in burnt forest are also skewed toward harder and bigger WD, with increased amount of snags (A. Endrestøl 2003, in prep.). Since all those WD qualities affect saproxylic insect abundance and richness, there is likely to be a different species composition between burnt and unburnt forest areas. My findings supports this, as whether the area was burnt or unburnt explained some of the variation in taxa distribution found in the CCA, using family level taxonomy. Didham et al. (1998) found that species composition of leaf-litter beetles changed significantly with decreasing distance from forest edge, and decreasing fragment area, but that rarefied species richness was roughly invariant across sites. If the same holds for saproxylic beetles, then the ICE estimator would not reflect the differences between burnt and unburnt forest areas. It is also likely that the number of rare taxa found in this study was too low to be reflected in the ICE estimator. As discussed above, one reason for the similarity found between burnt and unburnt forest areas, could be a restoration of the saproxylic fauna, because the fires occurred three years ago. As all of the taxa investigated in this study showed no differences in density between burnt and unburnt (except for one), this is likely to be reflected as a similarity in the Coleman richness analyses, which shows sample richness.

Methods

The methods I used for collecting saproxylic insects probably yielded a biased distribution of insects, even though dead wood is a quite well defined substrate. Because the sampling was based on hand- picking and physically investigating the wood, densities of insects in big and hard logs were underestimated, even though boreholes were investigated. The extent of the physical investigation of WD also varied between logs and snags, which made it difficult to compare within plot differences. Also, some of the taxa would easily escape hand-collection (especially Blattodea and Orthoptera). All the above influences both species densities and total densities, and would highly underestimate these. This also influences the richness estimators and the accumulation curves both within sample richness and total richness based on rarity.

The saproxylic insect community consisted of a wide variety of feeding guilds associated to different degrees with dead wood, and often varying between different life stages within the same taxa (Grove 2000). The method used in this study will therefore probably also bias the distribution of feeding guilds and stages of saproxylics found. For Coleoptera, Lepidoptera, and Diptera, this would probably be towards xylophagous and mycophagous larvae, and not so much include predators/parasites, or adults/imagos in general. Another problem is that the amounts of wood sampled in burnt and unburnt were different, and that the sampling effort was not great enough for the ICE estimator to stabilise. However, the results are useful as a comparison between different sites, since the method is consistent. Siltonen (1994) compared two methods for sampling saproxylic insects, where one included bark peeling and the other one, trunk window traps. He found it hard to obtain large enough sample units by bark peeling, because of great variation among plots, and that the window trap yielded large samples at small cost. Because of the cost, the sample sizes yield, and the destructive nature of my method, it cannot be recommended over other sampling methods.

My data consist of relatively low taxonomic resolution (orders, families, subfamilies, and genera). Nevertheless I have analysed the data using two taxonomical resolutions (highest possible, including subfamilies and genera vs. lumping to order and family level), with similar results. This supports the argument that analysis at family level can be sufficient to reveal general responses of invertebrate assemblages (Blanche *et al.* 2001; Orgeas & Andersen 2001), even though a more distinct separation of samples (species) in the ordination space might have been achieved using higher taxonomical resolution. It is also possible that the difference in taxonomic resolution between my two data sets was to small to reveal differences that might exist between e.g. species and family level.

Conclusion

An overall similarity was found between burnt and unburnt LDRF in both abundance and richness of saproxylic insects. The nature of the 1997-98 fires might have left some of the saproxylic fauna alive (Makihara *et al.* 2000), which could still be reflected at the time of this study due to extended life cycles of xylophagous insects (e.g. Harmon *et al.* 1986). The similarities could also be explained by a quick restoration of the saproxylic fauna (Makihara *et al.* 2000), as the substrate in the burnt forest might still be used by saproxylic insect (Wikars 1997; Michaels & Bornemissza 1999). Most of the saproxylic insects showed a preference towards a decay class of WD, and this was also the most important environmental parameter explaining the distribution of the saproxylic taxa, and their abundance and richness. Richness and abundance were also positively correlated to sample WD volume, and richness was additionally positively correlated with WD connectivity. Even though no differences were found in insect densities per ha in this study, this might still exist at a larger scale, both because abundance and richness was correlated with some of the WD characteristics, and because no differences in volume of WD could be detected in the sample plots, even though such a difference existed at a larger scale with a skewed structural distribution of WD characteristics (Endrestøl 2003, *in prep.*). The above also indicates that there is likely be a different species composition in burnt and unburnt forest.

This study has shown that burnt LDRF can still harbour many of the saproxylic insects found in an unburnt primary rainforest, at least on the subfamily or family level. Differences might still exist in species composition, which should be investigated through further research. The dynamics of input and output of WD are altered by the fires, which over years could affect the distribution and composition of saproxylic insects. Further research is recommended to acquire knowledge of the saproxylic insects in the tropics, and to further understand the effects of wild fires on the saproxylic fauna.

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Appendix 2.1: Insects encountered and identified.

Table A2.1.1. Data set I: Total number and mass (g) of identified taxa. Taxa in italics represent Coleoptera imagos. * represent taxa excluded from the CCA analysis. Total mass is the total number of individuals multiplied by average individual mass.

Taxon	Code in ordination	Individuals	Total mass (g)
ANOBIIDAE (major part)	*	1	0.020
ANTHRIBIDAE (major part)	*	3	0.181
ANTHRIBIDAE: Anthribinae	*	1	0.166
BRENTIDAE: Brentinae (major part)	BreBRE_L	29	1.471
BRENTIDAE: Cylanidae	*	1	0.036
BUPRESTIDAE (major part)	*	4	0.244
CALLIRHIPIDAE	CALLIR L	15	12.714
CARABIDAE (major part)	*	2	0.041
CARABIDAE (major part)	*	5	0.057
CERAMBYCIDAE: Cerambycinae	*	5	0.558
CERAMBYCIDAE: Cerambvcinae (maior part)	*	2	1.147
CERAMBYCIDAE: Lamiinae	LamCER L	144	15.736
CERAMBYCIDAE: Lamiinae (maior part)	*	2	0.087
CERAMBYCIDAE: Prioninae (maior part)	*	1	0.384
CHALCODRYIDAE	*	1	0.240
CLERIDAE (major part)	CLERID L	13	0.026
CURCULIONIDAE: Scolutinge (major part)	*	2	0.019
DYTISCIDAE (major part)	*	1	0.007
FI ATERIDAE: Cardionhorinae	*	2	0.119
FLATERIDAE: Denticollinae	DenFLA I	18	1 577
ELATERIDAE: Elaterinae	EleFLA I	25	1.103
ELATERIDAE: Magastriinae	*	5	0.161
ENDOMYCHIDAE (major part)	ENDOMY I	8	0.868
ENDOMICHIDAE (major puri)	*	8	0.003
EUCNEMIDAE (major part)	FUCNEM I	70	1 238
HISTERID AF (major part)	EUCINEM_L *	1	0.002
HVDPOPHI IDAE, Hydrophilings (major part)	*	1	0.002
I AEMOPHI OFID AE (major part)	*	1	0.008
LAEMOPHLOEIDAE (major pari)	*	1	0.010
LAMP I RIDAE: Lampyrinae (major part)	*	1	0.020
LANGORIDAE: Xenosceuni (major pari): Xenosceunae	LUCANIL I	3	0.090
LUCANIDAE	LUCANI_L	148	40.970
LUCANIDAE: Lucaninae (major part)		11	0.900
	MORDEL	3	0.067
MORDELLIDAE	MORDEL_L	10	0.291
PASSALIDAE	PASSAL_I	34	3.967
PASSALIDAE	PASSAL_L	48	4.823
PHILODACTYLIDAE: Ptilodactylinae	*	2	0.010
RHIPIPHORIDAE: Rhipidiinae (late instar)		1	0.075
SCARABAEIDAE	SCARAB_L	23	15.315
SCARABAEIDAE: Melolonthinae (major part)	т 4	1	0.059
SCARABAEIDAE: Scarabaeinae (major part)	*	1	0.021
		1	0.001
TENEBRIONIDAE (major part)	TENEBR_I	79	7.476
TENEBRIONIDAE (major part)	IENEBR_L	385	38.966
BLABERIDAE: Panesthia sp. (nymph)	BlaPan_n	52	38.774
BLABERIDAE: Panesthia sp. (adult)	BlaPan_a	16	52.150
BLATTODEA: stm (nymph)	BLAstm_n	44	8.157
BLATTODEA: sfm (adult)	*	4	1.540
DIPTERA	DIPTERA	223	1.430
LEPIDOPTERA	LEPIDOPT	59	0.811
ORTHOPTERA (unknown stage)	*	6	1.925
ORTHOPTERA (nymph)	*	7	0.539
ORTHOPTERA (adult)	*	4	1.281
PUPAE (generally)	PUPAE	77	16.951
SUM		1616	280 844

Table A2.1.2. Data set II; Total number and mass (g) of taxa after lumping lower taxa. Taxa in italics represent images. Taxa in **bold** are lumped (either from different subfamilies/genera or stadium taxa). * represent taxa excluded from the CCA analysis. Total mass is the total number of individuals multiplied by average individual mass.

Taxon	Code in ordination	Individuals	Total mass (g)
ANOBIIDAE (major part)	*	1	0.020
ANTHRIBIDAE	*	4	0.347
BRENTIDAE	BRENTI_S	30	1.507
BUPRESTIDAE (major part)	*	4	0.244
CALLIRHIPIDAE	CALLIR_L	15	12.714
CARABIDAE	*	7	0.098
CERAMBYCIDAE	CERAMB_S	154	17.912
CHALCODRYIDAE	*	1	0.240
CLERIDAE (major part)	CLERID_L	13	0.026
CURCULIONIDAE: Scolytinae (major part)	*	2	0.019
DYTISCIDAE (major part)	*	1	0.007
ELATERIDAE	ELATER_S	50	2.960
ENDOMYCHIDAE	ENDOMY_S	9	0.871
EUCNEMIDAE (major part)	EUCNEM_L	79	1.238
HISTERIDAE (major part)	*	1	0.002
HYDROPHILIDAE: Hydrophilinae (major part)	*	1	0.008
LAEMOPHLOEIDAE (major part)	*	1	0.010
LAMPYRIDAE: Lampyrinae (major part)	*	1	0.026
LANGURIIDAE: Xenoscelini (major part): Xenoscelinae	*	3	0.090
LUCANIDAE	LUCANI_S	159	47.876
LYCIDAE	*	3	0.067
MORDELLIDAE	MORDEL_L	10	0.291
PASSALIDAE	PASSAL_S	82	8.790
PTILODACTYLIDAE: Ptilodactylinae	*	2	0.010
RHIPIPHORIDAE: Rhipidiinae (late instar)	*	1	0.075
SCARABAEIDAE	SCARAB_S	25	15.395
STAPHYLINIDAE	*	1	0.001
TENEBRIONIDAE	TENEBR_S	464	46.442
BLABERIDAE: Panesthia sp.	BlaPan_S	68	90.924
BLATTODEA: sfm	BLAsfm_S	58	9.875
DIPTERA	DIPTERA	223	1.430
LEPIDOPTERA	LEPIDOPT	59	0.811
ORTHOPTERA	ORTHOP_S	17	3.745
PUPAE (generally)	PUPAE	77	16.951
SUM		1626	281.022

Appendix 2.2: Statistical results

All the tests were preformed using SigmaStat version 1.0

All tests were conducted using the non-parametric Mann-Whitney Rank Sum Test.

All densities given (either of biomass or individuals) are average values of the 0.04 ha sampling plots (SPs) (\pm SE). Summed orders and summed totals includes just taxa present in the tables. Densities calculated per ha includes just insects found in coarse woody debris, excluding fine woody debris. Densities calculated per m³ include both fine and coarse woody debris.

The number of repetitions (SPs) in burnt and unburnt forest was always 7 (14 total).

Tables A2.2.5 and A2.2.6 were produced in Canoco 4.0.

Table A2.2.1. *Statistical results*: No. of individuals in saproxylic insect taxa per ha tested between burnt and unburnt lowland dipterocarp rainforest (LDRF), East Kalimantan, Indonesia.

The table includes Blattodea (*Panesthia* sp. and Blattodea sfm.), Coleoptera (Brentidae, Callirhipidae, Cerambycidae, Cleridae, Endomychidae, Elateridae, Eucnemidae, Lucanidae, Mordellidae, Passalidae, Scarabaeidae, Tenebrionidae), Diptera, Lepidoptera, Orthoptera and all pupae found in coarse woody debris (CWD ≥ 10 cm diameter). Area extrapolated from the average of 14- 0.04 ha sampling plots.

Taxon	Т	р	No ind ha ⁻¹ (± SE)	No ind ha ⁻¹ (± SE) in	Total no ind ha ⁻¹	%
			in unburnt LDRF	burnt LDRF	(± SE) in LDRF	total
Brentidae	54.5	0.8048	85.71 ± 56.39	21.43 ± 17.62	53.57 ± 29.75	2.12
Callirhipidae	60.5	0.3176	46.42 ± 27.51	3.57 ± 3.57	25.00 ± 14.59	0.99
Cerambycidae	43.0	0.2593	221.42 ± 145.61	257.14 ± 92.53	239.28 ± 83.02	9.47
Cleridae	49.0	0.7104	0 ± 0	46.43 ± 46.43	23.21 ± 23.21	0.92
Elateridae	50.0	0.8048	53.57 ± 12.71	110.71 ± 49.36	82.08 ± 25.73	3.25
Endomychidae	53.0	1.0000	25.00 ± 25.00	3.57 ± 3.57	14.28 ± 12.49	0.57
Eucnemidae	66.0	0.0973	264.29 ± 214.77	17.86 ± 7.14	141.07 ± 108.74	5.58
Lucanidae	49.5	0.7104	153.57 ± 92.49	392.85 ± 251.93	273.21 ± 133.12	10.81
Mordellidae	58.5	0.4557	14.28 ± 7.43	7.14 ± 7.14	10.71 ± 5.05	0.42
Passalidae	49.0	0.7104	175.00 ± 154.78	85.71 ± 45.59	130.35 ± 78.49	5.16
Scarabaeidae	44.5	0.3176	14.28 ± 5.05	67.85 ± 37.28	41.07 ± 19.54	1.63
Tenebrionidae	48.0	0.6200	550.00 ± 103.36	892.85 ± 287.10	721.42 ± 154.10	28.55
Σ Coleoptera	50.0	0.8048	1603.57 ± 373.78	1907.14 ± 566.88	1755.35 ± 328.89	69.47
Blattodea sfm.	38.5	0.0728	64.28 ± 56.39	110.71 ± 39.28	87.50 ± 33.63	3.46
Panesthia sp.	40.5	0.1282	53.57 ± 20.72	157.14 ± 51.67	105.35 ± 30.35	4.17
Σ Blattodea	40.0	0.1282	117.85 ± 54.74	267.85 ± 57.66	192.85 ± 43.49	7.63
Diptera	45.0	0.3829	307.14 ± 191.92	389.28 ± 138.10	348.21 ± 114.15	13.78
Lepidoptera	47.0	0.5350	50.00 ± 18.09	132.08 ± 64.48	91.07 ± 34.13	3.60
Orthoptera	46.0	0.4557	32.08 ± 28.19	25.00 ± 9.44	28.57 ± 14.32	1.13
Pupae	45.0	0.3829	85.71 ± 31.27	135.71 ± 44.27	110.71 ± 26.94	4.38
TOTAL	47.5	0.5350	2196.42 ± 455.43	2857.14 ± 638.86	2526.78 ± 387.87	100.00

Table A2.2.2. Statistical results: No. of individuals in sag	proxylic insect taxa per m ³ tested between burnt and unburnt
lowland dipterocarp rainforest, East Kalimantan, Indonesia	ι.

The table includes Blattodea (Panesthia sp. and Blattodea sfm.), Coleoptera (Brentidae, Callirhipidae, Cerambycidae,
Cleridae, Endomychidae, Elateridae, Eucnemidae, Lucanidae, Mordellidae, Passalidae, Scarabaeidae, Tenebrionidae),
Diptera, Lepidoptera, Orthoptera and all pupae found in fine and coarse woody debris (5 cm \leq FWD \leq 10 cm diameter,
$CWD \ge 10 \text{ cm diameter}).$

Taxon	Т	р	No ind m ⁻³ (± SE) in	No ind m ⁻³ (± SE) in	Total no ind m ⁻³	%
			unburnt plots	burnt plots	(± SE)	total
Brentidae	54.5	0.8048	0.32 ± 0.21	0.05 ± 0.03	0.19 ± 0.11	1.33
Callirhipidae	65.0	0.1282	0.36 ± 0.17	0.01 ± 0.01	0.18 ± 0.10	1.26
Cerambycidae	51.0	0.9015	1.00 ± 0.44	0.94 ± 0.44	0.97 ± 0.30	6.81
Cleridae	49.0	0.7104	0 ± 0	0.28 ± 0.28	0.14 ± 0.14	0.98
Elatateridae	60.0	0.3829	0.64 ± 0.39	0.36 ± 0.19	0.50 ± 0.21	3.51
Endomychidae	57.0	0.6200	0.15 ± 0.10	0.02 ± 0.02	0.08 ± 0.05	0.56
Eucnemidae	68.5	0.0379	5.41 ± 5.20	0.06 ± 0.03	2.74 ± 2.60	19.24
Lucanidae	54.0	0.9015	0.61 ± 0.22	1.03 ± 0.45	0.82 ± 0.25	5.76
Mordellidae	56.0	0.7104	0.12 ± 0.07	0.06 ± 0.04	0.09 ± 0.04	0.63
Passalidae	53.5	0.9015	0.97 ± 0.81	0.23 ± 0.11	0.60 ± 0.41	4.21
Scarabaeidae	52.0	1.0000	0.17 ± 0.08	0.24 ± 0.13	0.21 ± 0.07	1.47
Tenebrionidae	64.0	0.1649	3.78 ± 0.69	2.57 ± 0.61	3.18 ± 0.47	22.33
Σ Coleoptera	62.0	0.2593	13.55 ± 6.23	5.85 ± 1.69	9.70 ± 3.28	68.12
Blattodea sfm.	42.0	0.2086	0.23 ± 0.16	0.25 ± 0.06	0.24 ± 0.08	1.69
Panesthia sp.	45.0	0.3829	0.27 ± 0.10	0.37 ± 0.10	0.32 ± 0.07	2.25
Σ Blattodea	47.0	0.5350	0.50 ± 0.17	0.62 ± 0.07	0.56 ± 0.09	3.93
Diptera	53.0	1.0000	4.93 ± 4.02	1.00 ± 0.24	2.97 ± 2.01	20.86
Lepidoptera	52.5	1.0000	0.30 ± 0.13	0.45 ± 0.27	0.38 ± 0.14	2.67
Orthoptera	48.5	0.6200	0.19 ± 0.15	0.10 ± 0.04	0.15 ± 0.08	1.05
Pupae	59.0	0.4557	0.56 ± 0.13	0.42 ± 0.12	0.49 ± 0.08	3.44
TOTAL	62.0	0.2593	20.03 ± 10.04	8.44 ± 1.87	14.24 ± 5.16	100.00

Table A2.2.3. *Statistical results*: Biomass of saproxylic insect taxa per ha tested between burnt and unburnt lowland dipterocarp rainforest (LDRF), East Kalimantan, Indonesia.

The table includes Blattodea (Panesthia sp. and Blattodea sfm.), Coleoptera (Brentidae, Callirhipidae, Cerambycidae,
Cleridae, Endomychidae, Elateridae, Eucnemidae, Lucanidae, Mordellidae, Passalidae, Scarabaeidae, Tenebrionidae),
Diptera, Lepidoptera, Orthoptera and all pupae found in coarse woody debris (CWD \geq 10 cm diameter). Area
extrapolated from the average of 14 0.04 ha sampling plots.

Taxon	Т	р	g ha ⁻¹ (± SE) in	g ha ⁻¹ (± SE) in burnt	Total g ha ⁻¹	%
			unburnt LDRF	LDRF	(± SE) in LDRF	total
Brentidae	54.5	0.8048	4.57 ± 3.09	0.81 ± 0.67	2.69 ± 1.61	0.58
Callirhipidae	60.0	0.3829	42.48 ± 35.87	2.92 ± 2.92	22.70 ± 18.14	4.89
Cerambycidae	45.0	0.3829	26.81 ± 16.99	32.76 ± 11.09	29.79 ± 9.78	6.42
Cleridae	49.0	0.7104	0 ± 0	0.09 ± 0.09	0.05 ± 0.05	0.01
Elateridae	52.0	1.0000	3.66 ± 1.04	6.70 ± 3.60	5.18 ± 1.85	1.12
Endomychidae	53.0	1.0000	3.03 ± 3.03	0.08 ± 0.08	1.55 ± 1.51	0.33
Eucnemidae	65.5	0.0973	3.87 ± 2.73	0.55 ± 0.29	2.21 ± 1.40	0.48
Lucanidae	51.0	0.9015	56.33 ± 46.77	65.09 ± 26.20	60.71 ± 25.78	13.08
Mordellidae	58.0	0.5350	0.13 ± 0.08	0.71 ± 0.71	0.42 ± 0.35	0.09
Passalidae	55.0	0.7104	22.20 ± 14.50	9.15 ± 4.65	15.68 ± 7.54	3.38
Scarabaeidae	47.5	0.5350	10.45 ± 8.65	44.51 ± 30.06	27.48 ± 15.75	5.92
Tenebrionidae	42.0	0.2086	54.58 ± 21.86	104.69 ± 46.16	79.64 ± 25.50	17.16
Σ Coleoptera	48.0	0.6200	228.11 ± 72.79	268.09 ± 73.32	248.10 ± 49.94	53.46
Blattodea sfm.	35.0	0.0262	5.04 ± 4.90	29.51 ± 25.88	17.27 ± 13.10	3.72
Panesthia sp.	37.5	0.0530	57.94 ± 33.84	260.06 ± 83.22	158.77 ± 51.49	34.21
Σ Blattodea	37.0	0.0530	62.53 ± 32.77	289.57 ± 91.65	176.05 ± 56.37	37.93
Diptera	46.0	0.4557	2.91 ± 1.90	2.10 ± 0.95	2.51 ± 1.03	0.54
Lepidoptera	40.0	0.1282	0.34 ± 0.11	2.34 ± 0.91	1.34 ± 0.52	0.29
Orthoptera	50.0	0.8084	10.74 ± 10.74	2.61 ± 1.78	6.68 ± 5.35	1.44
Pupae	38.5	0.0728	9.07 ± 3.00	49.72 ± 15.04	29.40 ± 9.28	6.33
TOTAL	39.0	0.0973	313.70 ± 94.60	614.43 ± 146.08	464.08 ± 93.43	100.00

Table A2.2.4. *Statistical results*: Biomass of saproxylic insect taxa per m³ tested between burnt and unburnt lowland dipterocarp rainforest, East Kalimantan, Indonesia.

The table includes Blattodea (*Panesthia* sp. and Blattodea sfm.), Coleoptera (Brentidae, Callirhipidae, Cerambycidae, Cleridae, Endomychidae, Elateridae, Eucnemidae, Lucanidae, Mordellidae, Passalidae, Scarabaeidae, Tenebrionidae), Diptera, Lepidoptera, Orthoptera and all pupae found in fine and coarse woody debris ($5 \text{ cm} \le \text{FWD} < 10 \text{ cm}$ diameter, CWD $\ge 10 \text{ cm}$ diameter).

Taxon	Т	р	g m ⁻³ (± SE) in	g m ⁻³ (± SE) in	Total g m ⁻³	%
			unburnt plots	unburnt plots	(± SE)	total
Brentidae	54.5	0.8048	0.016 ± 0.011	0.002 ± 0.001	0.009 ± 0.006	0.51
Callirhipidae	61.0	0.3176	0.279 ± 0.244	0.006 ± 0.006	0.142 ± 0.123	7.98
Cerambycidae	55.0	0.8048	0.108 ± 0.043	0.107 ± 0.039	0.108 ± 0.028	6.07
Cleridae	49.0	0.7104	0 ± 0	0.001 ± 0.001	0.0003 ± 0.0003	0.02
Elateridae	62.0	0.2593	0.038 ± 0.019	0.021 ± 0.013	0.029 ± 0.011	1.63
Endomychidae	56.0	0.7104	0.008 ± 0.008	0.0003 ± 0.0003	0.0042 ± 0.004	0.24
Eucnemidae	67.5	0.0530	0.073 ± 0.067	0.002 ± 0.001	0.037 ± 0.034	2.08
Lucanidae	45.0	0.3829	0.174 ± 0.130	0.374 ± 0.180	0.274 ± 0.110	15.39
Mordellidae	54.0	0.9015	0.001 ± 0.001	0.005 ± 0.004	0.0027 ± 0.002	0.15
Passalidae	56.0	0.7104	0.121 ± 0.079	0.023 ± 0.010	0.072 ± 0.040	4.04
Scarabaeidae	49.0	0.7104	0.060 ± 0.045	0.142 ± 0.109	0.101 ± 0.058	5.67
Tenebrionidae	54.0	0.8983	0.362 ± 0.145	0.261 ± 0.075	0.312 ± 0.079	17.52
Σ Coleoptera	59.0	0.4557	1.239 ± 0.279	0.945 ± 0.239	1.092 ± 0.181	61.32
Blattodea sfm.	35.0	0.0262	0.051 ± 0.051	0.064 ± 0.055	0.058 ± 0.036	3.26
Panesthia sp.	41.5	0.1649	0.301 ± 0.179	0.603 ± 0.144	0.452 ± 0.118	25.39
Σ Blattodea	42.0	0.2086	0.352 ± 0.171	0.668 ± 0.163	0.510 ± 0.122	28.65
Diptera	48.0	0.6200	0.035 ± 0.029	0.006 ± 0.004	0.021 ± 0.014	1.18
Lepidoptera	41.0	0.1649	0.002 ± 0.001	0.007 ± 0.003	0.005 ± 0.002	0.28
Orthoptera	47.0	0.5350	0.057 ± 0.057	0.007 ± 0.004	0.032 ± 0.028	1.80
Pupae	56.0	0.7104	0.088 ± 0.026	0.155 ± 0.062	0.122 ± 0.034	6.85
TOTAL	49.0	0.7104	1.773 ± 0.410	1.788 ± 0.328	1.780 ± 0.252	100.00
Table A2.2.5. *Statistical results*: The correlation matrix between the ordination axis and the different environmental parameters from data set I and II.

		Data	set I		Data set II						
	ENVI	ENVI	ENVI	ENVI	ENVI	ENVI	ENVI	ENVI			
	AX1	AX2	AX3	AX4	AX1	AX2	AX3	AX4			
Decay WD	.8545	.1392	.1037	1177	.7952	.1809	.0484	0566			
Log/snag	.1039	2015	.0115	.6254	.1545	.1068	2375	.4410			
Volume WD	.0008	.0734	0551	.0026	.0575	.0361	.0129	0605			
Canopy	.1496	0820	3603	.1891	.1740	.3527	.2253	.1639			
Soil temp.	.0785	5015	0738	2261	.1820	4636	.0721	1394			
Burnt/unburnt	.0565	2056	4838	.1097	.1260	.0802	.4234	.1477			
North	.0024	4264	.2927	.4435	.1067	1422	3620	.5705			
South	.0001	.0459	1546	2207	.0006	1646	0484	5739			
West	0027	.4034	1509	2425	1134	.3202	.4327	0111			
Slope	1281	.0328	.4597	.1292	1195	1472	4120	.0122			
HighFlat	0203	.0674	5388	0280	0516	.2973	.4352	.0331			
Alluvial	.2630	1709	.0748	1845	.3007	2325	.0127	0773			
Ants in WD	1405	4304	1193	0303	.0072	2883	0769	2800			
Termites in WD	.2962	.2414	.1003	2482	.2137	.1828	0247	3178			

Values stronger than 0.3 are highlighted in bold. Produced in Canoco 4.0 (ter Braak & Smilauer 1997).

Values higher than 0.3 are highlighted in bold. Underlined values denote mutually exclusive parameters. Produced in Canoco 4.0 (ter Braak & Smilauer 1997).

Decay WD	0 Decay WD	Log/snag	Volume WD	Canopy	Soil Temp.	Burnt/unburnt	North	South	West	Slope	HighFlat	Alluvial	Ants in WD	Termites in WD
Log/snag	-0.18	1.00												
Volume WD	-0.08	0.10	1.00											
Canopy	-0.02	0.13	0.17	1.00]									
Soil Temp.	-0.15	0.00	-0.01	0.32	1.00]								
Burnt/unburnt	-0.15	0.07	0.07	0.79	0.70	1.00	1							
North	0.01	0.19	0.19	0.35	-0.05	0.05	1.00	1						
South	-0.16	-0.14	-0.13	-0.31	0.49	0.09	<u>-0.54</u>	1.00	1					
West	0.15	-0.05	-0.06	-0.05	-0.45	-0.15	<u>-0.51</u>	<u>-0.46</u>	1.00	1				
Slope	-0.06	-0.05	-0.14	-0.34	0.43	0.07	-0.11	0.50	-0.39	1.00				
HighFlat	-0.01	0.07	0.13	0.53	-0.31	0.13	0.25	-0.48	0.16	<u>-0.83</u>	1.00	1		
Alluvial	0.12	-0.02	0.03	-0.27	-0.26	-0.35	-0.22	-0.20	0.44	<u>-0.40</u>	<u>-0.17</u>	1.00	1	
Ants in WD	-0.10	0.08	0.23	-0.15	0.02	-0.13	0.06	0.08	-0.15	0.01	-0.07	0.10	1.00	
Termites in WD	0.23	-0.02	0.23	0.10	-0.13	-0.08	0.13	-0.13	0.00	-0.17	0.20	-0.02	0.10	1.00

Table A2.2.6. *Statistical results*: The correlation matrix between the environmental parameters.

"J eg sitter å føler meg som en hersker og konge over hele denne opplyste herligheten rundt meg, konge over alle disse mennesker og over alt det land vi har hugd nakent og vristet fra jungelen. Det elektriske lyset og larmen fra sagbruket holder alle jungelens makter på avstand selv om natten.

Men i den dødende skumringen ser jeg et stykke borte hvordan den ødelagte jungelen strekker sine truende kjempehender mot himmelen. Svartbrente treskjeletter! At de aldri faller, de gamle døde kjempene! Jeg liker ikke særlig denne holdningen deres om kvelden. Det ligger både trussel og sorg i denne ville gestus mot himmelen. Det er som om de tydelig vil si meg at jeg ikke har kjempet for noen god sak, og at jeg ikke har vunnet kampen ennå. Da er det ikke morsomt å være konge mer.

Da forstår jeg at kampen mot jungelen ikke bringer noen ære, og at jeg lurer både meg selv og andre til å kjempe mot et gode [...] Det er som om vi simpelthen skader oss selv, noe inni oss, når vi ødelegger villmarken og agerer fortropper for kultur og sivilisasjon..."



- Eric Lundquist *-

^{*} Eric Lundquist: "I jungelens vold" Gyldendal Norsk Forlag, Oslo, 1954