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Vegetation indicates diversity of soil macroinvertebrates: a case study with termites along a land-use intensification gradient in lowland Sumatra

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Abstract

Macroinvertebrates have an important role in the maintenance of soil structural stability and fertility in many natural and man-modified habitats. Efficient cataloguing of these animals, as a part of rapid biodiversity assessments, is hampered by high species richness, inherent inaccessibility and a strong tendency towards aggregated distribution. Current debate concerning the relative merits of transects (rapid, but at best semi-quantitative) and alternative sampling approaches such as grid-based or randomised placements of monoliths or cores (labour intensive, but statistically preferable) has initiated a search for satisfactory indicator groups or surrogates of belowground faunal diversity. Here, we use well-characterised, forest-derived plant and termite assemblages to show there can be a key role for plant indicators. We catalogued all vascular plant species, plant functional attributes (PFAs), plant functional types (PFTs), and vegetational structure in seven IBOY-designated sites along a gradient of disturbance and land-use intensification in lowland Sumatra, using a rapid survey protocol. We simultaneously sampled the termite assemblage in the same sites by a more exhaustive process involving microhabitat exploration. There were highly significant, positive correlations between species richness of all termites (and of soil-feeders, the most important termite functional group) and, respectively, mean canopy height ($r > 0.96$), woody plant basal area ($r > 0.95$), the ratio of plant species richness to richness of PFTs ($r > 0.97$), and plant species richness ($r > 0.85$). There was no significant correlation between any individual plant and termite species. There were significant correlations between 18 individual PFAs and 24 of the 54 termite species, and between 12 PFTs and 38 termite species. In addition, 6 PFTs and 10 PFAs were highly correlated with termite species richness and relative abundance. Causal linkages between termites and their plant predictors are briefly discussed. Plant-based heterogeneity and aboveground habitat structure may therefore predict termite diversity response to disturbance. We conclude that for rapid, multi-taxon surveys including belowground macroinvertebrates, logistic efficiency may be achieved by the use of specific, readily observable plant indicators.

Key words: plants, termites, tropical forest, bioindicators, disturbance, land use

See also Electronic Supplement at **http://www.senckenberg.de/odes/03-05.htm**

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Introduction

Plants comprise most of the living biomass in terrestrial ecosystems and are the basis of energy and nutrient turnover in food webs: hence they are the primary determinants of terrestrial ecosystem structure, including microhabitat conditions for other organisms at secondary and tertiary trophic levels, and the consequent diversities of these consumers. As members of the belowground biotic community, plants share the soil environment with a suite of other organisms ranging from relatively large animals to prokaryotes. The latter community also shapes the ecosystem through soil biological processes, such as decomposition, nutrient cycling, bioturbation and suppression of pathogens, that are vital to service functions (Hole 1981, Brussaard et al. 1997, Lavelle et al. 1997, van Breemen & Finzi 1998). Plants affect niche availability for belowground organisms through the influence of vegetation cover on soil climate, the modification of soil structure and drainage by root penetration, and nutrient supply to soil organisms from a variety of litters and exudates, including products of photosynthesis transferred directly to microsymbionts (Swift & Anderson 1993, Angers & Caron 1998, Bignell et al. in press).

Primary lowland tropical forests are widely considered the world's most species-rich terrestrial habitats, with soil communities contributing much of the diversity (Giller 1996, Brussaard et al. 1997). Many pristine tropical forests are being disturbed, converted and fragmented with increasing intensity. The process is viewed as a global biodiversity crisis (acutely so in Indonesia, e.g. Jepson et al. 2001), but a lack of baseline information hampers the design of remedial measures and management strategies. The need to understand the impacts of habitat change on biodiversity has set in motion the search for cost-effective field protocols for rapid assessment of species richness across a variety of taxonomic groups (Pimm et al. 1995, Whitmore 1998, Lawton et al. 1998). Two key objectives in baseline studies are: (1) to define the permanent effects of forest disturbance, and (2) to seek indicator species which can be monitored to calibrate gradients of "land-use intensification", i.e. land-use change (e.g. progressive loss of primary tree species and canopy cover; sensu Lawton et al. 1998) or agricultural intensification (e.g. simplification of cropping regimes and shortening of fallow periods on forest-derived soils; sensu Matson et al. 1997). The rationale for such work concerns both the understanding (and therefore future management) of extinctions (e.g. Didham et al. 1998, Davies 2000) and the development of land uses that are compatible with the conservation of biodiversity and sustainable cropping systems (Giller et al. 1997, Bignell et al. in press). The central hypotheses are: (1) that strong dynamic links exist between belowground biodiversity and long-term soil fertility (Giller et al. 1997), and (2) that there is mutual dependence between high biodiversity aboveground and belowground (Hooper et al. 2000). In this paper we are concerned mainly with seeking evidence for the latter hypothesis.

Biodiversity studies commonly address insect faunas, which make up the majority of known eukaryote biodiversity and of which about 70% are associated with the litter and soil rather than the canopy (Stork 1988, Wilson 1992, Hammond et al. 1997). Termites are the dominant macroarthropod detritivores in many tropical soils, with highest diversity in lowland equatorial forests (Eggleton et al. 1996, 1999; Eggleton 2000). As 'ecosystem engineers' they contribute significantly to ecosystem processes including carbon fluxes, soil formation and soil conditioning (Lee & Wood 1971, Bignell et al. 1997, Bignell & Eggleton 2000). Termite species assemblages differ in different stages of post-logging forest succession (Eggleton et al. 1995, 1997), and may decline somewhat in overall species richness (Collins 1980). Severe disturbance, such as replacement of forest with agriculture, generally leads to a sharp decrease in diversity, with a disproportionate loss of some trophic functional groups (chiefly soil-feeders: Eggleton et al. 2002), or a marked dominance by a small number of savanna species adapted to drier soil conditions (Wood et al. 1982). Furthermore, if termites are efficiently sampled in any one place, a range of species (or particular balance of trophic functional groups) can usually be found that characterises the land use in question. This makes termites candidate taxa as biological indicators of disturbance, with the added advantage that their soil-forming and soil-conditioning activities link directly to medium- and long-term soil fertility and stability (Lavelle et al. 1997, Bignell & Eggleton 2000). Giller et al. (1997) cite evidence for very close correspondence between increasing agricultural intensification and reduced soil biodiversity, but argue that this is not in itself proof of causality. They recommend studying trends along gradients of intensification that should include field experiments with agricultural practices of differing intensity (see also Holt et al. 1996). Using species (or plant functional types) to forecast the impacts of land-use change along such gradients should derive from an improved understanding of the causes of biodiversity change. According to Sala et al. (2000), changing interactions between taxa, and between taxa and their physical environments, represent one of the largest uncertainties in projections of future biodiversity change. With this in mind we present evidence for the occurrence of potentially useful predictive correlates between plant community parameters and one functionally important insect group – termites.

The difficulties of sampling termites in rapid biodiversity assessments are similar to those encountered

with other soil macrofauna (for reviews see Eggleton & Bignell 1995, Bignell et al. in press). These include inaccessibility (most are subterranean), relative taxonomic intractability (identification may require morphometric comparisons and internal dissection of the alimentary canal), seasonal and interannual variations in diversity and abundance (Dibog et al. 1998), and patchiness (distinct clumping within the soil, making determination of the variances associated with estimates of abundance and biomass unreliable, and requiring labour-intensive replication of soil coring or monolith cutting to obtain acceptable means: see Eggleton et al. 1996). However, systematic sampling of microhabitats along extended (100 m) transects (Jones & Eggleton 2000) is a robust and relatively rapid method of estimating overall species diversity (about 35% of the assemblage are consistently discovered), demonstrating functional group composition (representatives of all groups present are generally recovered) and allowing relative abundance to be derived (as encounters per transect). This method is now the basis of comparisons of termite assemblages on all scales ranging from localities to biogeographical regions (Eggleton & Tayasu 2001, Davies et al. in press). The question of whether a single taxon, such as termites, is an adequate surrogate for all soil macrofauna in natural resource surveys is under debate, while methods for estimating biodiversity are still very uncertain (e.g. see Lawton et al. 1998, Hilty & Merenlender 2000, Lindenmayer et al. 2000). This is partly due to the broad, and therefore imprecise, definition of the term (biodiversity = the "diversity of all life"; Heywood & Baste 1995), but also to the inability of life scientists to calibrate predictors for the wealth of taxa and associated genetic variability to be found in almost any above- or belowground assemblage of organisms. Ideally, knowledge of the dynamic linkages between taxa, individuals and their physical environment would facilitate the selection of suitable surrogates, but such knowledge remains elusive in even the simplest of communities. Opinions vary about selection criteria for indicators. For example, Miller et al. (1995) suggested that key pollinators and seed dispersers should always be included, but since these cannot always be identified it is more common practice to broadly monitor the status of a cross-section of taxa (plants, mammals, birds, invertebrates). Considerable debate surrounds the largely correlative basis for predicting the occurrence of one set of taxa from another (Noss 1990; Cranston & Hillman 1992; Pearson 1995; Howard et al. 1996, 1997; Lawton et al. 1998; Lindenmayer et al. 2000). Selection criteria for indicators may include ease of sampling, and more inaccessible taxa may be excluded if time and resources are limited. For example, in a wide-ranging study of biodiversity in the Rwenzori National Park of Uganda, Howard et al. (1996, 1997) chose woody plants, five families of small mammals, birds, butterflies and two families of large moths. In Cameroon, Lawton et al. (1998) chose six insect groups (butterflies, flying beetles, canopy beetles, canopy ants, litter ants and termites) together with birds and soil nematodes; however, they found little evidence to support the use of one set of taxa to predict another. Among plant taxa, individual plant species tend to be the most frequently used indicators of biodiversity, despite the considerable problems of identifying species in tropical forests. For convenience, higher taxa (genera and families) are sometimes used, but the efficiency of this is questionable (Dale & Clifford 1976, Prance 1995). Although the species is the most common currency for biodiversity, species analysis in relation to lower and higher taxonomic ranks can give an added quantum of biodiversity via phylogenetic or 'taxic' richness (Vane-Wright et al. 1991, Stork et al. 1997). Regardless of the state of discussion, there is still an urgent need for indicators of habitat complexity, critical functional groups, population stability and overall taxonomic richness (Stork et al. 1997).

In this paper we show that there are corresponding distribution patterns between plants and termites when sampled along gradients of disturbance or land-use 'intensity' in a complex, tropical, lowland, forest-derived landscape mosaic. This relationship can be exploited to select indicators from the more readily observable plant features. We depart from the sole use of taxa to predict taxa. Instead, we explore the potential complementary value of other environmental-response-based plant indicators (Plant Functional Types or PFTs) as well as certain elements of vegetation structure. Part of the underlying rationale for their use is that because PFTs are demonstrably adapted to environmental change, they may provide a more logical basis than Linnean species for exploring causal relationships with associated fauna. Because their application in this context is relatively novel, it is necessary to provide some rationale. Functional Types are "sets of organisms showing similar responses to environmental conditions and having similar effects on the dominant ecosystem processes" (Diaz 1998; see also Cramer 1996, Cramer et al. 1999). Shugart (1996) used PFTs to connote species or groups of species with similar responses to a suite of environmental conditions.

In general, functional types are frequently associated with 'guilds' or groups of individuals that exploit an existing resource in a similar way, such as raptors, folivores, plant parasites, saprophytes etc. (Gillison 1981, Bahr 1982, Huston 1994, Gitay & Noble 1996, Shugart 1996, Gillison & Carpenter 1997, Gitay et al. 1999). They can be used to reduce complex species assemblages to more manageable groups for both ecological and biodiversity investigations. Functional types have been shown to influence ecosystem processes and in-

clude keystone species and those essential for ecosystem resilience by providing natural insurance capital (Folke et al. 1996). While PFT richness itself can be a useful indicator of biodiversity condition, differences in PFT composition can also help explain more of the variation in ecosystem processes, such as production and nitrogen dynamics, than the overall number of functional types or groups present (Hooper & Vitousek 1998). PFTs based on adaptive morphologies also influence soil organic carbon (SOC) distribution in the soil profile (cf. Jobbágy & Jackson 2000).

In an intensive, multitaxa baseline study in lowland Sumatra, PFTs and plant species were closely correlated with soil organic carbon, soil nutrient availability, aboveground carbon and land-use intensity (Gillison & Liswanti 1999, Gillison 2000, Hairiah & van Noordwijk 2000). The same study provided strong statistical support for the use of PFTs in combination with vascular plant species as indicators of certain groups of insects and birds along a lowland, tropical, forested land-use intensity gradient (Gillison 2000, Jones et al. 2003). Using the same study, this paper further explores the predictive relationships between PFTs, plant species and vegetation structure and termite species richness and relative abundance.

Materials and methods

Study sites

Sites were located at or near Pasir Mayang in Jambi Province, Central Sumatra. The area includes 900 ha of a forest reserve set aside for research by SEAMEO BIOTROP (SEAMEO = South East Asian Ministries of Education Organisation, Thailand; BIOTROP = SEAMEO Regional Centre for Tropical Biology, Indonesia), located within the Barito Pacific logging concession, and is a mosaic of pristine forest, logged-over secondary forest, softwood plantations, rubber and jungle rubber (regenerating secondary forest enriched with rubber trees, *Hevea brasiliensis*) with secondary mosaics of subsistence gardens and fruit orchards. The area surveyed represents a putative gradient of land-use intensification and disturbance (Murdiyarso & Wasrin 1995, Jones et al. 2003), derived from forest rich in plant species, and dominated by trees from the Dipterocarpaceae family (Table 1). Soils are mostly ultisols and represent a mixture of relatively low-nutrient, gibbsitic, kaolinitic and ferralitic types over recent alluvium, acidic pumice tuffs, tuffaceous sandstones, and carbonaceous mudstones, siltstones, sandstones and conglomerates. The region is drained by the Batangahari river which is also used to float log rafts down to Kota Jambi (Gillison 2000). The study was conducted during November 1997, as part of the establishment of a multi-taxon ecoregional database by the Alternatives to Slash and Burn Consortium (UNDP/ICRAF/CIFOR; Tomich et al. 2001). All sites were at elevations between 30 and 80 m a.s.l., with an annual rainfall of nearly 3000 mm, distributed in a wetter season of six months (wettest months December and January) and a drier season of six months (driest months July and August; Ketterings et al. 1999). The Sunda lowland forest region, which includes Sumatra, has been identified as one the world's top five biodiversity 'hotspots' (Myers et al. 2000) and is currently under extreme threat from land clearing.

Site selection and survey protocol

Sampling was preceded by a ground reconnaissance of a series of representative land-use types. Although only a limited number could be sampled, those land-use types chosen represented a range of extremes of subjectively assessed land-use intensification or forest disturbance, from pristine lowland tropical rain forest through logged-over forest and tree plantations to degraded *Imperata* grassland. To identify suitable sites, the 'gradsect' (gradient-oriented transect) model of Gillison & Brewer (1985) was employed. Where the primary aim is to maximise information about the distribution of plants and animals, the method is more efficient than purely random or systematic (e.g. grid-based) surveys (Austin & Heyligers 1991, Wessels et al. 1998). Prospective sites are clustered in a nested series of hierarchical environmental gradients (e.g. rainfall seasonality, parent rock type, drainage and soil catenary sequences, overlain by land use and vegetation pattern). Within this gradient we selected 16 sites that were broadly representative of variation in patterns of land-use types and the underlying natural resource. These formed the basis for selecting seven representative subsets of transects for sampling termites. Because animal habitat is closely coupled with vegetation cover and pattern, 40×5 m belt transects, placed along any visible contour, were used for all botanical surveys and as the focal point for fauna samples.

Sampling of plant-based variables

The variables recorded in each transect, including site physical and plant-based elements, are listed in Table 2. A field botanist recorded all vascular plant species for which voucher specimens were collected and later identified at the Herbarium Bogoriense (Bogor, Java, Indonesia). These were cross-referenced with PFTs (or functional modi; Gillison 1981) recorded using the classification method of Gillison & Carpenter (1997). Data were collated and stored in a laptop computer using the CIFOR 'VegClass'® (beta v. 1.5) Windows®-based software package (Gillison 2001, 2002). VegClass uses a standard protocol to collate, store and tabulate proforma data. It can be used to generate graphic output of meta-data and to export summary data to many spreadsheet and relational database programs (in the present case to Microsoft Excel®). A summary description of the method together with some case studies is available on the internet at http://www.cifor.cgiar.org and described in Gillison (2002; an electronic publication available at http://www.consecol.org/vol6/iss2/art3). The sites were also separately surveyed for aboveground biomass C, dead wood and litter accumulations, soil bulk density, and a suite of soil physical and chemical properties (details in van Nordwijk et al. 1997, Ketterings et al. 1999, Gillison 2000).

Table 1. Summary of site physical features and vegetation structure across seven sites along a land-use 'intensity' gradient in lowland Central Sumatra.

Site No.	Site Id.	Vegetation/Land-use type	Latitude/ Longitude	Elev	Slp	Asp	Lit	Terrain position	Mcan	Ccov	Ba-Av	WPlt	Bry	MFI	FIcv	BD
1	BS01	Intact rain forest. Dominated by dipterocarp species	01-04-47S 102-06-02 E	76	25	7	10	Upper slope	21.0	75	27.33	7	2	13.50	88.38	0.67
2	BS03	Secondary forest logged 1984	01-04-43 S 102-05-55 E	85	12	150	15	Ridge top	10.0	35	32.67	6	3	10.25	226.86	0.87
3	BS06	*Paraserianthes falcataria* 4 yrs old industrial soft-wood plantation	01-04-59 S 102-06-43 E	65	20	202	3	Upper slope	6.0	40	13.33	4	1	43.75	80.2	1.00
4	BS08	Rubber plantation – 8 yrs old	01-05-25 S 102-07-05 E	53	3	183	5	Upper slope – ridge	11.0	65	32.67	4	4	39.25	101.01	0.79
5	BS10	Jungle rubber – 15–38 yrs old mosaic with *Hevea brasiliensis*	01-10-12 S 102-06-50 E	30	0	0	8	Flat	14.0	50	27.33	6	3	38.50	99.45	0.65
6	BS12	*Imperata* grassland – fired annually	01-35-58 S 102-21-11 E	40	5	225	0.1	Ridge	1.0	90	32.67	1	1	0.00	0.00	1.12
7	BS14	Cassava plantation >10 yrs old	01-36-05 S 102-21-22 E	48	0	0	0.5	Ridge	1.8	50	13.33	5	1	98.75	2.25	1.31

Latitude (deg.min.sec); *Longitude* (deg.min,.sec.); *Elev*: Elevation (m.a.s.l.); *Slp*: Slope (%); *Asp*: Aspect (deg.); *Lit*: Litter depth (cm); *Mcan*: Mean canopy height (m); *Ccov*: Crown cover %; *Ba-Av*: Basal area average ($m^2 ha^{-1}$); *WPLt*: Woody plants <1.5 m tall; *Bry*: cover-abundance of bryophytes; *Mfi*: Mean Furcation index; *Ficv*: Furcation Index coefficient of variation %; *BD*: soil bulk density ($g\ cm^{-1}$)
(Ref. Table # and text for additional detail)

Table 2. List of data variables recorded for each 40 × 5m survey plot

Site feature	Descriptor	Data type
Location reference	Location	Alpha-numeric
	Date (dd-mm-year)	Alpha-numeric
	Plot number (unique)	Alpha-numeric
	Country	Text
Observer(s)	Observer(s) by name(s)	Text
Physical	Latitude deg.min.sec. (GPS)	Alpha-numeric
	Longitude deg.min.sec. (GPS)	Alpha-numeric
	Elevation (m a.s.l.) (aneroid and GPS)	Numeric
	Aspect (compass deg.) (perpendicular to plot)	Numeric
	Slope (%) (perpendicular to plot)	Numeric
	Soil depth (cm) (sample taken 0–10, 10–20 cm)	Numeric
	Soil type (U.S. soil taxonomy)	Text
	Parent rock type	Text
	Litter depth (cm)	Numeric
	Terrain position	Text
Site history	General description and land-use/landscape context	Text
Vegetation structure	Vegetation type	Text
	Mean canopy height (m)	Numeric
	Crown cover percent (total)	Numeric
	Cover-abundance (Domin Scale) – bryophytes	Numeric
	Cover-abundance (DS) woody plants <1.5 m tall	Numeric
	Basal area (mean of 3) (m^2 ha^{-1})	Numeric
	Furcation Index (mean and cv % of 20)	Numeric
	Profile sketch of 40 × 5 m plot (scannable)	Digital
Plant taxa (vascular)	Family	Text
	Genus	Text
	Species	Text
	Botanical authority	Text
Plant Functional Type	Plant functional elements combined according to published rule set	Text
Photograph	Hard copy and digital image	JPEG

Plant functional types

As described by Gillison & Carpenter (1997) and as applied here, PFTs are unique combinations of adaptive morphological or functional attributes (e.g. leaf size class, leaf inclination class, leaf form and type = distribution of chlorophyll tissue) coupled with a modified Raunkiaerean life form and the type of aboveground rooting system. PFTs are derived according to a specific grammar or rule set from a minimum set of 35 plant functional attributes (PFAs). For example, an individual with **mi**crophyll-sized, **ve**rtically inclined, **do**rsiventral leaves supported by a **ph**anerophyte life form would be a PFT expressed as mi-ve-do-ph. Although they tend to be indicative for a species, PFTs are independent of species in that more than one species can occur in one PFT and more than one PFT in a species. PFTs allow the recording of genetically determined, adaptive responses of plant individuals that can reveal intraspecific as well as interspecific response to environment (e.g. land use) in a way that is not usually contained in a species name. Because PFTs are generic, they have a singular advantage over species as they can be used to record and compare data sets derived from geographically distant regions where, for example, adaptive responses and environments may be similar but where species differ. Results from field studies across widely differing environments show that estimates of biodiversity (expressed as richness of taxa) can be improved by including descriptions of functional features or functional types. (Gillison 1981, 1988; Nix & Gillison 1985; Huston 1994; Collins & Benning 1996; Martinez 1996; Woodward et al. 1996; Gillison & Carpenter 1997).

Sampling termites

Because vegetation assessment takes about 20% of the time needed to sample termites, sample plots for the latter were restricted to a representative subset of seven of the overall 16 transects. A transect of 100 × 2 m was marked out, parallel with and adjacent to the vegetation survey plot and sampled for termites using the protocols given by Jones & Eggleton (2000) and Jones et al. (2003). The transect was divided into twenty (5 × 2 m) sections each of which was systematically explored by two experienced collectors for 30 minutes. Species richness is the number of species and morphospecies obtained over the whole transect. Relative abundance is the

number of encounters per transect, where the presence of a species in one section represents one encounter. The concept of the short survey plot (for plant and soil properties) and adjacent extended transect (for termites) follows Anderson & Ingram (1993) as modified by Swift & Bignell (2001). Most termites were identified to named species at The Natural History Museum, London. Remaining taxa were assigned to morphospecies, applied consistently across regional voucher collections (Eggleton et al. 1997, 1999; Jones & Brendell 1998; Gathorne-Hardy et al. 2001). After identification, all specimens were deposited in the Museum Zoologi, Bogor.

Statistical and multivariate analyses

Linear and polynomial regressions were used to seek out the most highly correlated variables within the entire data set using the MINITAB© statistical package. Certain key vegetation parameters (mean height, basal area, species and PFT richness, and species:PFT ratio) are known in many cases to vary predictably with certain measures of biodiversity and LUT (Gillison 2000). Their values can be integrated across all plots and expressed as a relative index (a "V-" or vegetation index). V-index values are derived by obtaining a single best eigenvector set of scores for each plot using a multi-dimensional scaling program or principal coordinate analysis (Belbin 1992). These scores are then standardised between 1 and 10 and used to rank LUTs – in this case the 16 plots of the present study. For the subset of seven sites sampled for termites, V-indices were extracted from the 16 plots and, for convenience, the scores again standardised between 1 and 10. The method is described in Gillison & Liswanti (1999) and the index has shown analogous values along similar agricultural intensification gradients in Brazil, Cameroon, Indonesia, Peru and Thailand. V-indices have been found to be highly correlated with certain animal groups and habitat features in lowland Sumatra and northern Thailand (Gillison & Liswanti 1999, Gillison 2000).

Results

Vascular plants and vegetation structure

A checklist of vascular plant taxa and PFTs is available in Appendix 1 (see Electr. Suppl. 03-xy, Pt 1) and summarised in Table 3. Of the vegetation structural variables given in Table 2, those that were found to be useful predictors are listed in Table 1 to characterise each site. Within the 16 original transects there is a highly significant correlation between species and PFTs ($r = 0.898$, $P < 0.001$). Within the subset of seven transects sampled for termites, the correlation differs only slightly ($r = 0.937$, $P < 0.002$). These correlations are consistent with baseline studies in other countries (Gillison 2000), implying that where it is useful to know species richness, but where identification is problematical, PFTs can be used to predict species richness with a high degree of confidence. The ratio of species richness to PFT richness has also been found to be potentially useful as an indicator of associated taxa, and in old growth tropical forests there tends to be a higher number of species per PFT. In disturbed conditions that offer a greater variety of available ecological niches, this ratio is usually reduced (Table 3) and may approach unity under conditions of very low nutrition or under extremes of temperature or moisture. Because the ratio also tends to reflect soil nutrient availability (Gillison 2000) this, in turn, can have implications for the prediction of associated fauna.

Termites

A total of 54 species was collected from the seven sites (listed in Appendix 2, see Electr. Suppl. 03-xy, Pt 2). The primary forest transect was the richest with 34 species and 110 encounters, followed by the logged forest with 23 species and 94 encounters, while the two non-forested sites were the most depauperate. Only two species (9 encounters) were found in the *Imperata* grassland transect, and just one species (1 encounter) in the cassava garden transect. The silvicultural sites were intermediate, with the jungle rubber (a system in which regenerating secondary forest is enriched with rubber trees and allowed to mature for approximately 30 years) showing the highest diversity (21 species and 82 encounters). The species sampled were affiliated to two families of lower termites (Kalotermitidae and Rhinotermitidae) and three subfamilies of higher termites (Termitidae: Macrotermitinae, Termitinae and Nasutitermitinae). The taxonomic composition of the whole assemblage (7 sites) generally resembled that of other Sunda assemblages sampled by the same transect method (e.g. Eggleton et al. 1997, Gathorne-Hardy et al. 2001), and there was a strong positive correlation between termite species richness and the relative abundance in each transect ($r = 0.981$, $P < 0.001$). A more detailed description of the Jambi assemblage, with notes on functional group composition, is given in Jones et al. (2003). The termite species most liable to extinction along the land-use intensification gradient were those in feeding groups III and IV (sensu Donovan et al. 2001), where the diet consists mainly or exclusively of mineral soil. Termites of this life type are generally distributed in the top 10 cm of the mineral horizon, where their extensive tunnelling and gallery construction contribute significantly to macropore formation and to the stabilization of complex organic matter. They are nonetheless susceptible to any disturbance that involves compaction of the soil and/or drying out as the result of a reduction of canopy cover (Bignell & Eggleton 2000).

Statistical relationships

We performed one-way product-moment correlation analysis on the plant and termite parameters with plant

Table 3. Summary of vascular plant and termite parameters across seven sites along a land-use intensification gradient in lowland Central Sumatra.

Site and land use	Plant species richness	PFT richness	Plant spp./ PFTs	V-index*	Termite species richness	Termite relative bundance#
1. Primary forest	102	35	2.91	10.00	34	110
2. Logged forest	50	24	2.08	5.48	23	94
3. *Paraserianthes* plantation	43	28	1.54	8.76	11	35
4. Rubber plantation	66	37	1.78	6.36	15	62
5. Jungle rubber	112	47	2.38	3.98	21	82
6. *Imperata* grassland	11	10	1.10	1.00	2	9
7. Cassava garden	15	12	1.25	1.43	1	1

* Index from multidimensional scaling of combined plant species richness, PFT richness, plant spp./PFT ratio, mean canopy height and basal area. See text for details.
# Encounters of individuals per transect.

Table 4. Pearson product-moment linear correlations between plant, soil and termite parameters.

Plant predictor	Termite species richness		Termite relative abundance	
Vascular plant species richness	0.850	$p < 0.016$	0.844	$p < 0.017$
Plant Functional Types (PFTs)	0.705	$p < 0.077$	0.732	$p < 0.061$
Plant species richness/PFT richness	0.975	$p < 0.0001$	0.944	$p < 0.001$
PFA 1 (ph) phanerophyte life form	0.962	$p < 0.001$	0.916	$p < 0.004$
PFA 2 (co) composite leaf inclination	0.904	$p < 0.005$	0.912	$p < 0.004$
PFA 3 (li) lianoid life form	0.879	$p < 0.009$	0.923	$p < 0.003$
PFA 4 (no) notophyll leaf size	0.887	$p < 0.008$	0.841	$p < 0.018$
PFT 1 (mi-la-do-ph-li)	0.925	$p < 0.003$	0.885	$p < 0.008$
PFT 2 (no-la-do-ct-ph)	0.911	$p < 0.004$	0.917	$p < 0.004$
PFT 3 (me-la-do-ph)	0.908	$p < 0.005$	0.883	$p < 0.008$
PFT 4 (me-la-do-ph-li)	0.827	$p < 0.022$	0.878	$p < 0.009$
Mean canopy height	0.963	$p < 0.001$	0.929	$p < 0.003$
Basal area, woody plants	0.955	$p < 0.001$	0.949	$p < 0.001$
V-index	0.932	$p < 0.002$	0.919	$p < 0.003$
Aboveground carbon	0.890	$p < 0.007$	0.789	$p < 0.035$
Soil bulk density	–0.878	$p < 0.009$	–0.905	$p < 0.005$

species richness, PFT richness, plant species, plant species:PFT ratio, individual PFAs and PFTs, mean canopy height, basal area of woody plants, aboveground carbon, and V-index as the predictors (Table 4). A more extensive summary of correlates between individual PFAs and PFTs and termite species richness where $P < 0.050$ is available in Appendices 3 and 4, respectively (see Electr. Suppl. 03-xy, Pts 3 and 4). The best correlations listed in Table 4 are those with the plant species/PFT richness ratio (Fig. 1), and these are better than those with plant species richness alone, but the latter are also significant. PFT richness, however, does not predict either termite species richness or termite relative abundance. Four individual PFAs and four PFTs are also strong predictors (examples in Figs 2, 3). Of the individual PFTs, PFT1 (mi-la-do-ph-li) plants with microphyll-sized, laterally inclined, dorsiventral leaves supported by a woody liane life form, appear to be the best predictor overall. This may be because the PFT is more widespread than others across most woody vegetation types within the region studied and where its relative abundance varies with the disturbance regime. Mean canopy height and basal area of all woody plants are the two strongest correlates with termite species richness and relative abundance (Figs 4, 5), followed by aboveground carbon (Fig. 6). The high level of correspondence between V-index values and the termite parameters (Fig. 7) reflects their covariation along the land-use intensity/disturbance gradient. As would be expected, there is an additional negative correspondence with soil bulk density (Fig. 8).

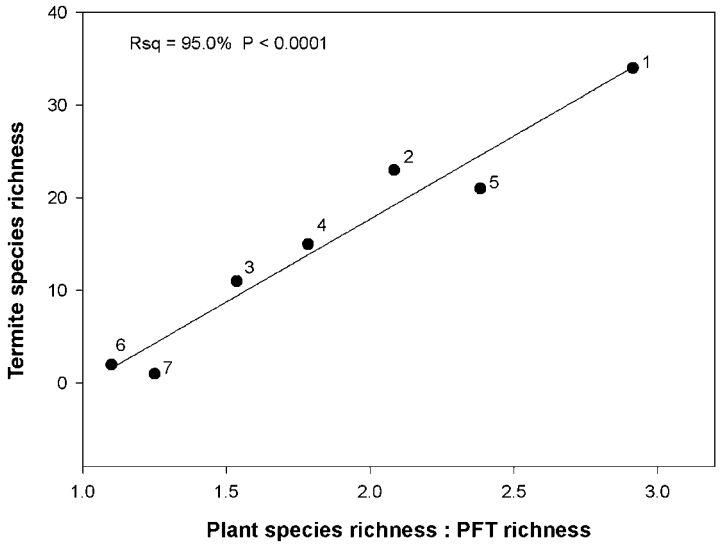

Fig. 1. Relationship between the plant species richness to PFT richness ratio and termite species richness.

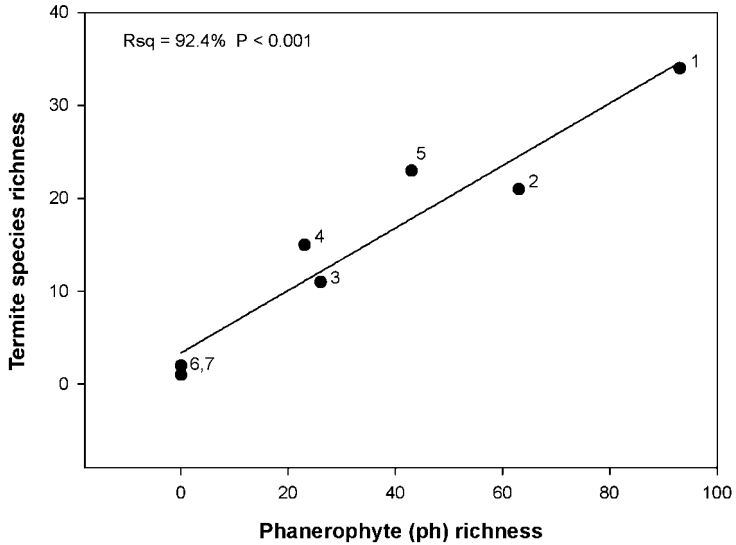

Fig. 2. Example of relationship between PFA (ph) richness and termite species richness.

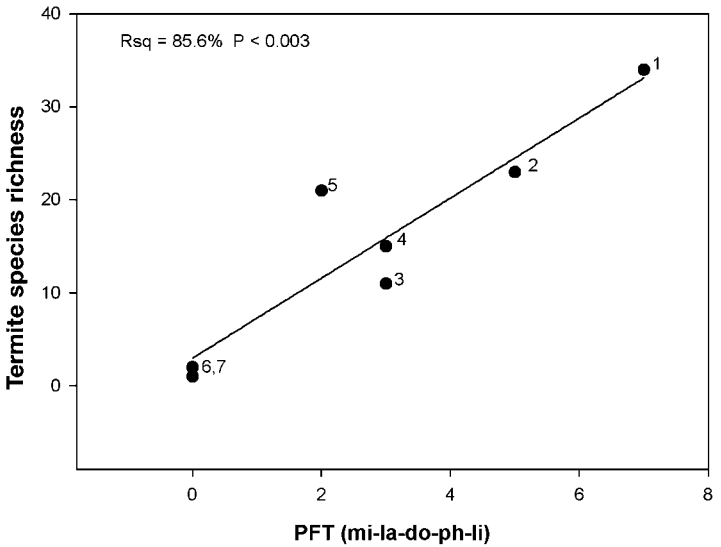

Fig. 3. Example of relationship between PFT richness and termite species richness.

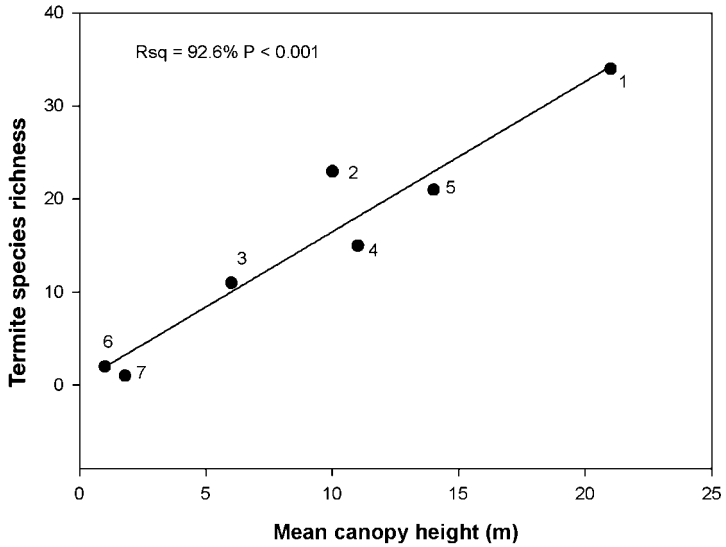

Fig. 4. Relationship between mean canopy height and termite species richness.

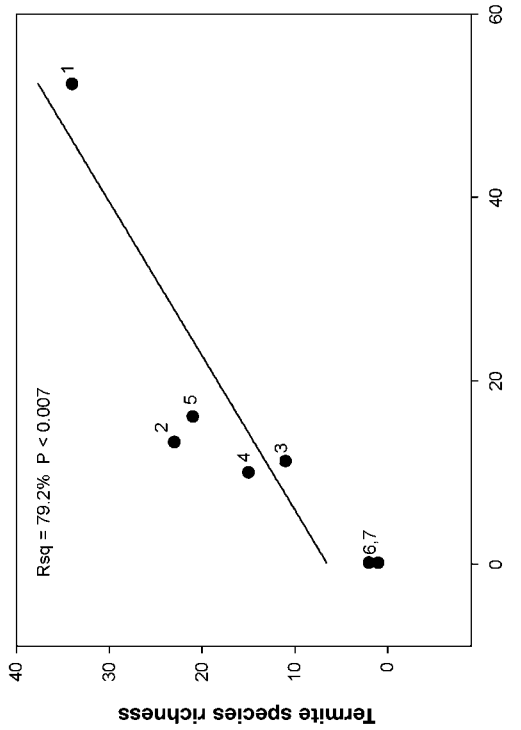

Fig. 6. Relationship between aboveground carbon and termite species richness.

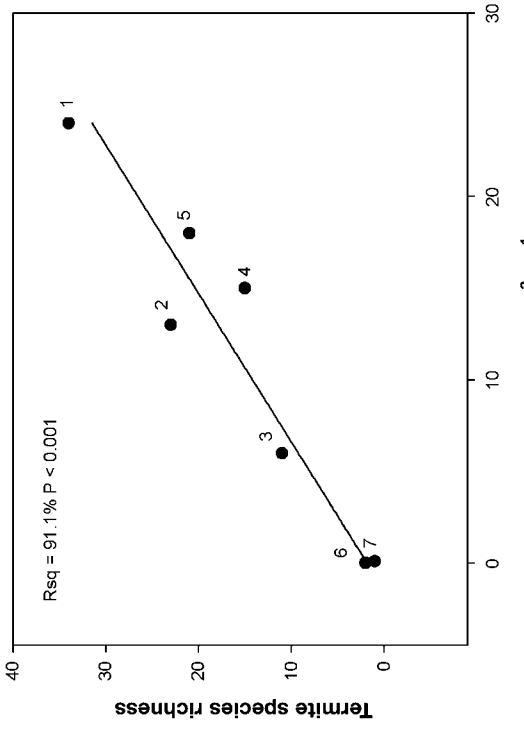

Fig. 5. Relationship between woody plant basal area and termite species richness.

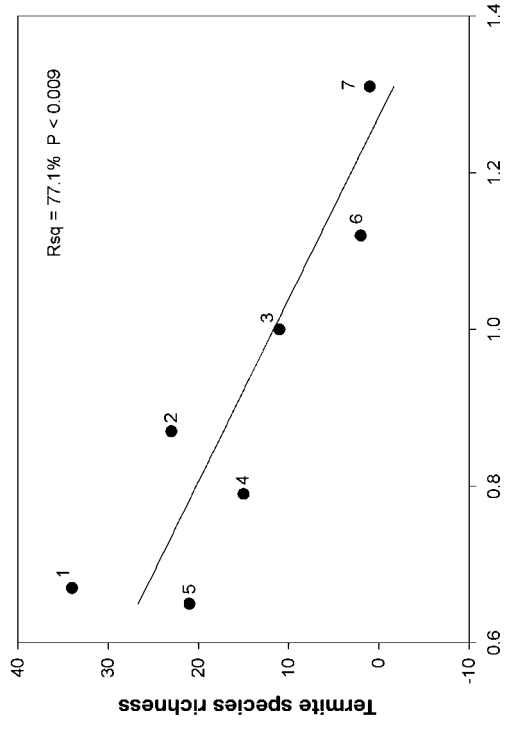

Fig. 8. Relationship between soil bulk density and termite species richness.

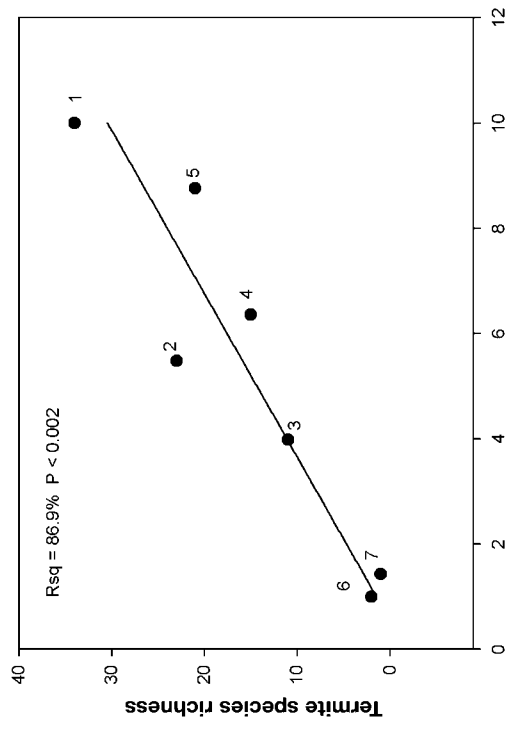

Fig. 7. Relationship between V-index and termite species richness.

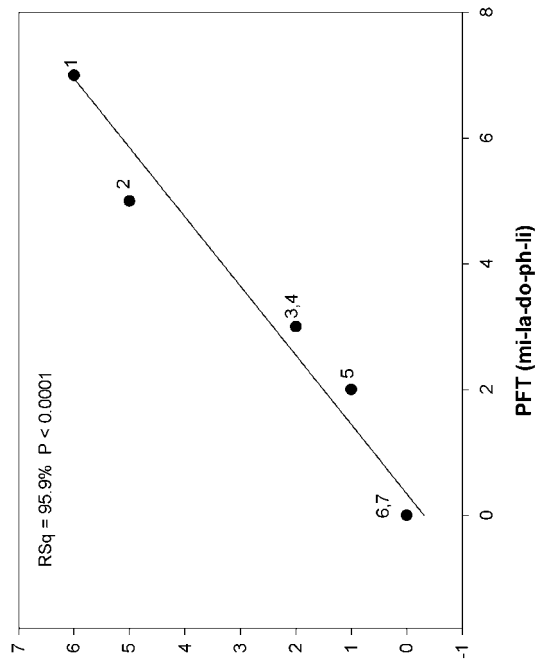

Fig. 10. PFT (mi-la-do-ph-li) as a predictor of the termite species *Dicuspiditermes santschii*.

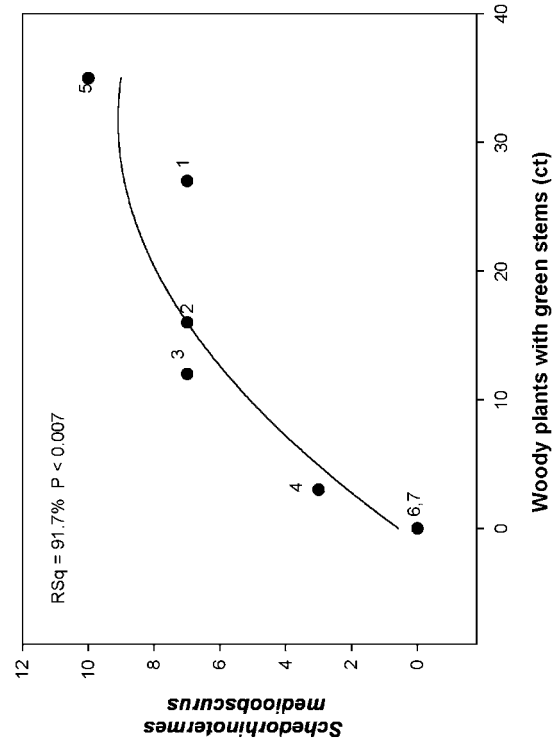

Fig. 9. PFA (ct), i.e. plants with green stems, as a predictor of the termite species *Schedorhinotermes medioobscurus*.

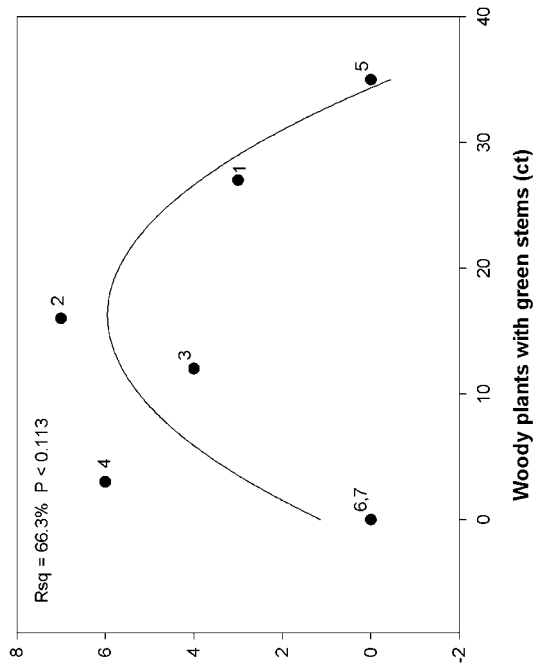

Fig. 12. PFA (ct), i.e. plants with green stems, as a predictor of the termite species *Dicuspiditermes santschii*.

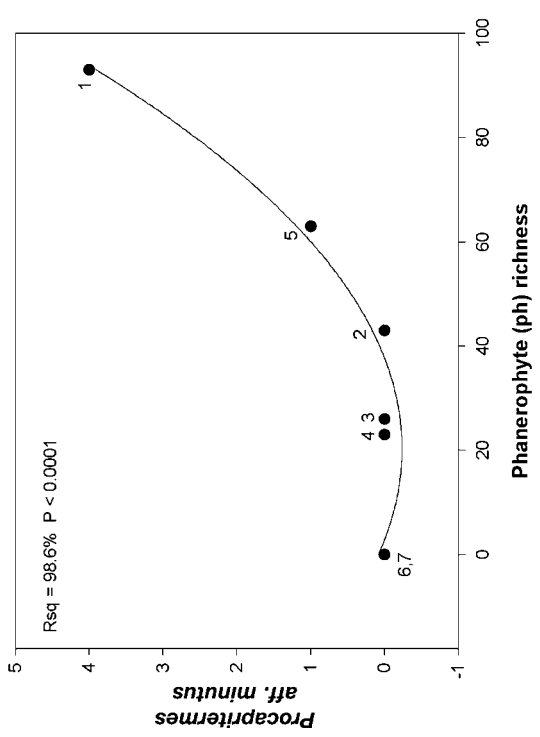

Fig. 11. PFA (ph), i.e. phanerophyte life form, as a predictor of the termite species *Procapritermes* aff. *minutus*.

In addition to examining the relationships between the summary data (richness and relative abundance), the study provided an opportunity to explore the value of plants for predicting the occurrence of named termite taxa. However, we found no significant correlation between any plant and termite species and, with some notable exceptions, the PFA and PFT data tended to be weakly correlated with most termite taxa. Significant linear correlations occurred between 18 individual PFAs and 24 termite species, and between 12 individual PFTs and 38 termite species (see Figs 9, 10 for examples of best fits). In addition, 6 PFTs and 10 PFAs were highly correlated with termite species richness and relative abundance (Appendices 3, 4; see Electr. Suppl. 03-xy, Pts 3 and 4). While there are numerous highly significant linear correlations, there is no consistent linear relationship between plant variables and termite species, with frequent improvements gained via polynomial fits (e.g. Figs 11, 12).

Discussion

The relatively small number of sites and the lack of replication of sampling do not favour a completely robust analysis. Nonetheless, the analyses reveal a series of very consistent trends between certain plant and termite parameters. This trend is unidirectional along the subjectively sampled gradsect and provides a strong argument for hypotheses that can be tested in future work. The data add to the accumulated evidence that land-use intensification gradients represent increasing habitat modification, with a progressive decline in the physical and biological complexity of the aboveground vegetation cover and, in turn, a corresponding reduction in termite diversity and relative abundance (cf. Jones et al. 2003). Adverse changes in microclimate, vegetation structure and canopy cover, as well as loss of microhabitats, increasing soil bulk density and the progressively more serious impact of fire will all contribute to the extinction of termite species. These various environmental factors appear to be most consistently reflected by changes in canopy cover and woody plant basal area, that together with mean canopy height can be readily and accurately determined by field survey (Gillison 2000). Soil-feeding termites (those showing the most response to habitat disturbance) are often associated with trees, where buttress and stilt roots can be used to support epigeal mounds and where deeper litter accumulations provide both food materials and suitable microhabitats. The effect of the gradient on other members of the soil macrofauna is less clear. In the same study, other invertebrate groups (ants, earthworms and epigeic insects) were sampled by the use of soil monoliths and pitfall traps, methods that are both laborious and generally unreliable (Swift & Bignell 2001, Bignell et al. in press). Nevertheless, these data (D. Bignell, unpublished) showed that ants were most species-rich in site 3 (*Paraserianthes* plantation), and earthworms, which have low species richness along the entire gradient, showed their highest relative abundance in site 5 (jungle rubber). Both distributions are consistent with the Intermediate Disturbance Hypothesis. Such observations support the view that individual taxa alone cannot serve as biodiversity surrogates (Lawton et al. 1998), although the case for termites having such a role remains stronger, at least in humid tropical forests and forest-derived ecosystems.

The distribution of plant species, functional groups and vegetation structure is consistent with the observed conditions of the land-use mosaic both in Sumatra and other similar geographic regions (Gillison 2000). One of the PFAs (ct – woody plants with a photosynthetic cortex or green stem) is highly sensitive to canopy opening and increased exposure to sunlight; plants with this attribute are strongly affected by disturbance. The high correlation between ct and the termite species *Dicuspiditermes medioobscurus* (an epigeal mound builder) suggests that while there may be no direct causal relationship between the two variables, they both respond similarly to canopy exposure.

Baseline studies to calibrate candidate indicator groups against other taxa are still rare, perhaps because they are also intensely resource-demanding (Eggleton & Bignell 1995, Lawton et al. 1998). Many inventories focussed on single taxa do include some information on plants, but this is often perfunctory, merely characterizing a habitat as “primary forest”, “logged forest”, etc. (e.g. Eggleton et al. 1995) or giving basic botanical data only, such as stems per unit area, tree species per unit area, and/or woody basal area (e.g. Eggleton et al. 1996). We suggest the use of plant variables, including PFTs, may improve predictions of biodiversity. While robust correlations between certain insect taxa and plant-based variables were found within a greater number of woody vegetation types in the 16-transect study (Gillison 2000), the strong signal obtained in the present study is no doubt partly due to the steep disturbance gradient from pristine rain forest through varying land-use types to degraded grassland. But it also reflects termite response to progressive modification of habitat structure, especially loss of vegetation cover and concomitant effects on soil microclimate. The ratio of plant species richness to PFTs, which closely predicts termite species richness, represents predictable shifts in richness in plant species and PFTs and in ratio values, all decreasing monotonically from forest to degraded grassland but with an ‘intermediate disturbance’ peak in jungle rubber. Thus, the highest values (for primary forest and jungle rubber) indicate that the greatest vegetation complexity is associated with these land uses, as well as the greatest

alpha diversities of plants. But the alpha diversity responses of termites suggest that vegetation complexity represented by combinations of both taxa and functional characteristics is more influential than plant species richness alone. In this study, evidence for the prediction of termite taxa from PFAs and PFTs also provides a stronger and more readily testable hypothesis than has existed so far for the use of functional types in the prediction of taxa and in rapid biodiversity assessment. These findings support the hypothesis that there is mutual dependence between high biodiversity aboveground and belowground. We recommend the use of inventories of plant functional types in future studies that aim to elucidate the links between aboveground and belowground biodiversities.

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