

Dung beetles as indicators of change in the forests of northern Borneo

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Summary

1. We reviewed the use of dung beetles as indicators of environmental change, highlighting the influence of natural forest dynamics on species distributions in primary forest and suggesting new ways in which this can be used to understand and interpret the effects of disturbance such as logging. These ideas were applied to rainforest dung beetle communities in Sabah, Malaysia.

2. Dung beetle samples, using baited pitfall and flight intercept traps, were examined from primary, logged and plantation forests. Cluster analysis on dung beetle assemblages from primary forest samples showed clear species associations that had a high degree of fidelity to a particular biotope or vegetation type. Beetles were grouped into riverine-edge, riverine, interior-primary and 'even' (equitable distribution between biotopes) associations. Although biotope-specific associations were spatially separate in primary forest, these associations overlapped at forest margins (riverine forest) and in logged forest (to form 'composite assemblages').

3. Species associations showed different responses to disturbance: the riverine association included many species that showed a positive response to at least some types of disturbance, whereas others were neutral or negative in response; the even association species were mostly neutral; the primary forest associations were almost entirely negative in response.

4. The greatest faunal similarities were found between logged forest and riverine assemblages. Diversity was lower in logged compared with primary forest, and the lowest species richness and diversity were recorded in plantation forest. Small-scale species richness in logged forest was generally higher than in individual transects from primary forest due to the presence of overlapping species ranges (composite assemblages) that were usually spatially separate in primary forest. Data suggested that increased species richness at a fine scale does not necessarily mean that species richness is greater at a larger scale, and that species mixing in derived ecosystems is dependent on the type of disturbance. Forest management should aim to minimize the mixing of the components of different biotopes, by implementing low impact (i.e. reduced-impact logging) harvesting techniques.

Key-words: bioindicator, community structure, diversity, logging.

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Introduction

There is currently much speculation about the consequences of human-generated disturbance on tropical

rainforest biodiversity, particularly impacts on species composition (Whitmore & Sayer 1992; Laurance & Bierregaard 1997) and the possibility of irreversible changes in tropical forests following logging (Reid & Miller 1989; Reid 1992). Over recent decades, the harvesting of timber has become the major source of human disturbance in tropical forests. The total loss in tropical forests in the decade 1981–90 was 154 million

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ha, representing an annual loss of 0.81% of the total forest cover in 1980 (FAO 1993, 1995), with tropical moist forests counting for the largest forest area lost (85% of the total; Whitmore 1997). Not all tropical rainforests are cleared through deforestation, and selective logging constitutes a substantial impact on remaining forests, especially in Asia. From 1981 to 1990, 5.6 million ha were logged each year, of which 2.6 million ha were in the Americas, 2.1 million ha in Asia and 0.9 million ha in Africa, representing 0.3%, 0.7% and 0.2% of the respective forest areas (Whitmore 1997). Within Asia the greatest logging impact was on forests in the Malay Archipelago (which includes the island of Borneo), where 1.8 million ha year⁻¹ were logged (compared with 0.4 million ha year⁻¹ on the continent of Asia). In 1989 it was estimated that only 0.1% of remaining natural tropical forest was under active sustainable management and only 3% set aside for the conservation of biodiversity (Holmberg, Bass & Timberlake 1991).

South-east Asia has the tallest tropical rainforests in the world (some emergent trees can reach 70–80 m) with the greatest timber volumes (dominated by the Dipterocarpaceae), which accounts for the high levels of logging in this region. This is particularly true for forests in Borneo, where current fellings in the primary forest in Borneo may, over limited areas, yield greater than 100 m³ ha⁻¹ compared with the regional average of 45 m³ ha⁻¹ (Collins, Sayer & Whitmore 1991). Borneo, at the heart of Sundaland, is a centre of biological diversity, with a very rich flora and fauna (e.g. 265 of the 390 species of dipterocarps are found there; Collins, Sayer & Whitmore 1991). In terms of forests throughout Malaysia, rainforests cover 200 450 km², of which 36 000 km² are found in Sabah (Sarawak being the other Malaysian state in Borneo). Management of forests in East Malaysia (Malaysian Borneo) is under state control, although under overall Federal policy (Sabah Forestry Department 1986; FAO 1987). In 1992, about 60% of Sabah's total land area (73 710 km²) was under forest cover of some sort, with 45% under Permanent Forest Estate (PFE) and 3.3% in State Parks (Marsh 1995). Of the PFE, 2530 099 ha were classified as Commercial Forest Reserve (i.e. can be exploited for logging; Marsh 1995). In 1974 it was estimated that 6.4 million ha (88% of the total land area) was forested, whereas only 4.5 million ha remained in 1985 (i.e. a 30% reduction in 11 years; Marshall 1992). The main cause of degradation and deforestation in Sabah has been from logging: between 1985 and 1990 the annual deforestation rate was 800 km² compared with 2210 km² for the whole of Federal Malaysia. Sabah's commercial forest has steadily been depleted over the past three decades: by 1997 only 365 879 ha of virgin forest remained within the Commercial Forest Reserve, compared with 2.7 million ha in 1970 (Chai 1997). Undisturbed lowland dipterocarp forest is becoming particularly scarce, and rapidly being diminished by logging (Marsh & Greer 1992).

SPECIES DIVERSITY IN TROPICAL RAINFORESTS

Theories regarding the generation and maintenance of rainforest diversity (Connell 1978) are plentiful (Wallace 1878; Aubréville 1938; Richards 1952; MacArthur 1965, 1972; Baker 1970; Ricklefs 1973; Grubb 1977; Leigh 1983; Gentry 1988; Martínéz-Ramos *et al.* 1988). It has become clear that natural disturbance and non-equilibrium dynamics generate high diversity (Jacobs 1988; Huston 1994), as do variations across environmental gradients generated by topographical and edaphic landscape features in the forest (see seminal work by Richards 1952).

Plant ecology has for many years described ecological processes in terms of changes along gradients (Austin 1985). In rainforest, predictability of disturbance (e.g. tree-fall gap formation) has been shown to be an important factor in vegetational differentiation of closely related species across microsites (Ashton, Gunatilleke & Gunatilleke 1995; reviewed by Brown & Jennings 1998). The distribution of animals in tropical rainforests has also long been linked with environmental factors (Allee 1926; Janzen & Schoener 1968), and predictable environmental gradients in the forest landscape (i.e. river edge to forest interior) may be expected to provide a strong correlative base to insect distribution patterns in primary rainforest, just as it has for plant communities. Species distributed along environmental gradients may be divided into discrete associations linked to particular biotopes (*sensu* Whittaker, Levin & Root 1973) in the landscape. We use the terms 'habitat' and 'biotope' according to the definitions of Samways (1994), i.e. where habitat is an autecological concept emphasizing the interaction between the species and the physical habitat structure, and biotope refers to the physical local area where a species, or association of species, lives (Samways 1994). We also make a distinction between 'association' and 'assemblage': an association is a group of species showing high correlation in abundance pattern across biotopes, and sometimes showing high fidelity to a particular biotope, whereas an assemblage is the mixture of species from different associations found in any particular biotope (or sample). Vertical environmental gradients have been studied in rainforest, correlated to changes in microclimate from the ground to canopy (Allee 1926; Kato *et al.* 1995; Davis *et al.* 1997), and natural breaks in the forest created by large rivers may provide similar extreme conditions to those found in the upper forest canopy (Davis & Sutton 1998). Here we suggest that examining species distributions across natural environmental gradients in primary forest may be a useful way of looking at, and understanding, species distributions in disturbed ecosystems.

INDICATOR ORGANISMS

Although ecologists are graduating from a study of pattern to a study of process and ecosystem function

(Hanski 1989; Didham *et al.* 1996), there is still a great ignorance of pattern in tropical forest insect communities, particularly in relation to ecosystem disturbance through such events as logging (Sutton & Collins 1991). Para-taxonomic approaches, such as insecticidal fogging, produce extensive species lists and are an effective way of tackling the problem of insect super-diversity (Stork 1991), but, because of the large number of organisms collected, pose problems in interpreting underlying patterns. These studies present particular problems when examining the effects of disturbance. Similarly, whole community surveys, while currently much vaunted, often succumb to the same problem (Robinson *et al.* 1992), where inferences about overall effects of disturbance are difficult to make (see arguments by Crome 1997). To counter these problems, specific groups of organisms (indicators) can be singled out for special attention, and examined in detail (Pearson 1994; McGeoch 1998). The relative merits of various indicator groups, and their uses in studying the effects of disturbance, have been discussed extensively in the literature (Landres, Verner & Thomas 1988; Andersen 1990; Brown 1991; Holloway & Stork 1991; Sutton & Collins 1991; Kremen 1992; Halffter & Favila 1993; Kremen *et al.* 1993; Sparrow *et al.* 1994; Brown 1997; Crome 1997; Dufrêne & Legendre 1997; Lawton *et al.* 1998; McGeoch & Chown 1998; McGeoch 1998; New 1998).

Dung beetles are important decomposer organisms, involved with nutrient recycling, seed dispersal and the control of vertebrate parasites (by removal of source of infection), and are therefore an important component of tropical forest systems (Hanski & Krikken 1991). The local distribution of dung beetles is strongly influenced by vegetation cover and soil type (Nealis 1977; Doube 1983; Janzen 1983), and the physical structure of the forest appears to be an important determining factor in the composition and distribution of dung beetle assemblages (Davis & Sutton 1998). Consequently, dung beetles are a useful indicator group because they reflect structural differences (i.e. architectural, abiotic) between biotope types; thus, they differ from insects that reflect floristic differences (i.e. species composition, biotic) through biotope fidelity via plant-feeding specializations (e.g. moths and butterflies). Dung beetles have been used in several studies to investigate the effects of environmental disturbance on forest diversity and structure (Howden & Nealis 1975; Klein 1989; Nummelin & Hanski 1989; Halffter, Favila & Halffter 1992; Hill 1995; Davis & Sutton 1998; Davis 2000a). The rationale for using dung beetles as indicators of disturbance has been reviewed by Halffter & Favila (1993). Groups where interspecific competition is strong, such as the dung beetles (Hanski & Cambefort 1991a), may be expected to show species associations with a high degree of fidelity to a particular biotope. Work in Australia has demonstrated high degrees of biotope specificity in dung beetle species between rainforest and more open areas (Hill 1996). If the distribution of biotopes in the landscape changes through disturbance,

dung beetle assemblage structure can be expected to mirror these changes.

In this study we examined the effects of logging and conversion to plantation forest on rainforest dung beetle assemblages. Dung beetle taxonomy, behaviour and ecology have been studied extensively in South-east Asia (Hanski 1983; Hanski & Krikken 1991), providing valuable information for such studies. Previous research into the effects of habitat disturbance on dung beetles has shown that forest clearance reduces species richness (Howden & Nealis 1975) and that habitat fragmentation reduces richness and abundance (Klein 1989). However, studies on the effects of logging have been carried out where logging intensity was relatively low (Nummelin & Hanski 1989; Nummelin 1996) and where effects were negligible, or the total sample size was low and sampling effort insufficient to reveal more than very gross underlying patterns (Holloway, Kirk-Spriggs & Chey 1992). There are few published studies on the effects of conversion to plantation forest on tropical insect communities (Holloway, Kirk-Spriggs & Chey 1992; Chey, Holloway & Speight 1997; Davis, Huijbregts & Krikken 2000). As far as we are aware, only one previous published report has examined the effects of conversion to plantation on dung beetle assemblages, where species richness and diversity was seen to be reduced in plantation forest but no other patterns were discernible (Nummelin & Hanski 1989). There has been one previous publication relating to the effects of plantation conversion on dung beetle assemblages relating to this current study (Davis, Huijbregts & Krikken 2000).

Methods

STUDY SITE

The study was undertaken at the Danum Valley Field Centre, which lies on the eastern edge of the Danum Valley Conservation Area (4°58' N, 117°48' E): a 438-km² area of primary forest within the Ulu Segama Reserve in south-eastern Sabah (north-east Borneo). Much of the Conservation Area is lowland (< 760 m) evergreen dipterocarp forest, where dipterocarps comprise up to 80% of the canopy trees (Newbery *et al.* 1992). Forest within the Ulu Segama Reserve, which surrounds the Danum Valley Conservation Area, contains logged forest coupes of different ages, and exotic tree plantations within the logged forest mosaic (Marsh & Greer 1992). The annual rainfall average at Danum is 2744.7 mm (January 1986 to December 1991; Manchester University/Danum Valley Hydrology Unit, unpublished data). Mean daily maximum and minimum temperatures in primary forest near to the field centre have been recorded at 28.4 °C and 21.2 °C, respectively (Brown 1990).

SAMPLING TECHNIQUES

An extensive trapping programme was carried out between May 1990 and May 1992, using baited pitfalls

Table 1. Number of pitfalls per transect used in analysis, and description of each transect site

Transect	Trapping effort*	Description of transect
Riverine A	33	Primary forest adjacent to large river. Traps at river's edge (< 10 m from edge)
Riverine B	35	Primary forest adjacent to large river. Traps > 10 m, < 50 m, from river's edge
Primary A	25	Primary forest site in DVCA†. 300 m from large river
Primary B	30	Primary forest site in DVCA. 700 m from large river
Primary C	30	Primary forest site in DVCA. 1000 m from large river
Logged A	30	Forest site logged in 1988
Logged B	30	Forest site logged in 1989
Logged D	29	Forest site logged in 1981
Plantation A	27	Adjacent <i>Acacia</i> and mahogany plantations
Plantation B	30	Cocoa plantation with albizia shade cover

*Number of pitfall traps per transect.

†Danum Valley Conservation Area.

and flight interception traps (FIT) (Davis 1993). Traps were placed in primary forest (the Danum Valley Conservation Area), logged forest and plantations. Pitfall traps were made from plastic containers, 12.5 cm in diameter and 13 cm deep, covered by a plastic plate (c. 20 cm above the pitfall) to protect the trap from rain. Pitfalls in the main collecting programme were baited with human faeces: a proven attractant to dung beetles in rainforests, which attracts a wide spectrum of species, from dung specialists through to those that feed on carrion and other resources (Howden & Nealis 1975; Hanski 1983). Insects falling into the trap were killed by a solution of water, chloral hydrate and detergent. Traps were put at intervals of 20 m, and were left out for 3 days and nights. In general, 10 traps were deployed per transect, although numbers varied according to local conditions (see below for further information on transects). Because of limitation of bait availability each transect was sampled sequentially, with each transect sampled on at least three separate occasions during the trapping programme (see below). Although the conditions at Danum are essentially aseasonal (Walsh 1996), where possible transects were sampled at different times of year to ensure the widest possible temporal coverage. Locations for transects were selected by choosing sites at varying distances from the Segama river (a major river that is adjacent to the Danum Valley Field Centre), incorporating river edge, riverine and forest interior biotopes, so that transects sampled a gradient of change from riverine through to interior-primary forest (maximum distance was 1 km from forest edge) (Davis, Huijbregts & Krikken 2000). FIT were placed in locations corresponding to the sites of existing pitfall transects between January and May 1992 (see details below for exact location of each trap). FIT consist of a vertical wall of black terylene netting measuring 2.4 × 1.1 m, over which a plastic rain-cover is suspended. The black net forms an invisible barrier to insects flying through the dark forest interior; any that fly into the net fall down into aluminium foil collecting trays (18 × 11 cm internally and 4 cm deep) on both sides of the vertical wall. A solution of water, detergent and chloral hydrate ensures that insects

falling into the trays are killed quickly. FIT passively collect insects flying through the forest rather than using an attractant (Hammond 1990).

We analysed data collected from four sites in primary forest (riverine and interior), three in logged forest and two plantation sites, representing a total of 299 pitfall traps (897 trap nights) and five FIT traps placed in three primary (one of them riverine), one logged and one plantation site, representing five trap weeks (one week per trap). This represented the majority of the total collecting effort during the 2-year study (Davis 1993; Davis 2000b). Table 1 contains a list of the number of pitfalls used at each site, and a summary of the location of each transect. Trapping effort per transect varied according to local conditions (i.e. some transects sampled narrow biotopes, such as riverine-edge habitat; riverine transect A; Table 1), which used fewer pitfalls, and had to be sampled on a greater number of occasions to make up for trap sample size; also some traps were lost through natural disturbances (Davis 1993), but total trapping effort for each transect, over the 2-year sampling period, was approximately equal for each transect (Table 1). Collections in riverine forest next to the Segama were divided into those within 10 m of the river's edge (riverine A) and those not immediately at the river's edge (> 10 m but < 50 m from the river's edge; riverine B). Primary site A was situated 300 m from the Segama, primary site B was further into the interior of the Danum Valley Conservation Area, and primary site C was the furthest from the Segama river (Table 1). The three logged forest sites covered different logging coupes: site A, logged in 1988; site B, logged in 1989; site D, logged in 1981. Logging intensities in the logged forest sites (total coupe averages) were: logged site A, 75.9 m³ ha⁻¹; logged site B, 97.5 m³ ha⁻¹; logged site D, 145.2 m³ ha⁻¹ (Sabah Softwoods Sdn Bhd, unpublished data). Plantation transects were placed in an acacia *Acacia mangium* Willd. and mahogany *Swietenia macrophylla* King plantation (plantation site A), and a cocoa plantation *Theobroma cacao* L. interplanted with albizia *Paraserianthes falcataria* (L.) Nielsen (plantation site B). Plantation site A was surrounded by selectively logged forest, whereas

plantation site B was part of an extensive area of cultivated land some distance from natural forest. Transect names correspond to those referred to in Davis & Sutton (1998) and Davis, Huijbregts & Krikken (2000). FIT were located at riverine site B, primary sites A and B, logged site D and plantation site B.

A full reference collection (voucher material and type specimens) of all species from this study is kept at the Naturalis Museum (the National Museum of Natural History) in Leiden, the Netherlands (Postbus 9517, 2300 RA Leiden, the Netherlands).

ANALYSIS

Data from pitfall transects and FIT collections were analysed using Shannon, Berger–Parker, and alpha diversity indices (Magurran 1988). Rank–abundance graphs (Whittaker 1972) were also examined (see below). The Shannon index (H') is used widely in the analysis of dung beetle communities (Hanski 1983; Klein 1989; Halffter, Favila & Halffter 1992; Holloway, Kirk-Spriggs & Chey 1992): because H' is calculated by summing the proportional value of each value to the total number of individuals in the sample (Magurran 1988), increased evenness (E) results in higher values of H' , and so as dominance plays a role (i.e. one abundant species can significantly reduce the relative properties of other species, thereby reducing the index value) the index reveals much about competitive asymmetries present within communities (ideal when examining assemblages where competition plays such a major role, such as dung beetle communities). The Berger–Parker index (d) has been described as one of the most satisfactory diversity measures available (May 1975), and is calculated simply by dividing the number of individuals in the most abundant species by the total number of specimens present in the sample (Magurran 1988). An increase in the value of d accompanies a decrease in diversity and an increase in dominance, and the index is therefore inversely related to values of H' but is much easier to calculate (and interpret). The alpha index is more applicable for speciose groups with samples containing large numbers of singletons, and is not generally used to analyse dung beetle communities, which normally contain only moderate numbers of species, but is used here for comparative purposes.

Data accumulated through faunal surveys can be analysed in two complementary ways: (i) transect samples can be classified in terms of faunal composition (Q-mode analysis), and (ii) species can be analysed according to their representation across samples (R-mode). The first leads to calculation of beta-diversity and gives measures of similarity/dissimilarity between site samples, and the second to species being divided into associations, which represent distinct coincidences of species abundance patterns across the samples. These associations in turn may prove to be strongly correlated with a particular biotope or vegetation type. A range of clustering, ordination and other methods is available

for performing such classifications (Holloway 1977, 1998). Here we used the R-mode analysis following the methodology outlined by Holloway (1977) (see also Intachat, Holloway & Speight 1997). The coefficient of association is calculated by expressing the distribution of individuals of each species across the samples on a percentage basis, then summing the percentage overlap of each pair of species in each sample. If 20% of the individuals of species A occur in sample X , 30% in sample Y and 50% in sample Z , and if species B has a distribution of 50%, 25% and 25% in X , Y and Z , then the coefficient is the sum of 20% overlap in X , 25% in Y and 25% in Z , a total of 70%. Single-link (nearest-neighbour) cluster analysis is used to generate dendrograms giving a preliminary indication of groupings (clusters) of the species. The criticism that the method gives poor results when the clustering structure involves much chaining is misplaced (Jardine & Sibson 1968). The cohesion and distinctiveness of single-link clusters, and revelation of any clusters obscured by chaining, can be assessed by constructing a linkage diagram. Such diagrams use an arbitrary level of similarity, and identify clusters where within-cluster linkages are generally more numerous than between-cluster ones (although some taxa may be placed in more than one cluster, i.e. the method is non-hierarchical). This is essentially an *ad hoc* application of the non-hierarchical B_k clustering procedure of Jardine & Sibson (1968); it was first applied to quantitative sample data for moths by Holloway (1977, 1979). These three publications indicate why this approach is more appropriate than the more commonly used averaging or centroid methods of clustering, such as the unweighted pair-group method using arithmetic average (UPGMA). Although somewhat more cumbersome, it gives a better retrieval of the information contained in the original data. R-mode analysis is more effective than other methods, such as canonical correspondence analysis (CCA), in revealing the integrity of species associations, and allowing these associations to be segregated and their rank/abundance curves to be examined independently. Recognizing associations of species with a similar pattern of representation across the samples is an essential first step towards understanding how site diversity is constituted: as will be seen later, the different associations may have very different species abundance curves. It also provides a baseline for assessing the ways in which these potentially distinct ecological components of local diversity respond to various types of ecological disturbance and habitat modification such as logging or conversion to plantation. Examples from moth data are given by Holloway (1998).

R-mode and Q-mode analysis was carried out for each transect and FIT collection. R-mode analysis followed the methodology outlined above and was applied to species represented by over five individuals in complete tables (i.e. including disturbed sites) in Appendices 1 and 2. Analyses were performed on primary (riverine and interior forest) sample data only

and on the full suite of data including logged and plantation sites. For Q-mode analysis, the Sorensen index (C_N) was used to calculate similarity indices between transects, and also between FIT (beta-diversity) (Southwood 1978; Magurran 1988). Because of competitive asymmetries within dung beetle communities, assemblages may be dominated by one species, and so beta-diversity measurements need to avoid sensitivity to the most abundant species as this can mask more subtle differences between sites: the Sorensen index overcomes the problem of sensitivity to the most abundant species and so avoids these problems (Magurran 1988). In contrast, another frequently used measure of beta-diversity, the Morisita–Horn index, although virtually independent of sample size and diversity (Wolda 1981), is sensitive to the abundance of the most abundant species (Magurran 1988) and so was not used here.

Species abundance distributions are frequently used to examine the relationship between species assemblages and their habitat. Log-normal distributions are generally believed to reflect complex assemblages at equilibrium, whereas log-series distributions are taken to represent more simple assemblages at non-equilibrium (Ugland & Gray 1982; Tokeshi 1993; see review by Hill & Hamer 1998). The appropriate level at which these models should be applied is much debated (Buzas & Hayek 1996; Basset *et al.* 1998; Hill & Hamer 1998). It is generally recognized that the study of species abundance distributions should be limited to well defined taxonomic groups (Magurran 1988) that form distinct guilds of interacting species. Within such groups, relationships can be examined within assemblages first by carrying out R-mode cluster analysis of species across samples to identify associations, then the species–abundance relationships within these and their relationship to biotopes can be looked at independently (Holloway 1977; Intachat, Holloway & Speight 1997; Holloway 1998).

Species abundance distributions were analysed using the Kolmogorov–Smirnov one-sample goodness-of-fit test (Daniel 1990). In each case, observed distributions are fitted to two statistical models, the log-series and the log-normal (Magurran 1988). Unlike the chi-squared test, the Kolmogorov–Smirnov does not assume that distributions are normal, and is more appropriate when samples are small (Tokeshi 1993; Sokal & Rohlf 1995; Hill & Hamer 1998). Calculation of both log-series and log-normal statistical models followed Magurran (1988). In the calculation of the log-normal predicted distributions, the model uses the value S^* (estimated number of species in the association or assemblage; Magurran 1988) rather than S (actual number of species recorded), leading to a disparity in N (Sokal & Rohlf 1995) in the Kolmogorov–Smirnov test between observed and predicted species distributions; to rectify this problem, each value in the predicted distribution is multiplied by $1 - p_o$ (a parameter used in the calculation of the log-normal distribution; Magurran 1988), effectively S/S^* , to reduce or increase the value of N in the predicted distribution model to that of the observed

distribution. In this way, for each observed and predicted log-normal distribution, the area under the distribution curve is the same.

To estimate potential species richness overall in our assemblages of samples, we applied the extrapolation methods advocated by Colwell & Coddington (1994) to the pitfall data and FIT data independently. Chao 1 estimates richness as $(S + a^2/2b)$, where a is the number of species represented by singletons in the total sample and b the number represented by doubletons. Chao 2 estimates richness in a similar manner but a is the number of species occurring in only one of the individual samples and b is the number occurring in only two.

Results

The material analysed here represents 86 species from 35 279 identified specimens. Application of richness estimators gave predicted species numbers of 78 (Chao 1) and 79 (Chao 2) for the pitfall data and 88 (Chao 1) and 85 (Chao 2) for the FIT data. These results suggest that FIT give a more comprehensive sample of the beetle species present in a given area. The species richness and composition of the full collection from Danum stands at 97 species from 68 481 specimens (Davis 2000b). Because of problems with taxonomy, the data analysed excluded the genera *Aphodius* Illiger and *Panelus* Lewis; both genera exist on the margins of dung beetle communities in the Bornean rainforest (Cambefort 1991; Hanski & Cambefort 1991b), therefore these omissions should not affect analysis of community structure. Species in these genera represented seven of the total of 97. A further four species were rare and not collected in the main trapping programme analysed here.

Both pitfall and FIT data showed clustering of species into several distinct associations, each association having a distinct ecological character or shared habitat. Pitfall data (Fig. 1) had a higher resolution and greater degrees of freedom than the FIT data (Fig. 2) as more traps were used in the pitfall sampling, and more biotopes sampled, than in the FIT collections. Associations could broadly be defined as riverine, interior-primary (although in figures this is simply referred to as primary) and ‘even’ (evenly distributed across biotopes). The interior-primary forest species were divided into two distinct associations (P1 and P2). Some species lay between these associations (riverine and interior-primary) and were therefore intermediate in ecological character. Pitfall data showed a greater degree of clumping, with the riverine association made up of river edge (R1), river bank (R2) and riverine non-edge/bank (R3) components. The river edge component was located at the very margin of the forest, whereas the river bank association was found under forest cover by the river.

The pitfall and FIT results showed much concordance in assignation of species (Table 2) except with regard to the even associations. The general riverine association of the FIT analysis shared 14 species with

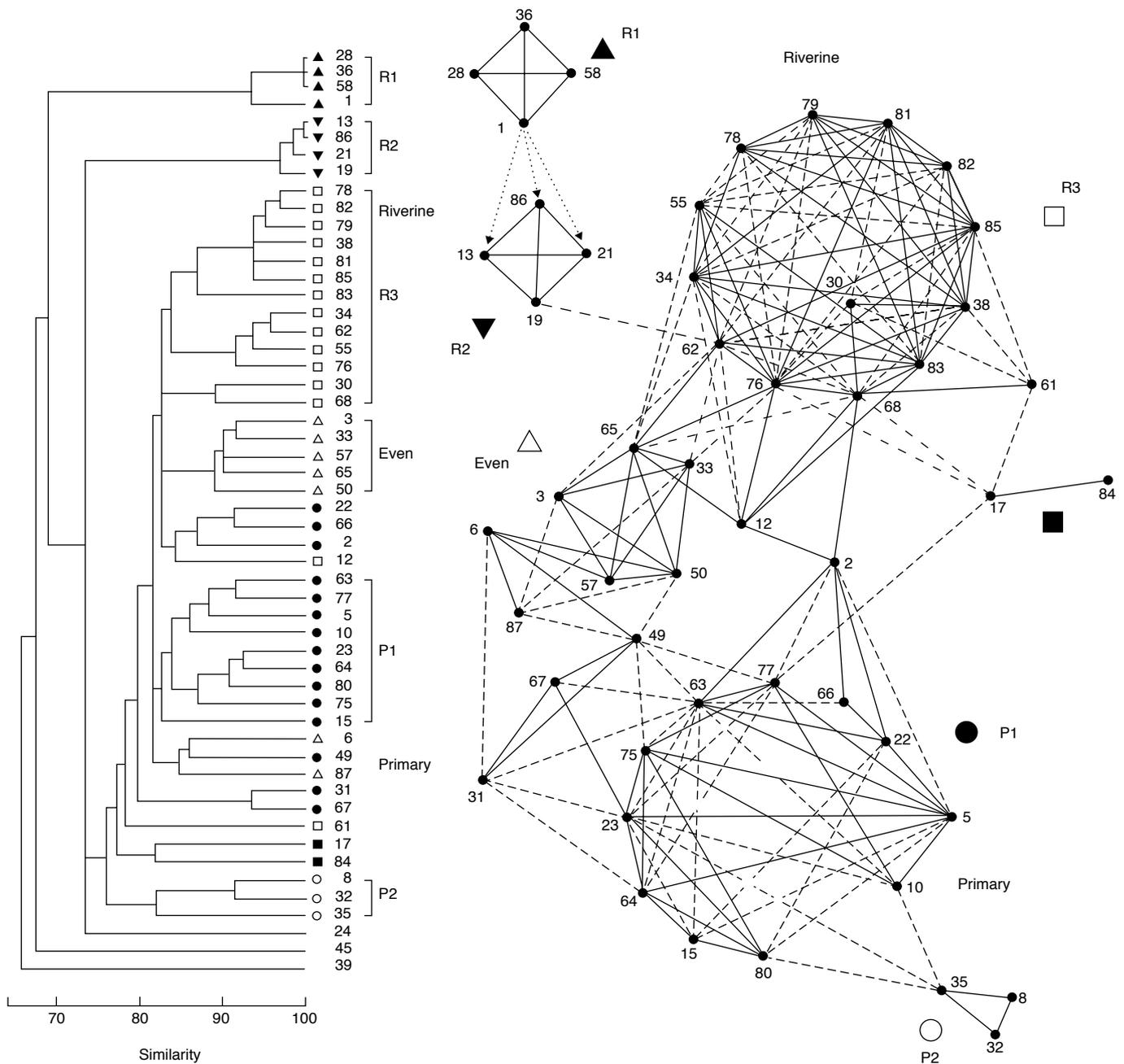


Fig. 1. R-mode single-link cluster analysis dendrogram and linkage diagram for dung beetle species represented by two or more individuals, collected by baited pitfall trap from primary forest traps in the Danum Valley Conservation Area. Species associations recognized from clusters in the linkage diagram are indicated on the dendrogram by the same symbol in both diagrams. The black square symbol represents species that form part of a general riverine cluster (R1 + R2 + R3) but cannot be directly attributed to any one riverine association. Numbers indicate species as in Appendix 1. In the linkage diagram, linkages of 90%+ similarity are indicated by thick solid lines, those of 80–89% by solid lines, and those of 75–79% by broken lines. Dotted lines with arrows indicate linkages below 75% in a minimum spanning tree. Line length has no significance, and the points are distributed to ensure the diagram is clear, rather than being placed through an ordination method. Three species, represented by a small number of individuals, cannot be attributed to an association (i.e. 24, 39 and 45) and these outlying species are not included in linkage diagram.

the three pitfall riverine associations. Only one species, *Onthophagus aphodioides* Lansberge, was classed as riverine in the FIT analysis and interior-primary in the pitfall analysis. Six of the FIT interior-primary species fell into the pitfall interior-primary associations, and only one into the even association. However, five of the FIT even species were placed in the larger pitfall interior-primary association. An R-mode analysis including both pitfall and FIT data was not attempted

as it would have yielded some clusters influenced by methodological bias. In subsequent discussion, greater emphasis will be placed on the pitfall results because of the greater number of samples involved.

Figures 3, 4 and 5 show species abundance distributions in various biotope samples for each association identified through cluster analysis (i.e. riverine, interior-primary and even associations). In this way, the whole assemblage of species was divided into ecological

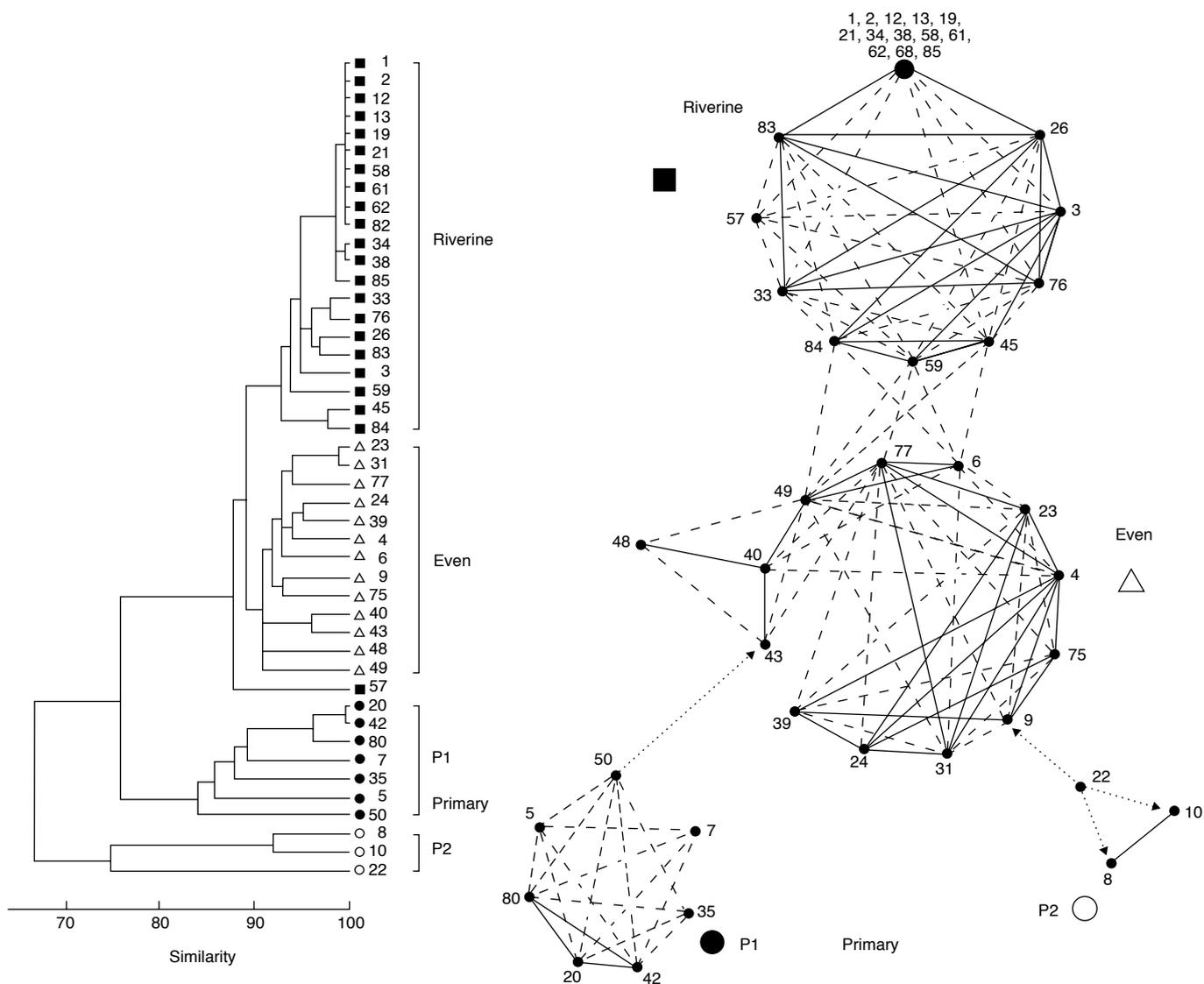


Fig. 2. R-mode single-link cluster analysis dendrogram and linkage diagram for dung beetle species represented by two or more individuals, collected by flight intercept trap from primary forest traps in the Danum Valley Conservation Area. Format as for Fig. 1 but numbers indicate species in Appendix 2.

Table 2. Comparison of species caught by pitfall trap and flight intercept trap (FIT), showing degree of concordance between trapping methods. Species are divided into the associations demonstrated in Figs 1–4. Concordance is indicated in bold. The main difference is in assignation of species to the even categories. See Figs 1 and 2, and text, for description of each association

	Association	FIT			
		Riverine	Even	P1	P2
Pitfall	R1	2			
	R2	3			
	R3	9			
	Even	3	1	1	
	P1	1*	5	2	2
	P2			1	1

**Onthophagus aphodioides*.

associations, and each association could then be examined independently. For clarity, curves in these and other figures are displaced along the x-axis rather than superimposed. Data were taken from primary (riverine and interior forest), logged and plantation forests. Figure 3 clearly shows the differing behaviour of each association along the environmental gradient, with the highest abundance and species richness recorded from the transect representing the ‘core biotope’ of each association, with the exception of the even association which showed little change in the rank–abundance curves. For example, species abundance and richness within the riverine non-edge association (Fig. 3b) were greatest in the riverine B transect, which represented the core biotope for this association. The riverine-edge association showed a dramatic decline in richness and abundance from riverine into interior-primary forest, whereas the other associations were better represented on all transects, and spread into sites away from their

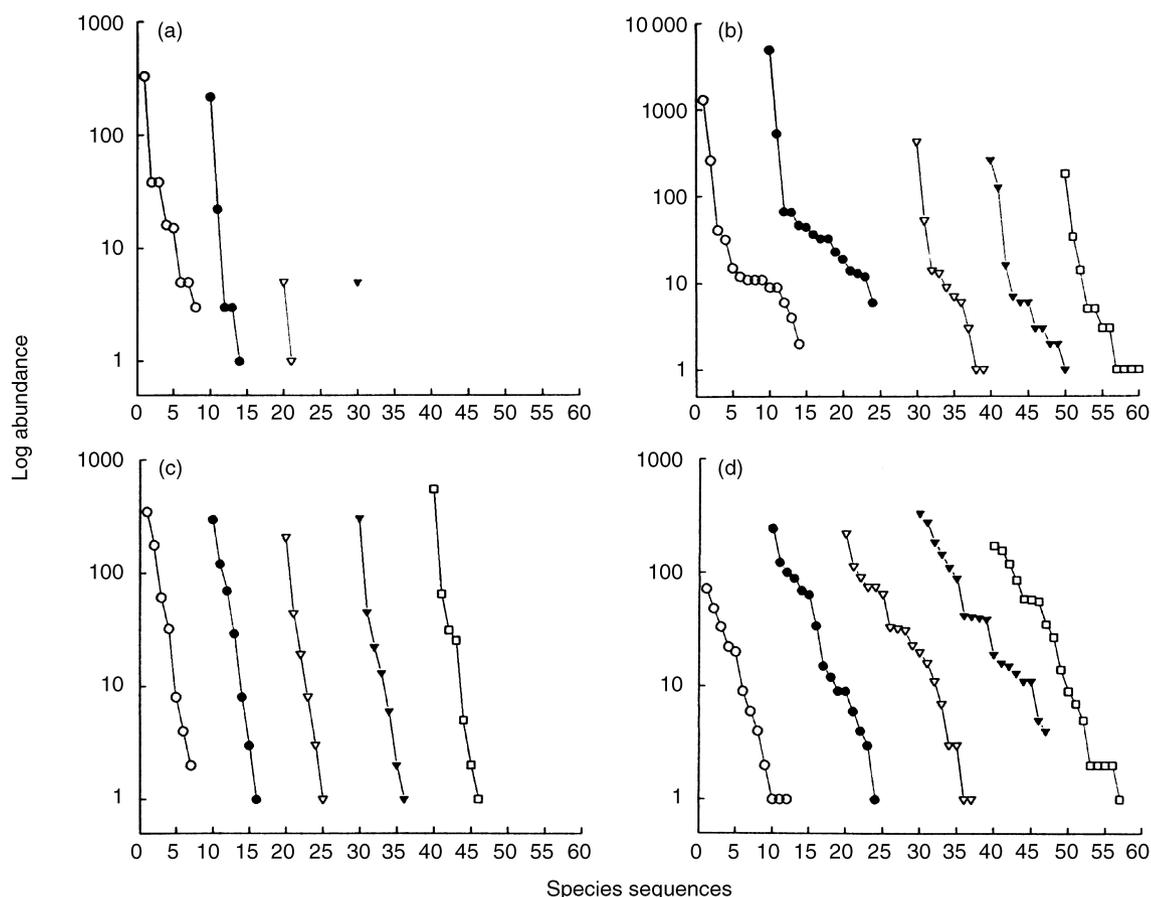


Fig. 3. Rank–abundance curves for samples of dung beetles collected by baited pitfall trap from primary forest in the Danum Valley Conservation Area in Sabah. Species are divided into associations identified by cluster analysis (Fig. 1), separated along an environmental gradient from riverine-edge habitat (riverine A; Table 1), riverine non-edge (riverine B), to deep interior forest (primary C). Each curve represents samples from a different transect (Table 1); the symbols used replicate, for convenience, those shown in other figures (Figs 1 and 2, 7 and 8) but here represent transects and not the associations. For clarity, curves are displaced along the x-axis rather than superimposed. Associations are: (a) riverine-edge association (R1); (b) riverine non-edge association (R2 + R3); (c) even association; (d) interior-primary association (P1 + P2). Transects: open circles, riverine A; closed circles, riverine B; open triangles, primary A; closed triangles, primary B; open squares, primary C.

core biotope, but with decreased richness and abundance in all cases (with the exception of the even association, as already mentioned). Pitfall data from disturbed forests (Fig. 4) showed that all associations were represented, but this representation varied in each assemblage (sample). All logged forest transects varied from the primary forest samples shown in Fig. 3a. The riverine-edge association (R1) was not strongly represented, or was entirely absent, in interior-primary transects (primary B and primary C; Fig. 3a), but was well represented in plantation transects and logged site D and present in logged site B, suggesting that this association had spread beyond its natural compass in these forests. All logged forest sites supported a well-developed riverine non-edge association (Fig. 4b), closely resembling the curves from riverine non-edge habitat in pristine forest (i.e. 10–50 m from the river, riverine transect B; Fig. 3b), as did plantation transect A. The interior-primary association (Fig. 4d) showed a reduction in richness and abundance in all disturbed transects compared with the core biotope curves in

Fig. 3d, with the greatest reduction in plantation forests. The curves for the even association (Fig. 4c) in general showed a reduction in species richness, most pronounced in plantation forest, although the general shape of each curve was similar to those in Fig. 3c. Figure 5 for the FIT data shows the same trends shown in Figs 3 and 4, with a well represented (in terms of species richness and abundance) riverine association in logged forest and a reduced interior-primary association in both logged and plantation forest, although resolution was poorer due to the lower number of sites sampled than the pitfall collections. It is of interest that the shape of the curves for all associations tended to be maintained across all biotopes for the pitfall data (much less so for the FIT data) except where abundance and richness were drastically reduced.

When individuals in each association were pooled from across all samples, the shape of the major pitfall association curves varied considerably (Fig. 6a), with the main riverine association being distinctly sigmoid,

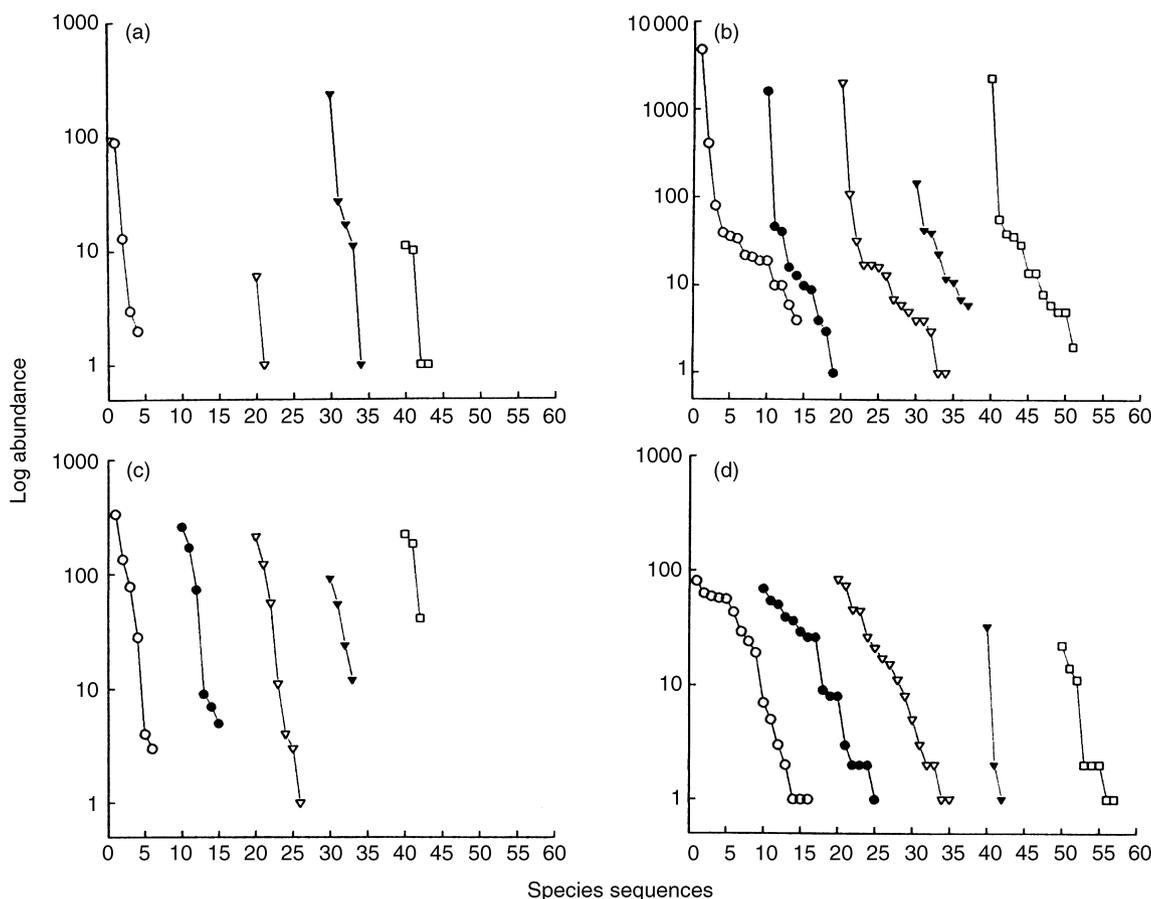


Fig. 4. Rank–abundance curves for samples of dung beetles collected by baited pitfall trap from logged and plantation forest in the Ulu Segama Reserve, Sabah. Species are divided into separate associations following the same method employed in Fig. 3. Associations are: (a) riverine-edge association (R1); (b) riverine non-edge association (R2 + R3); (c) even association; (d) interior-primary association (P1 + P2). Transects: open circles, logged D; closed circles, logged A; open triangles, logged B; closed triangles, plantation B; open squares, plantation A.

with some dominance, but with greater packing or evenness of middle-ranking species than in the other associations. Consistency of curve shape between pooled samples and individual samples for each association suggested pooling of samples in this way was valid, and followed the same principle as combining samples through time (e.g. accumulation of insects in a trap over several days) or space (e.g. the initial pooling of samples from individual pitfalls in each transect). The even and interior-primary associations had more linear curves but the latter showed greater equitability, packing in more species over a lesser abundance range (Fig. 6a). The curves from the combined FIT data were more similar (Fig. 6b), also being somewhat sigmoid. However, the FIT data did not separate the two small R1 and R2 associations of the pitfall analysis, and five of the FIT even association species were assigned to the interior-primary association in the pitfall analysis (Fig. 6b). These differences could be reconciled by (i) combining the R1, R2 and R3 clusters (Fig. 6b) to form a riverine association equivalent to the riverine association in Fig. 6a, and (ii) adding species that were in even and P2 associations in the FIT analysis, but assigned to P1 in pitfall analysis, to the P1 curve in

Fig. 6b to create an ‘augmented P1 curve’ equivalent to P1 in the pitfall analysis (Fig. 6a).

In disturbed forests, pitfall data (Fig. 7) showed that interior-primary forest clusters (P1 and P2) from the earlier analysis (Fig. 1) had persisted relatively unchanged, as had the even cluster. The riverine clusters, however, had been disrupted, with the development of a new, loosely associated, cluster (encircled star; Fig. 7) consisting of species that were common in plantation forests and moderately represented in logged ones. These species were drawn from all three riverine associations but also with one even association species and two (39, 45) that were placed as outliers in Fig. 1 (i.e. not assigned to an association), being represented by only a small number of individuals in the undisturbed biotopes. Remnants of the old riverine associations persisted, with one species from R1 and three from R2 showing little penetration of disturbed biotopes. Those from R3 and the even association were more strongly represented in all disturbed biotopes, whereas representation of P1 and P2 was weaker and concentrated in the logged ones.

A similar pattern emerged in an analysis performed on the full suite of FIT samples, illustrated in Fig. 8. The P1 and P2 clusters from Fig. 2 largely persisted

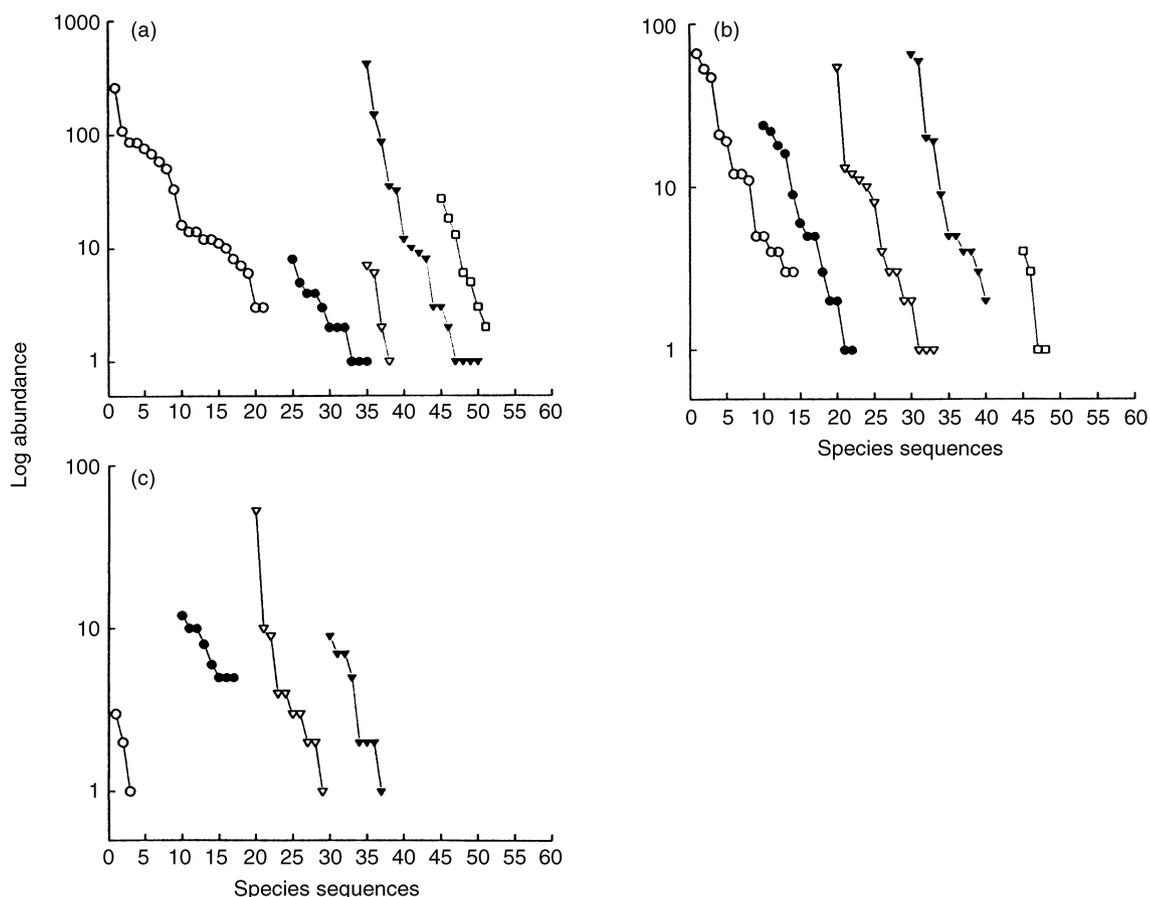


Fig. 5. Rank–abundance curves for samples of dung beetles collected by flight intercept trap from primary, logged and plantation forest in the Ulu Segama Reserve, Sabah. Species are divided into associations identified by cluster analysis (Fig. 2), separated along an environmental gradient from riverine-edge habitat (riverine B; Table 1) to deep interior forest (primary B). Each curve represents samples from a different trap (Table 1). Associations are: (a) riverine association (see Fig. 2); (b) even association; (c) interior–primary association. Transects: open circles, riverine B; closed circles, primary A; open triangles, primary B; closed triangles, logged D; open squares, plantation B.

(one P2 species was displaced). The even cluster was divided into two, with a cluster of four species showing little penetration of disturbed biotopes, and a larger cluster of eight that was well represented in the sample from logged forest. Only one species in the smaller cluster was included in the pitfall analyses, and that was placed in the P1 cluster although in a somewhat intermediate position between it and the even cluster. The large riverine cluster of Fig. 2 had disintegrated, with a group (solid square) showing little penetration of the disturbed biotopes, but the others showing it in varying degrees, such as moderate, strong to predominant (closed, open and encircled stars) in the logged sample, or strong in the cocoa sample (open square).

There were some differences compared with the pitfall result, particularly in the composition of the most disturbed clusters (encircled stars) of each. Both included species 57 and 84, but 10 (a primary species) and 19 (riverine) showed little penetration of disturbed biotopes in the pitfall analysis (where 9 was not represented).

The Kolmogorov–Smirnov one-sample goodness-of-fit test was carried out for each abundance distribution in Figs 3–5, for both log-series and log-normal models. As goodness-of-fit was applied to data with discrete

distributions, corrections were not applied to the calculations (Daniel 1990). In the majority of cases, results were not significant ($P > 0.2$) and in only two cases did observed distributions vary significantly, both from the log-series distribution (primary B transect; Fig. 3d; $D_{max} = 0.3261$, $N = 18$, $P < 0.05$) and the interior–primary association from the FIT at primary site A (Fig. 5c; $D_{max} = 0.5963$, $N = 8$, $P < 0.01$).

The results of calculations for alpha for pitfall data were inconclusive (Table 3), although values were lowest in plantation forest. For other diversity measures, for both pitfall and FIT samples, diversity was lower in logged compared with interior–primary forest, with the lowest diversity again recorded from plantation forest (Table 3). Data showed that species richness in logged forest was generally higher than individual transects from primary interior–forest, closer to species richness in riverine forest (Table 3): the reasons for this will be discussed later. Species richness was lowest in plantation forest. From pitfall data, the mean number (\pm SE) of species was 41.67 ± 1.45 from primary interior forest, 45.67 ± 4.49 from logged forest, 48.0 ± 0.0 from riverine forest and 29.0 ± 4.0 from plantation forest (Table 3). The same trends were shown in the FIT

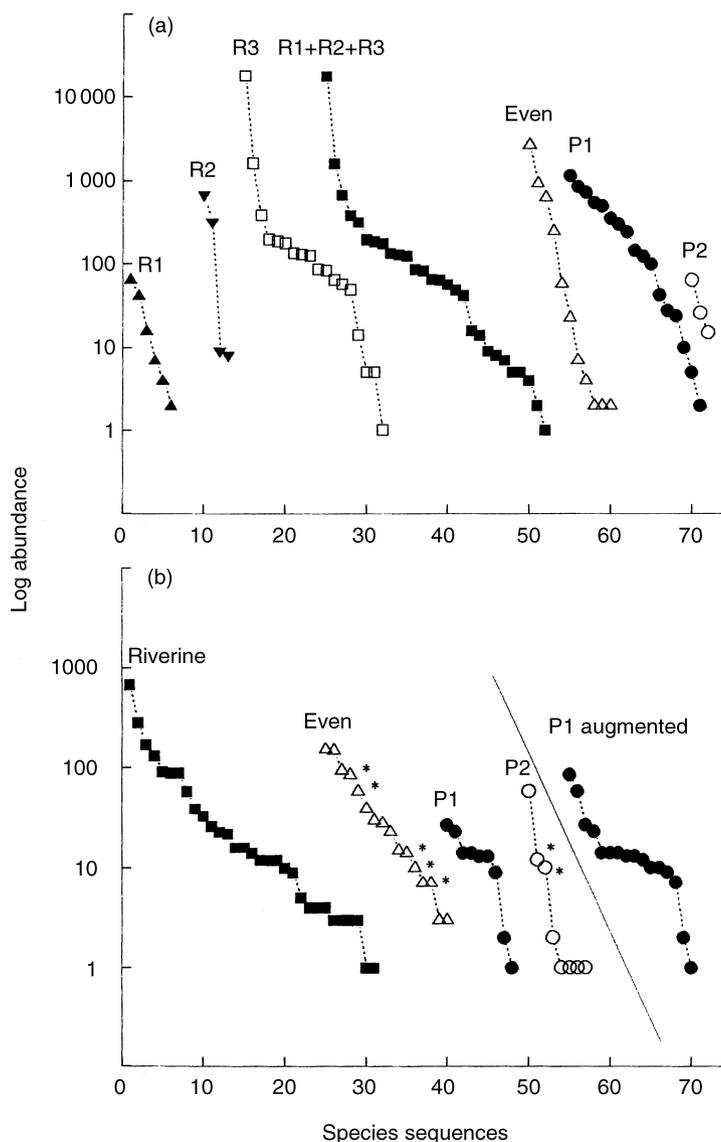


Fig. 6. (a) Species abundance curves, from pitfall trap data, obtained by pooling individuals in each association from across all the samples, both primary and disturbed. Species represented in the total sample by five individuals or less are assigned subjectively to the associations with which their distribution coincides most closely, as are those included in the analysis but placed as outliers or intermediates. Riverine associations are shown both separately (R1, R2, R3) and combined (R1 + R2 + R3). The combined riverine curve is equivalent to riverine curve of the flight intercept trap analysis (Fig. 6b). (b) Species abundance curves, from flight intercept trap data, obtained as in (a). Species in even and P2 associations with an asterisk can be assigned to P1 in pitfall analysis: these are added to the P1 curve here to create an 'augmented' P1 curve (far right of figure) that is therefore equivalent to P1 in pitfall analysis (Fig. 6a).

data (Table 3). Evenness was lowest, and dominance highest, in riverine and logged forest (Table 3). In terms of beta-diversity (Tables 4 and 5), in both pitfall and FIT samples greatest faunal similarities were found between logged forest and riverine communities, between pitfall samples in plantation A and riverine forest (Table 4), and between similar habitats (Tables 4 and 5).

Discussion

EDGE EFFECTS

In this study, species from discrete associations in primary forest (interior-primary and riverine) were

recorded as coincident in disturbed forests, thus, with the generally distributed even associations, increasing species richness at a fine scale (i.e. within a particular forest type) but not at the larger scale. Increased edge in logged and plantation forest seems to increase the numbers of edge species in these forests (Fig. 4; Appendix 1). Disturbance does not increase species richness *per se*, but species distributed along environmental gradients in primary forest (riverine edge through to interior forest; understorey to canopy) are mixed at the same spatial location in logged and plantation forest (Davis & Sutton 1998; Davis, Huijbregts & Krikken 2000). Species diversity (a combination of species richness and abundance) actually decreases in disturbed forests,

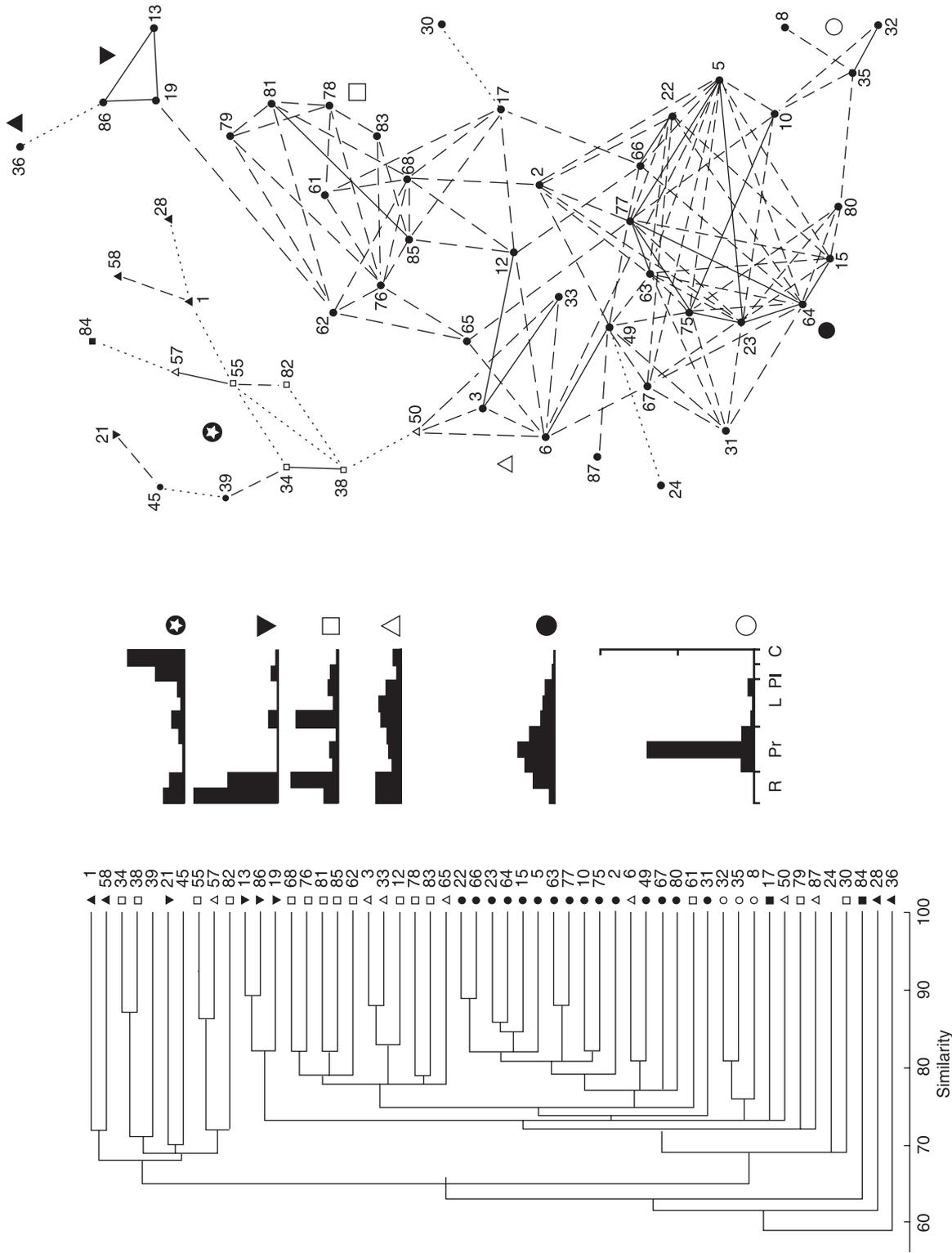


Fig. 7. Single-link dendrogram and linkage diagram for an R-mode analysis of species in all pitfall samples. Conventions are as in Fig. 1, including small symbols representing membership of clusters recognized in the earlier analysis (associations: closed upward triangle, R2; open upward triangle, R1; closed downward triangle, R3; open square, R4; open circle, P1; open circle, P2). Solid lines indicate links of 80% and above, broken ones those of 70–79%. Dotted lines indicate links of lower values that unite the various clusters or bring in outliers (part of the minimum spanning tree). Smaller symbols for species in the ‘encircled star’ cluster indicate from which undisturbed cluster (Fig. 1) the species are drawn, the small dots indicating outliers in Fig. 1. Histograms indicate the average percentage representation across the samples of species in each cluster (these also give an indication of proportional representation across the samples from undisturbed biotopes). In the linkage diagram, a new cluster has formed (encircled star) consisting of species that are common in plantation biotopes and moderately represented in logged ones, formed largely by the breakdown of the riverine clusters (Fig. 1). The histograms are placed approximately opposite the relevant cluster in the dendrogram, with larger symbols enabling the clusters to be located in the linkage diagram. The bottom histogram indicates the blocks for riverine (R), interior-primary (Pr), logged (L), plantation (PI) and cocoa (C) samples.

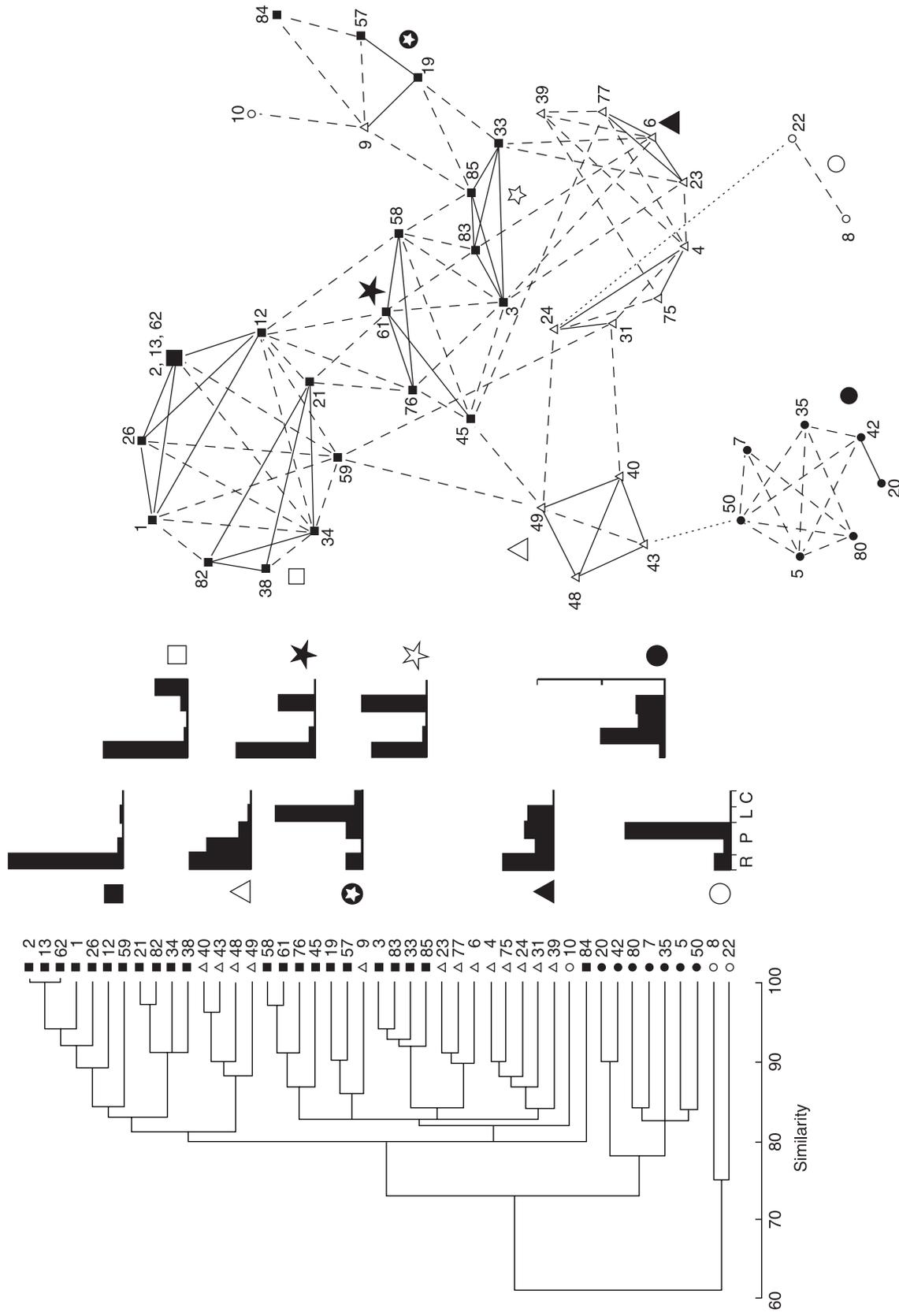


Fig. 8. Single-link dendrogram and linkage diagram for an R-mode analysis of species in all flight intercept trap samples. Conventions are as in Figs 1, 2 and 7. Solid lines in the linkage diagram indicate links of 85% and above, broken lines those of 75–84%, and dotted lines those of lower value that are part of the minimum spanning tree uniting the clusters. Three new clusters are formed (closed star, open star and encircled star), formed largely by the breakdown of the riverine and even clusters (R), interior-primary (P), logged (L) and cocoa (C) samples.

Table 3. Species richness, number of specimens, alpha diversity measurement, Shannon and Berger–Parker diversity indices for samples collected by two trapping methods from riverine, interior-primary, logged and plantation forest

Trapping method	Location*	S†	N	Alpha		Shannon		Berger–Parker	
				α	SD	H'	SD	E	d
Pitfall	Riverine A	48	3082	8.10	1.17	2.20	0.03	0.57	0.42
	Riverine B	48	7410	6.87	0.99	1.64	0.02	0.42	0.66
	Primary A	39	1648	7.17	1.15	2.63	0.03	0.72	0.26
	Primary B	42	2253	7.33	1.13	2.75	0.02	0.74	0.15
	Primary C	44	1755	8.19	1.24	2.51	0.03	0.66	0.31
	Logged A	37	2695	6.07	1.00	1.74	0.03	0.48	0.61
	Logged B	52	3081	8.89	1.23	1.62	0.03	0.41	0.66
	Logged D	48	6721	6.99	1.01	1.41	0.02	0.36	0.72
	Plantation A	33	3083	5.16	0.90	1.18	0.03	0.34	0.74
	Plantation B	25	810	4.89	0.98	2.37	0.04	0.74	0.29
FIT	Riverine B	50	1242	10.45	1.48	3.02	0.03	0.77	0.21
	Primary A	38	214	13.43	2.18	3.20	0.06	0.88	0.11
	Primary B	34	239	10.84	1.86	2.71	0.08	0.77	0.23
	Logged D	42	1010	8.85	1.37	2.24	0.05	0.60	0.41
	Plantation B	14	86	4.74	1.27	2.05	0.12	0.78	0.31

*See Table 1.

†S, number of species; N, number of specimens; α , alpha diversity measurement; SD, standard deviation of diversity index; E, measurement of evenness; FIT, flight intercept trap.**Table 4.** Similarities between samples collected by baited pitfall trap in riverine, interior-primary, logged and plantation forest, measured using the Sorensen index (C_N). Index values greater than 0.5 are highlighted in bold

Transect*	Riverine B	Primary A	Primary B	Primary C	Logged A	Logged B	Logged D	Plantation A	Plantation B
Riverine A	0.50	0.44	0.40	0.40	0.72	0.68	0.52	0.58	0.18
Riverine B	–	0.32	0.32	0.25	0.47	0.55	0.52	0.52	0.07
Primary A	–	–	0.72	0.65	0.51	0.47	0.30	0.34	0.14
Primary B	–	–	–	0.70	0.42	0.40	0.28	0.24	0.12
Primary C	–	–	–	–	0.42	0.37	0.26	0.23	0.15
Logged A	–	–	–	–	–	0.84	0.55	0.72	0.15
Logged B	–	–	–	–	–	–	0.61	0.82	0.15
Logged D	–	–	–	–	–	–	–	0.58	0.09
Plantation A	–	–	–	–	–	–	–	–	0.17

*See Table 1.

with the lowest diversity found in logged and plantation forest, due to decreased equitability in the overall assemblage resulting from the increased dominance of some species. Species assemblages in disturbed biotopes are therefore 'composite', in that the whole assemblage contains a mixture of species associations from different biotopes that tend to be spatially separate in interior-primary forest. Some mixing of species associations is seen in riverine forest (also increasing measures of species richness), particularly up-slope away from the river, suggesting that this

phenomenon may be common to both edge-rich and marginal habitats.

Extensive research has been carried out on the importance of edge effects in fragmentation studies (Lovejoy *et al.* 1986; Kapos 1989; Laurance & Yensen 1991; Laurance 1991; Kapos *et al.* 1993; Murcia 1995; Didham 1997; Turton & Freiburger 1997), although data from the current study suggest that edge effects may play an important role in understanding the effects of logging and conversion to plantation. The interspersed of landscape elements in an increasingly finer mosaic

Table 5. Similarities between flight intercept traps in riverine, interior-primary, logged and plantation forest, measured using the Sorensen index (C_N). Index values greater than 0.5 are highlighted in bold

FIT location*	Primary A	Primary B	Logged D	Plantation B
Riverine B	0.21	0.20	0.58	0.13
Primary A	–	0.51	0.18	0.11
Primary B	–	–	0.16	0.08
Logged D	–	–	–	0.07

*See Table 1.

FIT, flight intercept trap.

leads to greater amounts of edge and often to increased wildlife diversity (Roth 1976), as has been noted in pioneering work on edge effects that has shown that the density and diversity of wildlife increased where two habitats meet (Leopold 1933).

Our observations from Danum concur with previous published studies. Spitzer *et al.* (1997) showed that species adapted to forest-gap microsites (i.e. another type of edge habitat) fared better in logged forest than stenotopic species confined to closed-canopy habitat, thereby increasing the number of these species (and therefore overall species richness) in disturbed habitats. Similarly, a study in Papua New Guinea (Bowman *et al.* 1990) demonstrated that the formation of secondary vegetation created the opportunity for certain species limited to small cleared areas (i.e. forest gaps) to expand their distribution in disturbed habitat, although this disturbance had catastrophic impacts on other species adapted only to survive in primary forest. Janzen (1987) noted that the localized opening up of a large pristine forest block by agriculture raised the species richness in the site overall, particularly if fields and pastures were subsequently abandoned, as many species characteristic of secondary succession (absent from the primary forest block) entered the site and so raised the overall number of species. Several other studies have recorded that butterfly densities and diversities are high in some secondary habitats and along secondary edges in primary forest fragments (Cheverson & Thomas 1985; Lovejoy *et al.* 1986). In all these cases disturbance raises species richness at the fine scale. Holloway (1998) noted, in a traditional shifting cultivation system in Seram, Indonesia, that moth diversity declined after initial clearance, but rose to levels recorded in undisturbed forest after abandonment, although with some change in faunistic composition and dominance effects. Again, associations of species were identified that appeared to respond positively to disturbance. Such observations need to be met with the caveat that disturbance may irretrievably alter the composition of natural species assemblages, such that increases in species richness within disturbed forests may not necessarily be a 'good thing' from a conservation perspective, and may actually be damaging for species assemblages in disturbed forests (Davis, Huijbregts & Krikken 2000).

EFFECTS OF DISTURBANCE

Cluster analyses performed in the R-mode for the full suites of data (both primary and disturbed sites) demonstrated clearly the differential response to disturbance of the major associations recognized by this method across samples from pristine forest types (riverine, even and interior-primary). While the interior-primary cluster retained its character, the riverine cluster or clusters of the 'undisturbed' analysis totally disintegrated and its components re-associated into a number of new clusters that reflected the extent to

which the species were able to survive, penetrate and thrive in the disturbed biotopes. For example, for the pitfall data, the eight species of riverine clusters R1 and R2 either showed little penetration of disturbed biotopes (13, 36, 86) or, conversely, a capacity to penetrate logged forest (19 and possibly 58) or plantation (1, 21, 28). Clear examples of all three types of response can be seen in Appendix 2 (e.g. 13, 58 and 34). The even cluster showed an intermediate response to those of the riverine and interior-primary clusters.

The data show decreased dung beetle diversity in logged and plantation forest, concordant with other studies that have shown a decline in insect diversity with disturbance (Holloway, Kirk-Spriggs & Chey 1992; Hill *et al.* 1995; Intachat, Holloway & Speight 1999) and further reduction in conversion to agriculture (Holloway 1987; Wolda 1987). Results presented in this paper suggest that dung beetle assemblages in selectively logged forest following traditional practices closely resemble riverine rather than interior-forest assemblages. The lowest species richness and diversity measures were recorded from plantation forest. This suggests that traditional logging practices, where large amounts of timber are removed and major damage to the residual stands occurs, lead to an ecosystem that departs significantly from primary forest, but some elements of natural forests are maintained, unlike plantation forest where there is a greater reduction in richness and diversity.

Damage to the remnant stand has been shown to be proportional to the amounts of timber removed (Cannon *et al.* 1994; Bertault & Sist 1997; Sist *et al.* 1998), and harvesting intensity clearly needs to be considered when considering the impacts of selective logging on faunal diversity. Recovery in a forest very much depends on the intensity of the original disturbance (Busschbacher, Uhl & Serrao 1988). Moderate human disturbance, which leaves a relatively high tree species diversity, has been shown to have surprisingly little, if any, effect on insect diversity (Wolda 1987). This may explain why forest disturbance in Uganda, where amounts of timber removed were much lower than in Sabah, did not significantly affect dung beetle diversity (Nummelin & Hanski 1989; Nummelin 1998).

SPECIES ABUNDANCE DISTRIBUTIONS

All species abundance distributions except two fit both the log-series and log-normal models, a result that could be expected by chance alone. This suggests that the statistical method used here is not sufficiently sensitive to analyse biotope-specific associations, and that other techniques may be needed to analyse species abundance patterns from discrete species associations, where there is likely to be low species count and low abundance. It is possible, however, that this methodology is more suited to more species-rich groups, and that trends can be more readily identified statistically in such communities.

Our observations that the curves for associations tend to retain their shape (predominantly an indicator of

equitability rather than richness) in different biotopes, including disturbed ones, can be contrasted with the results of Holloway (1977, 1996) where the shape of curves for moth associations on Norfolk Island was strongly affected by variation in rainfall, including prolonged periods of drought. This may suggest that environmental disturbance and environmental stress involved different processes. The Norfolk Island associations showed increased equitability in response to drought stress. As indicated here, the dung beetle assemblages in disturbed forest show decreased equitability, while the equitability of individual associations may be less affected. The differences in association curves between pitfall and FIT surveys shown in Fig. 6a,b indicate that sampling method may also influence curve shape: in this case a baited method is contrasted with a passive trapping method.

CONCLUDING REMARKS

Species forming different associations may exhibit very different species abundance relationships (Basset *et al.* 1998). Even though traditional analysis of log-normal distributions in assemblages assumes that they comprise many patches (Ugland & Gray 1982), each patch forms part of the same species pool, and clumping of that pool into separate associations is not taken into account. Here R-mode cluster analysis separated species into discrete associations; these results confirm previous analysis of the data, whereby species were divided into riverine and interior-forest assemblages on the basis of regression analysis of species abundance against distance from the Segama (Davis, Huijbregts & Krikken 2000). These data suggest that analyses that do not carry out these procedures will be unable to differentiate between (i) a single closely integrated 'community' with shared habitat (*sensu* Samways 1994) parameters, or (ii) a conglomeration of disparate species abundance distributions from several independent associations. Data presented here show that species distribution patterns for individual associations within discrete biotopes respond to disturbance, with different associations responding in different ways: the riverine association includes many species that show a positive response to at least some types of disturbance, whereas others are neutral or negative in response; the even association species are mostly neutral; the primary forest associations are almost entirely negative in response. Such results indicate that this approach can complement comparisons from whole assemblages (which may cross several biotopes) and possibly provide a more subtle tool for analysing the effects of disturbance on species associations than methods traditionally used, such as Q-mode analysis, ordination or partitioning methods such as TWINSpan.

Data suggest that increased species richness at a fine scale does not necessarily mean that species richness is greater at a larger scale, and that species mixing in derived ecosystems is dependent on the type of disturbance. This work not only emphasizes the utility of

dung beetles as biological indicators, where change is apparent across natural forest ecotones and following anthropogenic disturbance, but also demonstrates that examining species distributions across natural environmental gradients in primary forest can be an effective way of looking at, and understanding, species distributions in derived forest ecosystems. Small-scale species richness in logged forest is generally higher than in individual transects from primary forest due to the presence of overlapping species association ranges (composite assemblages) that are usually spatially separate in primary forest. Caution is therefore needed in interpreting species richness measures from disturbed forests. Management of tropical forests could be evaluated on the extent to which the different biotope elements remain spatially distinct (minimal mixing); this could be achieved by using low impact techniques (i.e. reduced-impact logging; Pinard & Putz 1996) that harvest forest more within the boundaries of natural forest dynamics than traditional methods.

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Appendix 1 Continued

Species number	As'n*	Species	Author	Transect										
				Riverine A	Riverine B	Primary A	Primary B	Primary C	Logged A	Logged B	Logged D	Plantation A	Plantation B	
47		<i>Onthophagus</i> sp. 30								1				
48		<i>Onthophagus vethi</i>	Krikken	1				1						
49	●	<i>Onthophagus vulpes</i>	Harold	33	64	31	89	120	39	73	43	11		
50	△	<i>Onthophagus waterstradti</i>	Boucomont	8	8	3	6	5	9	3	4		12	
54		Unidentified female								1				
55	□	Arboreal 1		9	14	3		1	13	17	19	57	43	
56		Arboreal 2		1	1				1	1	1		1	
57	△	<i>Proagoderus schwaneri</i>	Vollenhoven	32	29	8	13	25	74	56	78	225	92	
58	▲	<i>Oniticellus tessellatus</i>	Harold	3						2	1	1	1	
61	□	<i>Caccobius binodulus</i>	Harold		6	1	2			1	4			
62	□	<i>Caccobius unicornis</i>	Fabricius	32	47	7	6	3	1	1	19	14		
63	●	<i>Catharsius molossus</i>	Linnaeus	72	246	221	279	157	54	45	63	14	32	
64	●	<i>Copris agnus</i>	Sharp	1	9	33	42	27	8	8	19			
65	△	<i>Copris ramosiceps</i>	Gillet	61	70	19	22	31	7	11	28			
66	●	<i>Copris sinicus</i>	Hope	4	70	75	39	14	29	15	57	2		
67	●	<i>Microcopris doriae</i>	Harold		12	32	41	58	50	17	29	2	2	
68	□	<i>Microcopris reflexus</i>	Fabricius	11	67	13	16	14	3	16	36	14	7	
69		<i>Cyobius</i> sp. 1								1				
72		<i>Liatongus femoratus</i>	Illiger								1			
75	●	<i>Paragymnopleurus maurus</i>	Sharp	48	89	91	335	174	36	26	56	1		
76	□	<i>Paragymnopleurus sparsus</i>	Sharp	261	532	53	126	34	47	109	409	36	12	
77	●	<i>Paragymnopleurus striatus</i>	Sharp	22	123	75	146	86	26	11	59			
78	□	<i>Phacosoma</i> sp. 1		12	33					4	34			
79	□	<i>Phacosoma dytiscoides</i>	Boucomont	9	33	1		1		5	6	2		
80	●	<i>Phacosoma</i> sp. 2				3	4	2		1				
81	□	<i>Phacosoma</i> sp. 3		6	19		1	1		6	10	6		
82	□	<i>Phaeochridius derasus</i>	Harold	11	37					7		39	40	
83	□	<i>Phaeochroops gilleti</i>	Benderitter	15	45	14	3	1	9	13	80	5		
84	■	<i>Phaeochroops silphoides</i>	Fairmaire		1		1		2	4	5	36		
85	□	<i>Sisyphus thoracicus</i>	Sharp	1299	4877	425	261	181	1631	2044	4821	2295	11	
86	▼	<i>Synapsis cambeforti</i>	Krikken	5	3									
87	△	<i>Tiniocellus sarawacus</i>	Gillet	2	1		1	2		1				

*Association.

Appendix 2

Total number of dung beetles collected by flight intercept trap in riverine, interior-primary, logged and plantation forest within the Ulu Segama Reserve. Identification numbers and symbols indicating association for each species are the same as appear in Figs 2 and 8.

Species number	As'n*	Species	Transect				
			Riverine B	Primary A	Primary B	Logged D	Plantation B
1	■	<i>Onthophagus aereopictus</i>	85			1	5
2	■	<i>Onthophagus aphodioides</i>	10				
3	■	<i>Onthophagus</i> sp. 1	12	2		12	
4	△	<i>Onthophagus batillifer</i> †	12	5	8	5	
5	●	<i>Onthophagus borneensis</i>	1	5	1	2	
6	△	<i>Onthophagus cervicapra</i> complex	53	18	13	59	4
7	●	<i>Onthophagus</i> sp. 3		10	2	2	
8	○	<i>Onthophagus</i> sp. 4		5	53		
9	△	<i>Onthophagus deflexicollis</i>	12	5	12	65	
10	○	<i>Onthophagus dux</i>			3	7	
12	■	<i>Onthophagus incisus</i>	14			2	
13	■	<i>Onthophagus</i> sp. 6	58				
14		<i>Onthophagus</i> sp. 7		1		1	
15		<i>Onthophagus laevis</i>			1		
19	■	<i>Onthophagus mulleri</i>	3			9	2
20	●	<i>Onthophagus</i> sp. 9		5	2	7	
21	■	<i>Onthophagus obscurior</i>	8			1	3
22	○	<i>Onthophagus ochromerus</i>	3		9		
23	△	<i>Onthophagus pacificus</i>	21	6	11	19	1
24	△	<i>Onthophagus</i> sp. 10	66	22	54	9	
26	■	<i>Onthophagus pavidus</i>	11	1			
27		<i>Onthophagus penicillatus</i> †	2			1	
28		<i>Onthophagus</i> sp. 12					1
29		<i>Onthophagus</i> sp. 14	4				
30		<i>Onthophagus</i> sp. 15				3	
31	△	<i>Onthophagus rorarius</i>	4	1	2		
32		<i>Onthophagus</i> sp. 16		1			
33	■	<i>Onthophagus rudis</i>	108	8	6	149	13
34	■	<i>Onthophagus rugicollis</i>	68	2		1	18
35	●	<i>Onthophagus sarawacus</i>		12	10	5	
38	■	<i>Onthophagus semiaureus</i>	50	1		10	27
39	△	<i>Onthophagus semicupreus</i>	5	1	4	5	
40	△	<i>Onthophagus</i> sp. 19	11	9	3		
41		<i>Onthophagus</i> sp. 21	4				
42	●	<i>Onthophagus</i> sp. 22		10	4	9	
43	△	<i>Onthophagus taeniatus</i>	3	3	1		
44		<i>Onthophagus</i> sp. 23	3				
45	■	<i>Onthophagus</i> sp. 24	7	2		3	
48	△	<i>Onthophagus vethi</i>	19	16	1	3	
49	△	<i>Onthophagus vulpes</i>	47	24	10	4	
50	●	<i>Onthophagus waterstradti</i>	2	6	3	2	
51		<i>Onthophagus</i> sp. 25			2		
52		Unidentified female			1		
53		Unidentified female		1			
55		Arboreal 1	3				
57	■	<i>Proagoderus schwaneri</i>	4		1	20	3
58	■	<i>Oniticellus tessellatus</i>	14			8	
59	■	<i>Anoctus</i> sp. 1	12	3	1		
60		<i>Bolbochromus catenatus</i> †	3	1			
61	■	<i>Caccobius binodulus</i>	6			3	
62	■	<i>Caccobius unicornis</i>	33				
63		<i>Catharsius molossus</i>				1	1
66		<i>Copris sinicus</i>				1	
67		<i>Microcopris doriae</i>				1	
68		<i>Microcopris reflexus</i>				1	
69		<i>Cyobius</i> sp. 1	2		1		
70		<i>Cyobius</i> sp. 2			1		
71		<i>Haroldius</i> sp. 1	2		1		
72		<i>Liatongus femoratus</i>					1

Appendix 2 Continued

Species number	As'n*	Species	Transect				
			Riverine B	Primary A	Primary B	Logged D	Plantation B
73		<i>Ochodaeus</i> sp. 1	1				
74		<i>Ochodaeus</i> sp. 2	4	1			
75	△	<i>Paragymnopleurus maurus</i>	3	2	3	2	
76	■	<i>Paragymnopleurus sparsus</i>	86	5	7	32	
77	△	<i>Paragymnopleurus striatus</i>	5	2	2	4	1
79		<i>Phacosoma dytiscoides</i>	2	1			
80	●	<i>Phacosoma</i> sp. 2		8	4	1	
82	■	<i>Phaeochridius derasus</i>	16			1	6
83	■	<i>Phaeochroops gilleti</i>	76	4	2	86	
84	■	<i>Phaeochroops silphoides</i>	3	1		35	
85	■	<i>Sisyphus thoracicus</i>	260	4		418	
87		<i>Tiniocellus sarawacus</i>	1				

*Association.

†Species not in Appendix 1; author: *Onthophagus batillifer* Harold; *Onthophagus penicillatus* Harold; *Bolbochromus catenatus* Lansberge.