Termite (Blattodea: Termitoidae) functional diversity across a forest disturbance gradient in Sabah, Malaysia

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Abstract

Tropical landscapes are suffering from widespread deforestation due to logging and conversion to agriculture. This has major effects on tropical biodiversity. In this study, changes in functional diversity are explored along a tropical forest habitat disturbance gradient in Sabah, Malaysia, for a major group of soil invertebrates, the termites. Studies of functional diversity have various advantages over traditional measures of diversity. Rather than just assessing how species assemblages change in response to habitat disturbance, functional diversity studies provide an understanding of the effects on ecosystem functioning.

Six functional traits primarily relating to diet were used to calculate three functional diversity indices (FRic, FEve and FDiv). Changes in each functional diversity index, along with changes in species richness and abundance were analysed across three habitat types (old growth, secondary forest and oil palm plantation), and their relationships with forest quality and environmental conditions also investigated.

Old growth forest was found to have a higher FRic, species richness and termite abundance than secondary forest and oil palm. Species richness and abundance also had a positive relationship with forest quality. Species richness was shown to have a unimodal relationship with air temperature.

No significant changes were found for the other two indices (FEve and FDiv). This contrasted with a similar study in ants, which found that FEve and FDiv change with habitat type but FRic and species richness do not. This is likely to be due to different environmental tolerances between the two groups.

The results suggest that termite functional diversity is at least partially reduced by habitat disturbance. Thus it is important to carefully manage habitat conversion and logging, in order to conserve termite functional diversity and preserve their important contribution to ecosystem functioning. Future studies on termite functional diversity need to sample many more species, as this will allow for a greater resolution in the statistical analysis.

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Introduction

Tropical forests and ecosystem functioning

Tropical forests are some of the most diverse ecosystems on the planet, with 15 (of the 25) major global biodiversity hotspots dominated by tropical forests (Myers *et al.,* 2000). They are home to over two-thirds of the terrestrial biodiversity on the planet (Gardner *et al.,* 2009). The processes carried out by the assemblages of species in tropical forest ecosystems, as well as the complex interactions between them make up the natural functioning of these ecosystems. The benefits thus afforded to human communities and economies are termed ecosystem services (Boyd and Banzhaf, 2007).

There are four categories of ecosystem services (Costanza *et al.,* 1997), which involve: provisioning of resources and raw materials such as food, water, timber and medicines, regulation processes including carbon sequestration and climate regulation, pollination, biological pest control, flood control, disease control, waste regulation and water quality, cultural benefits (recreational, aesthetic and spiritual) and supporting services such as soil formation, photosynthesis and nutrient cycling (Aerts and Honnay, 2011). The ecosystem services provided by tropical forests have been estimated to be worth almost 4 trillion US dollars per year to humanity (Costanza *et al.,* 1997).

High biodiversity is linked to improved and more stable ecosystem functioning (Tilman, 1997). For example, tree diversity has been shown to be a major influence on carbon storage in tropical forests (Ruiz-Jain and Potvin, 2010). However, around the world there is extensive tropical deforestation, with about half the natural tropical forests on Earth already destroyed and the land put to alternative uses (Wright 2005). Of all anthropogenic effects on tropical forest biodiversity, land-use change is thought to have the biggest impact (Sala *et al.,* 2000), and deforestation is especially detrimental to tropical forest biodiversity where species have a limited range (Morris, 2010).

Loss of tropical forest habitats

Southeast Asia is home to 11% of the remaining tropical rain forests on the planet (Koh and Wilcove, 2007), and these forests have been shown to be amongst the most diverse in the world (Myers *et al.* 2000). However, in the last two decades, they have come under unparalleled threats from the oil palm cultivation (Koh and Wilcove, 2007). Habitat destruction in Southeast Asia generally follows a disturbance gradient from old growth (primary) forest, through secondary (logged, regenerating) forest to oil palm plantations (Koh and Wilcove, 2007). Conversion of old growth and secondary forests to oil palm causes significant biodiversity losses (Koh and Wilcove, 2008, Foster *et al.,* 2011). Not only are oil palm forests home to many fewer species than both old growth and secondary forests, they are also less species rich than many other forest crop habitats (Fitzherbert *et al.,* 2008).

Termites as ecosystem engineers

Some taxa inevitably play a more important role in ecosystem functioning than others. If we are to predict how ecosystems will be affected along a habitat disturbance gradient, it is most important to assess changes in species compositions and biodiversity with respect to these taxa.

Termites (Blattodea: Termitoidae) are one such group. They are a dominant invertebrate group in tropical forests (Eggleton *et al.,* 1996, Donovan *et al.,* 2001). In lowland tropical rainforests in Sabah, Malaysia, they can make up as much as 95% of soil insect biomass (Donovan *et al.,* 2007). They are the main invertebrate decomposers in tropical forests (Eggleton and Tayasu, 2001), and, by feeding on dead plant material, play a major part in the decomposition of plants (Donovan *et al.,* 2001), and thus the cycling of nutrients and carbon (Eggleton *et al.,* 1997, Jones and Eggleton 2000), which is key for climate mediation. They also play essential roles in regulation of soil formation, structure, humification and conditioning, as well as breaking-up of organic detritus and nitrogen-fixation (Eggleton *et al.,* 1996). The structural effect of termite presence in soil dramatically increases infiltration rates of water (Lavelle *et al.,* 1993), which may have important benefits for flood prevention and soil erosion by regulating water-runoff (Lavelle *et al.,* 2006). Jouquet *et al.* (2011) review the ecosystem functions and services carried out by termites.

In their role as soil engineers, termites not only supply a number of ecosystem services themselves, but also have a positive effect on faunal and floral biodiversity and ecosystem stability (Jouquet *et al.,* 2011). This, in turn, provides a range of other ecosystem services. Thus, termites are of immense ecological value (Eggleton and Tayasu, 2001).

Habitat disturbance and termite diversity

The diversity and relative abundances of termites have been shown to decrease in response to habitat conversion along a disturbance gradient (Eggleton *et al.,* 1995, Jones *et al.,* 2003). Logging of tropical forests has been shown to decrease species richness by almost two-thirds (Donovan *et al.,* 2007). Various studies have shown that different feeding groups of termites respond differently to habitat disturbances, with soil feeders being the most at risk to the loss of primary forests (Eggleton *et al.,* 1995, Eggleton *et al.,* 1996, Eggleton *et al.,* 1997, Eggleton and Tayasu, 2001). Wood feeders are more resistant to disturbance, and in some cases are more diverse in mature secondary forest than primary growth (Eggleton *et al.,* 1997).

The importance of ecosystem functions provided by termites means that it is important to assess how habitat loss affects termite diversity. Habitat loss is expected to decrease termite diversity, leading to negative effects on ecosystem functioning. Termite diversity has been studied from various angles, the traditional method being to measure species richness. However, there is not necessarily a direct correlation between species richness and

ecosystem functioning. It is the array of functional traits carried by a range of species that is the principal mediator (Hooper *et al.,* 2005, Villéger *et al.,* 2008). For this reason, over the last decade or so, another relevant measure of biodiversity has gained importance, functional diversity. Functional diversity refers to the value and range of traits in a group of organisms in an ecosystem (Diaz and Cabido, 2001), and is an important driver of ecosystem function (Villéger *et al.,* 2008).

Global termite diversity has been studied with respect to the classification of species into functional groups (Eggleton and Tayasu, 2001). Donovan's 'feeding groups' (Donovan *et al.,* 2001) gathers species into five groups according to their food substrates (see **Table 1**). Termite mandibles have various adaptations to diet, and can be split into two groups: grinding and pounding (Eggleton, 2011). In the grinding type, the teeth are short and the distance between the apical tooth and first marginal tooth are also short. These teeth are for tearing wood fibres. In addition, the molar plates are extensively ridged, which aids with grinding up wood and other dead plant material. In the pounding type, the distance between the apical and first marginal tooth is long, as is the length of the apical tooth. This is for carving out lumps of soil. The smooth molar plates of these mandibles are convex and concave (right and left mandibles respectively), and fit into each other to pound soil and humus (Eggleton, 2011).

Table 1. *Termite functional group definitions from Donovan* et al. *(2001).*

Functional group definitions
Group I: Feed on dead wood and/or grass; with flagellate protists in their guts
Group II: Feed on grass, dead wood and leaf litter
Group IIF: Feed on grass, dead wood and leaf litter, with the help of fungal mutualists grown inside the nest ("Fungus-growing termites")
Group III: Feed in the organically rich upper soil layers ("Humus feeders")
Group IV: Feed on organically very poor soil ("True soil feeders")

Past studies into functional diversity have often used functional group richness as a proxy for functional diversity. There are a few drawbacks associated with such an approach, as Villéger *et al.* (2008) point out. First, information is lost when species with continuous traits are placed into discrete groups. Second, some species are more abundant than others, and will this be more influential on the function of an ecosystem. However, many studies using functional group richness ignore abundance. Finally, differing conclusions may arise about functional diversity when different functional group classifications are used.

Functional diversity indices

To overcome these issues, Villéger *et al.* (2008) advocate the use of quantitative trait values and continuous measures of functional diversity. They argue that these measures of functional diversity should meet a set of criteria, including being able to deal with multiple traits, taking abundance data into account, and evaluating all aspects of functional diversity.

They propose the use of three functional diversity indices (originally proposed by Mason *et al.,* 2005), which alone do not satisfy all these criteria, but meet the criteria when viewed together. These indices are functional richness, functional evenness and functional divergence (FRic, FEve, and FDiv, Villéger *et al.,* 2008). Functional richness is a measure of the total volume of trait space occupied by a group of species. Functional evenness measures the regularity of the distribution of species functional traits, with respect to their abundance. Functional divergence measures how species abundance is spread within the trait space filled by the group of species.

Aim of this investigation

Termite sampling was part of a study of co-variation and trophic interactions in ant and termite assemblages along a tropical forest disturbance gradient in Sabah, Malaysia by Luke (2010), which found that genus richness and abundance of termites decreased with increasing habitat disturbance, with soil feeders being more affected than wood feeders.

As termites are such an important taxon in tropical forest ecosystems, it is important to quantify how their functional diversity changes with habitat disturbance, as it is this that influences ecosystem functioning and services. In this study, the functional diversity of termites is assessed along a habitat disturbance gradient, from old growth forests, through secondary regenerating forest, to oil palm plantation. The three indices proposed by Villéger *et al.* (2008) are used, as they allow for the analysis of functional diversity with respect to multiple continuous traits (rather than relying on functional group richness as a proxy). This study also aims to compare the findings for termites, with the findings from a similar functional diversity study by Bishop, (2012) on the ant data collected by Luke (2010).

Functional diversity correlates with species richness, (Villéger *et al.,* 2008). Therefore functional richness is expected to decrease along the disturbance gradient, as this is the pattern followed by species richness (Eggleton *et al.,* 1995, Jones *et al.,* 2003, Donovan *et al.,* 2007). The responses of functional evenness and divergence are less easy to forecast. They are independent of species richness, and as the indices are relatively new there is not much previous work (none on termites) to make predictions from (see Villéger *et al.,* 2010, and Pakeman, 2011 for studies using these indices and yielding differing results, on tropical fish and temperate plant communities, respectively).

Materials and methods
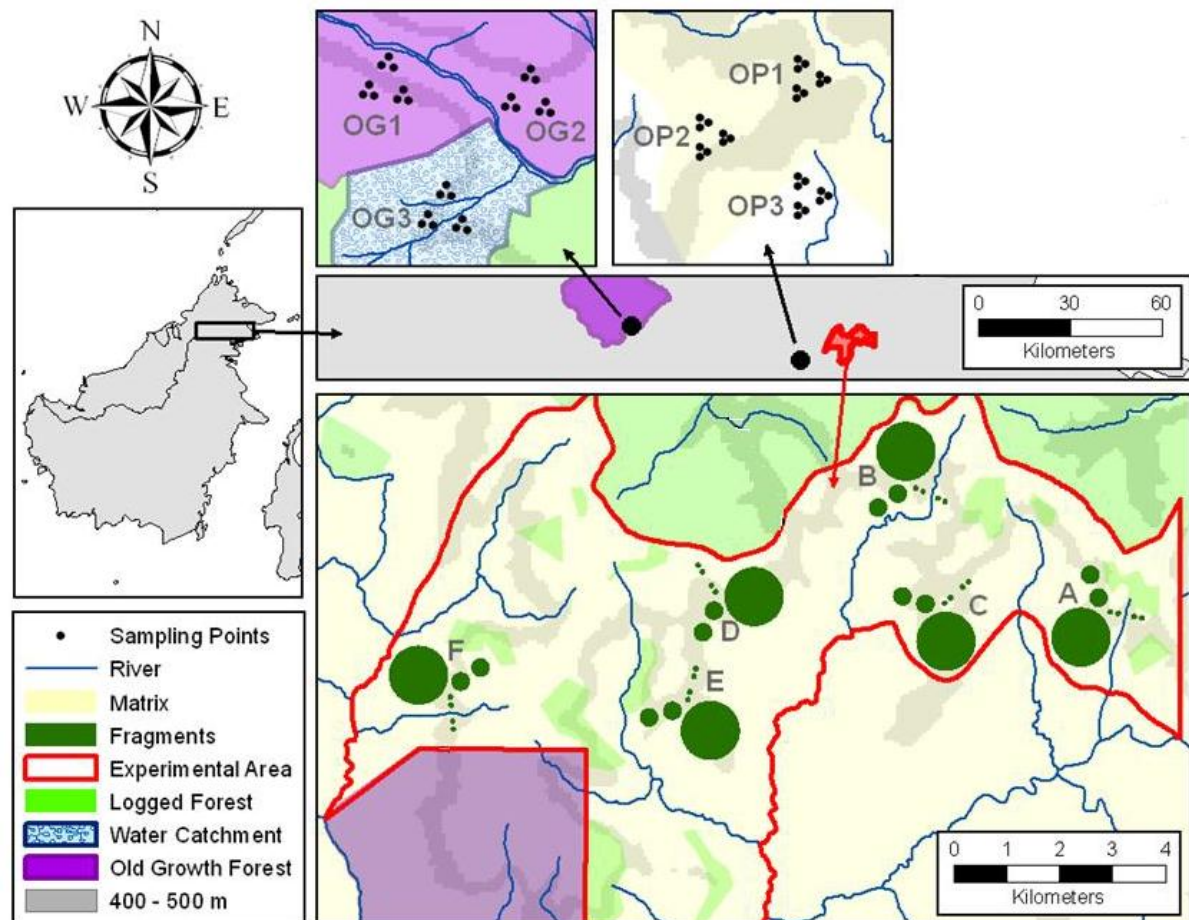
Study sites

The sampling for this study took place in Sabah, Malaysia, as part of the Stability of Altered Ecosystems (SAFE) project: an investigation into the effects of habitat conversion and fragmentation on lowland tropical forest ecosystems in Borneo (see Ewers *et al.,* 2011). Sampling of termite species was carried out in parallel to ant sampling, as part of an MSc

project into the composition of ant and termite assemblages along a disturbance gradient by Luke (2010).

Survey points

The SAFE project survey points form a triangular fractal arrangement, spanning the old growth, secondary forest and oil palm sites (**Figs. 1** and **2.**). First-order triangular networks are centred on the vertices of second-order equilateral triangles (of length 178 m), which are, in a similar fashion, placed within third and fourth-order triangles (Ewers *et al.,* 2011). In this study a total of 59 second-order survey points were sampled. These were split into 18 old growth (OG), 32 secondary forest (SF) and 9 oil palm (OP) survey points. SF had the highest number of survey points in order to capture the high-expected level of heterogeneity. OP had the fewest to reflect the homogeneous nature of the habitat.

Figure 1. *Location of study sites in Borneo, from Luke (2010). Old growth forest (OG) and oil palm (OP) second-order survey points are shown above, and fragments of secondary forest below. In this study, the second-order survey points at OG1, OG2 and OP1 were used, as well as second-order survey points from secondary forest fragments C and F (**Fig. 2.**).*

Old growth

Old growth forest data was collected in the Maliau Basin Conservation Area. These sites are protected and have never been subject to commercial logging. Some areas have been lightly

logged to build the field centre but this is not judged to have affected forest quality or species composition substantially (Ewers *et al.,* 2011).

Secondary forest

Secondary forest data was collected from sites in Benta Wawasan. These sites have undergone two rounds of selective logging.

Oil palm

Oil palm data was collected from a plantation in Benta Wawasan. The plantation is a monoculture of *Elaeis guineensis* (African oil palm).
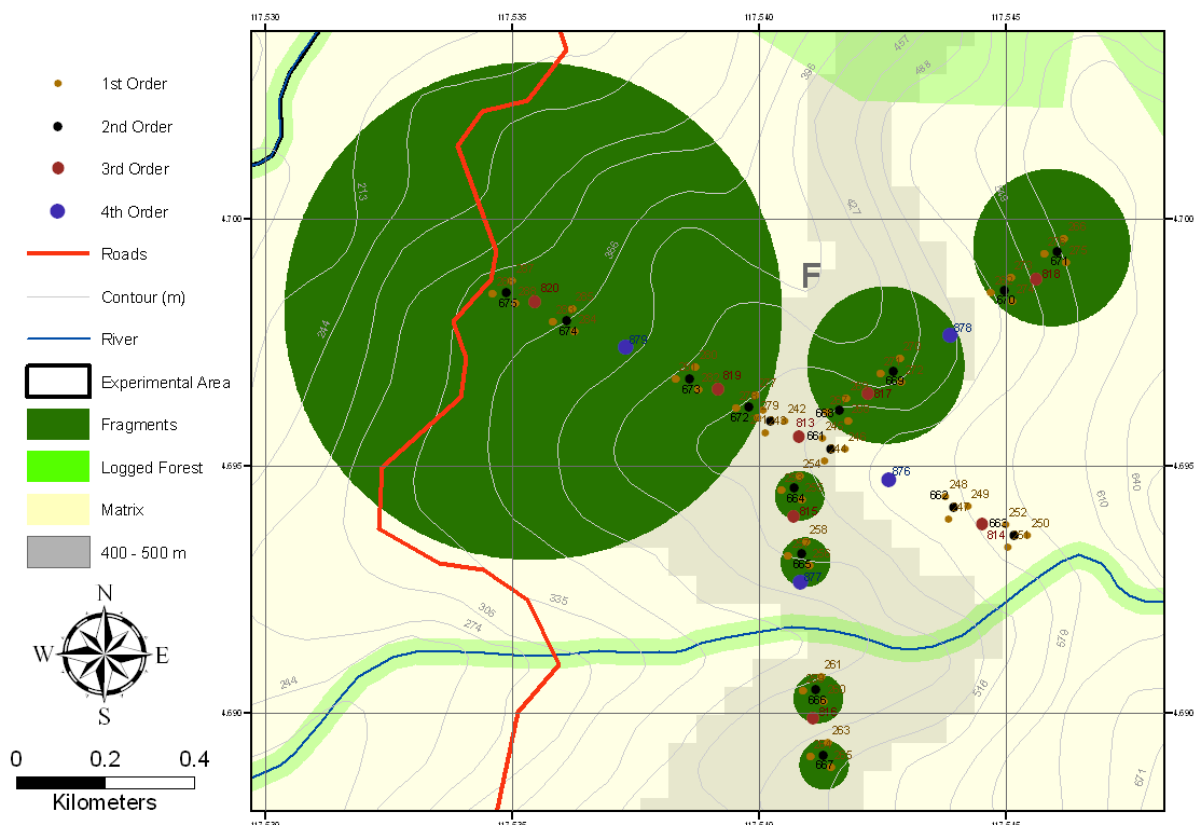
Figure 2. *Detailed locations of 16 second-order survey points (black) in secondary forest fragment F, from Luke (2010). The 16 points in fragment C are arranged similarly.*

Termite sampling

Data collection was carried out in April and May 2010. A quadrat of 4 x 4m was centred on each second order survey point (located using GPS), with its top edge pointing east-west. Where it was impossible to centre the quadrat directly on the survey point due to paths or obstacles (fallen trees or particularly dense vegetation), the quadrat was placed as close to the survey point as possible. Soil pits, of dimension 12 x 12cm wide x 10cm deep, were dug in the middle of each square metre of the quadrat, making a total of 16. The soil extracted from these pits was searched for termites for a total of 10 person-minutes (usually two people for 5mins). Whenever any large wood (diameter wider than 5cm, up to 2m high) was

found within the sample site, bark was removed and any holes searched, once per metre of wood (following Davies, Hernandez *et al.,* 2003). All termites found were stored in 80% ethanol (Luke, 2010).

Termite identification

Termite soldier keys (Thapa, 1982, Gathorne-Hardy, 2004) were used to identify soldiers (along with the workers with which they were sampled) to species level. The Natural History Museum termite collection in London was also used as a reference. Where these resources were not enough for species level identification, species were assigned to morphospecies. In addition, where individuals of the same genus differed markedly in their functional traits, these were separated into morphospecies. This tactic reduced the risk of losing diversity information caused by lumping two functionally different taxa together. Morphospecies are henceforth referred to as species for simplicity.

**Trait measurement and abundance data**

To build a matrix of functional trait data, six traits (five quantitative and one categorical) were chosen to represent differences between species. These traits were:

1. Head width
2. Hind femur length
3. Distance between the apical tooth and first marginal tooth
4. Distance between the first and second marginal teeth
5. Distance between the second marginal tooth and molar plate
6. Extent of ridging on the molar plate

Traits were only measured for workers, because it is they who are responsible for foraging behaviour, whereas traits in soldiers and reproductives will be linked to defensive and sexual behaviour respectively (see Eggleton, 2011). Measurements were taken using a microscope graticule at 50 times magnification. A maximum of 6 individuals were measured per species, with an average of 4.86 individuals per species.

Head width was measured at its maximum distance, and was used as a surrogate measurement for body size. All other lengths were standardised by dividing by this measurement. This prevented the functional analysis being biased towards size, due to the overestimation of its importance. Hind femur length (measured on the right hand side) to represents leg length. Leg length can be expected to vary with diet, as it will effect movement. For example, longer legs can increase the speed of an organism, but cost more to make. As the ground becomes too uneven, longer legs lose their advantages over shorter legs (the size-grain hypothesis, see Kaspari and Weiser, 1999). This will affect foraging efficiency, and femur length measurements thus aim to capture differences in foraging behaviour.

As functional diversity in termites is believed to be driven by diet differences along a humification gradient (Donovan *et al.,* 2001), traits linked to diet (e.g. mandible or gut traits) should form the main basis of a functional analysis. Consequently, four out of the six chosen traits were mandibular. Analysis of gut traits would clearly have been a useful exercise in this regard, but was beyond the scope of this investigation, and also much more difficult to standardise. All mandibular traits were measured on the right mandible. Distances between teeth were measured between the points of the teeth. The distance between the second marginal tooth and the molar plate was measured from the tip of the second marginal tooth to the point where the molar plate begins to plateau. The extent of ridging on the molar plate was assessed qualitatively on a scale of 0 to 2, where 0 = 'no ridging observed', 1 = 'ridges present,' and 2 = 'extensive ridging.'
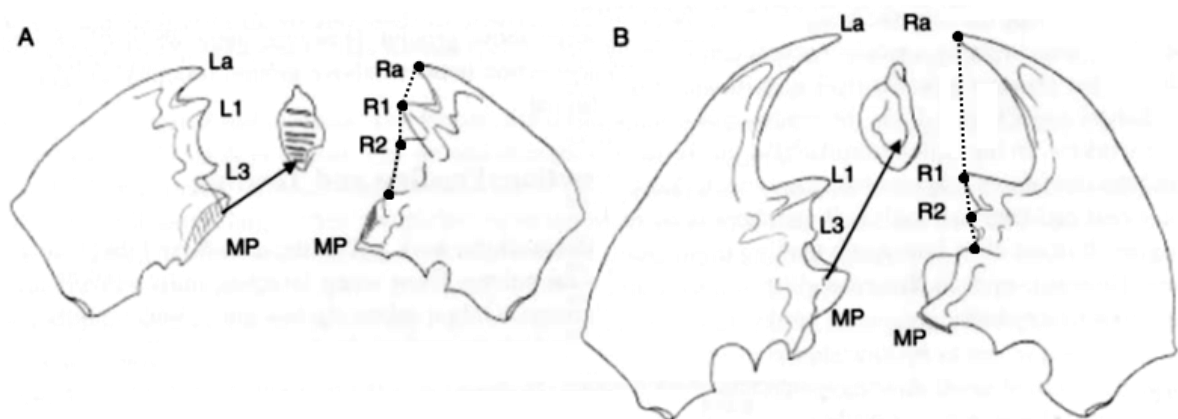
Figure 3. *Mandibles of wood feeding* Microcerotermes strunckii *(A) and soil feeding* Megagnathotermes notandus *(B) workers. Left (La, L1 and L2) and right (Ra, R1 and R2) apical, first marginal and second marginal teeth, and molar plates (MP) are labelled. Dotted lines illustrate measurements made. Adapted from Eggleton (2011).*

Given that workers were the only individuals measured, they alone were included in abundance data. This gave a total of 759 individuals, representing 36 species (and morphospecies).

Forest quality data and environment data

Forest quality data at each survey point was assessed using the SAFE project scale, see **Table 2.**

At each survey point various environmental conditions and measurements of vegetation cover were recorded (hereafter referred to as environment data). An electronic meter was hung from vegetation at the centre of the quadrat to measure air temperature and humidity. Canopy openness was measured using a spherical densiometer (the number of open quarter squares was counted to the north, east, south and west of the survey point). The percentage cover of leaf litter, bare ground, low vegetation and trees was also recorded at each survey point.

Table 2. *SAFE project standardised forest quality scale.*

Forest type	Forest quality	Description of vegetation around sample point
0	Oil palm	Oil palm
1	Very poor	No trees - open canopy with ginger/vines or low scrub
2	Poor	Open with occasional small trees over ginger/vines
3	OK	Small trees fairly abundant/canopy partially closed
4	Good	Lots of trees, some large, canopy closed
5	Very good	Closed canopy with large trees, no logging

Data analysis

The standardized trait measurements were averaged for each species, and from these figures a data frame was constructed. Likewise, a data frame of species abundances at each site was also constructed. The fractal nature of the sampling meant that habitats could be analysed at various levels. In this case, the sites analysed were of roughly equally sized sampling areas. OGa, OGb and OP all contain 9 second-order survey points, with SFa, SFb, SFc and SFd containing 8. Analysing the abundance at a lower level is impossible because some of the survey points had very low species richness and, in order for the functional diversity indices of Villéger et al. (2008) to work, the number of species found at each site cannot be much lower than the number of traits analysed. Analysing the abundance at a higher level would have given uneven sized sites, thus overestimating functional diversity in SF and underestimating in OP (which had the most and fewest numbers of survey points respectively). As a result this was the only level of resolution possible that gave roughly equal sized sites and allowed the functional diversity indices to work.

The trait and abundance data matrices were analysed using a principal coordinates analysis (PCoA), to establish the axes of variation within the data set. Where there are more axes of variation than species, a subset of these axes are taken, (with a consequent loss of information). The quality of the reduced space representation indicates how much information is lost, and is interpreted like a R^2-like ratio; the higher the value (between 0 and 1) the lower the information loss.

The PcoA axes of variation (or the subset) are then used to plot the data in *T*-dimensional space (where *T* is the number of traits – 6). This allows for the calculation of the functional diversity indices of Villéger *et al.* (2008) for each site. The functional diversity indices were then compared for each habitat type (OG, SF or OP) using analysis of variance (ANOVA) tests.

The functional richness index (FRic) measures the volume of trait space occupied by a group of species. In a single-trait analysis, this refers to the difference between the maximum and minimum values of the trait. In a two-trait analysis, functional richness is the area contained within the perimeter joining the most extreme trait values of the group of species. For a multi-trait analysis, functional richness estimates the *T*-dimensional volume occupied by the group, where *T* is the number of traits analysed. This is referred to as the minimum convex

hull (Cornwell *et al.,* 2006). Any species with less extreme trait values than others in the group will fall within the convex hull, and will not count towards functional richness of the community. FRic is not weighted using abundance data, so the functional richness value will not change if a species' abundance changes (unless a species becomes absent, in which case it no longer influences the functional richness index).

The functional evenness index (FEve) measures the regularity of the distribution of species functional traits, with respect to their abundance. This is calculated using the minimum spanning tree that links all trait values in T-dimensions, which is weighted using species abundance data. FEve will increase as species abundances become more evenly spread, or when functional distances between species become more uniform.

The functional divergence index (FDiv) measures how species abundance is spread within the T-dimensional trait space filled by the group of species. It describes how species trait distances diverge from the centre of the gravity of the trait space. This index is also weighted by abundance. When highly abundant species have extreme trait values compared to species with lower abundances, FDiv is high.

Both FEve and FDiv are independent of species richness, and both range between 0 and 1. FRic is not independent of species richness, and has no upper bound as it measures total trait space.

In addition to functional diversity analyses, species richness and abundances were compared at each site, using generalised linear models. In these cases the individual second-order survey points were compared across habitats (rather than as groups of 8 or 9 survey points) as this did not involve calculation of the functional indices, and thus it did not matter if some survey points had low species richness.

Linear regressions were used to determine how the results for each functional index, along with the species richness and abundances vary with forest quality (as measured by the SAFE project standardised scale), and how they vary with the environment data.

If the species richness seemed to have an optimum value, when plotted against the environmental variables, the apparent unimodal relationship was explored further. Jamil and ter Braak (2013) show that generalised linear mixed models (GLMMs) can be used to determine whether a data set has a unimodal relationship with environmental variables, rather than a straight-line relationship. This is tested statistically by fitting two GLMMs, the null model stating that the relationship is linear and the alternative model stating that the species richness depends quadratically on the environmental variable. There is evidence of a unimodal response if an ANOVA test comparing the fit of the GLMMs states that the quadratic model gives a significantly better fit. As this method only uses presence/absence data and not abundance data, it was only suitable for analysing unimodal relationships of

species richness (and not abundance, or the functional diversity indices). Jamil and ter Braak (2013) explain the method in more detail.

All statistical analysis was performed using the software R 2.13.1 (R Development Core Team, 2011). The functional indices for each site were calculated using the FD package in R (Laliberté and Legendre, 2010, Laliberté and Shipley, 2011). Where the results of ANOVAs were significant, Tukey's Honest Significant Differences were used to determine the cause of the significance. All GLMs used Poisson errors (as no data was normally distributed) except when data was over-dispersed, in which case quasi-Poisson distribution was used.

Results

Functional diversity indices

ANOVAs of mean functional richness between habitats were very significant (F = 36.1, p < 0.01). Tukey's HSD test indicates that old growth had significantly higher functional richness than both secondary forest (p < 0.01) and oil palm (p < 0.05). However, no significant differences in FRic were found between SF and OP (p = 0.172) (**Fig. 4.A.**).
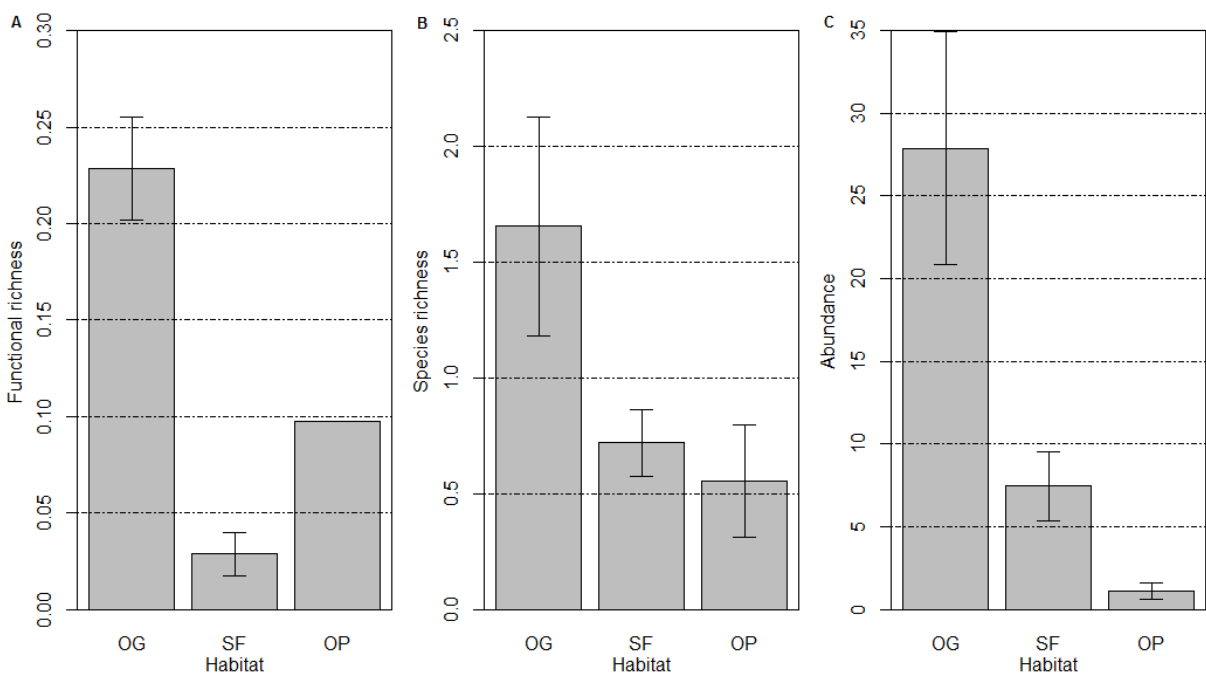
Figure 4.A. Mean termite functional richness per site (groups of 8 or 9 survey points) for each habitat type (N = 2 sites for OG, 4 for SF and 1 for OP). B. Mean termite species richness per 2nd order survey point for each habitat (N = 18 survey points for OG, 32 for SF and 9 for OP). C. Mean termite abundance per 2nd order survey point for each habitat (N = same as B). In each case, values for OG are significantly higher than SF and OP, and there is no significant difference between SF and OP. Error bars represent ± 1 standard error of the mean.

ANOVAs of mean functional evenness and divergence showed no significant differences between habitats (F = 1.45, p = 0.336, and F = 1.12, p = 0.411, respectively).

The quality of the reduced space representation (as a result of there being less species in some sites than axes of variance in the PCoA) is 0.319.

Species richness and abundance

Generalised linear models (GLMs) of species richness across habitat types show a very significant difference between OG and SF (z = -5.12, p < 0.001) and between OG and OP (z = -2.91, p < 0.01), with species richness higher in OG in both cases. There was no significant difference between OP and SF (z = 0.00, p = 1.00) (**Fig. 4.B.**).

GLMs of abundance across habitat types also show a very significant difference between OG and SF (t = -3.73, p < 0.001) and a significant difference between OG and OP (t = -2.25, p < 0.05), with species richness higher in OG in both cases. There was no significant difference between OP and SF (t = 1.31, p = 0.195) (**Fig. 4.C.**). Because of over-dispersion, GLMs of abundance data used quasi-Poisson distribution.

**Functional diversity vs. forest quality**

There is an apparent trend towards an increase in FRic with increasing forest quality, but linear regression analysis demonstrated that this relationship was not significant (t = 1.68, p = 0.155). Likewise linear regression revealed that the apparent relationship between decreasing FEve and increasing forest quality was non-significant, (t = -1.02, p = 0.356). There was no demonstrable relationship between FDiv and forest quality (t = 0.005, p = 0.997) (**Fig. 5.**).
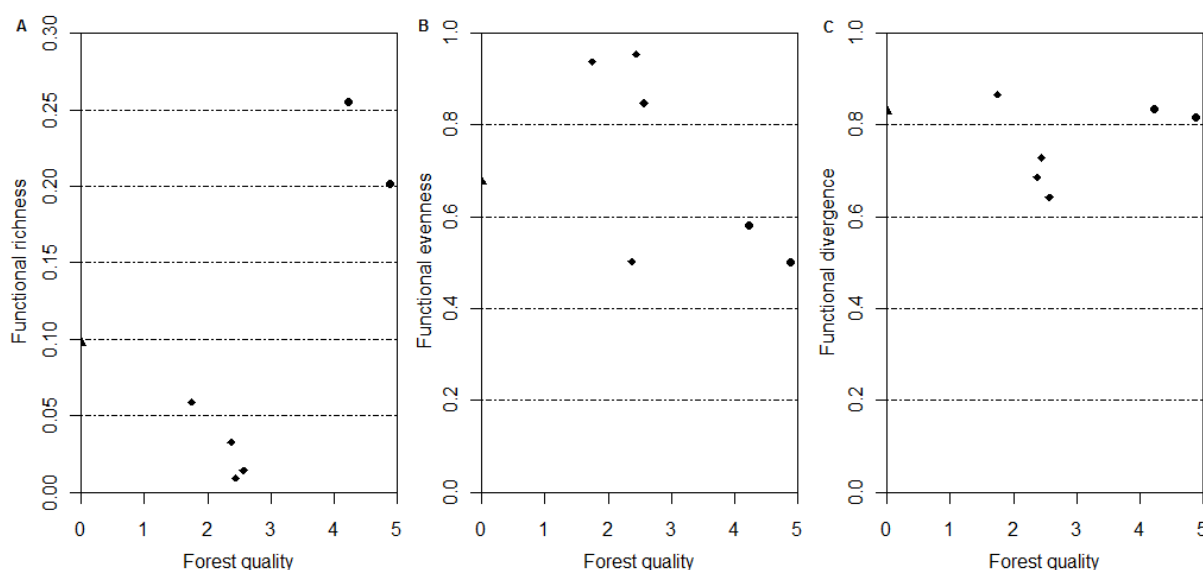
Figure 5. *The relationship between forest quality and functional richness (**A**), forest quality and functional evenness (**B**), and forest quality and functional divergence (**C**), for each site (groups of survey points).* ● *= OG,* ◆ *= SF and* ▲ *= OP sites. None of these relationships are statistically significant. N = 2 sites for OG, 4 for SF and 1 for OP for each graph.*

Species richness and abundance, vs. forest quality

Linear regression showed a very significant positive relationship between species richness and forest quality (t = 4.27, p < 0.001). A very significant positive relationship was also found between abundance of termites and forest quality (t = 3.93, p < 0.001) (**Fig. 6.**).
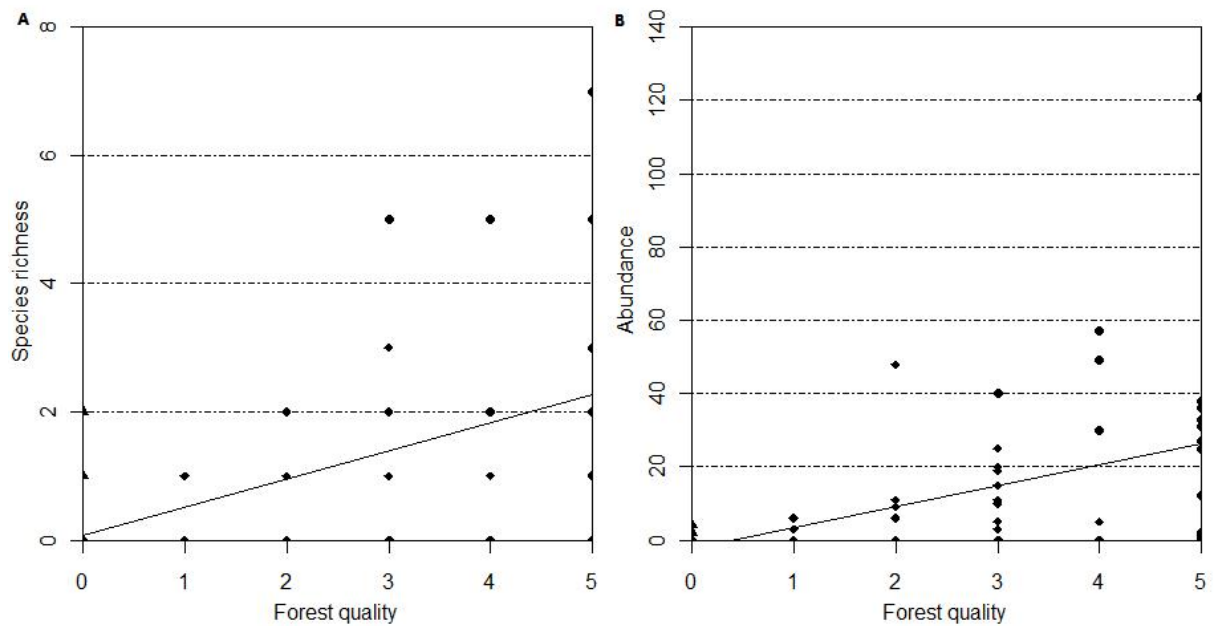
Figure 6. The relationship between forest quality and species richness (**A**), and forest quality and abundance (**B**), 2nd order survey point for each habitat type. ● = OG, ◆ = SF and ▲ = OP sites. Both these relationships are statistically very significant, and are illustrated with linear regression lines. N = 18 survey points for OG, 32 for SF and 9 for OP for both graphs.

Functional diversity vs. environment data

Linear regression analysis exploring the relationship between the environment and the functional diversity indices found no significant correlation, see **Table 3.**

Table 3. Summary of the regression analyses of the relationship between the environment data, and the functional diversity indices, along with species richness (SR) and abundance.

	FRic		FEve		FDiv		SR		Abundance	
	t-value	p-value	t-value	p-value	t-value	p-value	t-value	p-value	t-value	p-value
Air temperature	-0.412	0.697	0.311	0.768	0.790	0.465	-2.11	0.0397 *	-2.07	0.0427 *
Humidity	0.362	0.732	-0.120	0.909	-0.740	0.493	1.40	0.166	1.43	0.158
Canopy openness	1.54	0.185	-0.804	0.458	1.71	0.147	-0.0890	0.929	-0.100	0.921
Leaf litter	0.595	0.577	-0.400	0.706	-0.820	0.450	1.51	0.136	1.58	0.119
Bare ground	-0.802	0.459	0.294	0.780	0.040	0.969	-1.24	0.220	-1.38	0.172
Low vegetation	-1.16	0.300	1.72	0.146	-0.301	0.776	-2.14	0.0370 *	-1.23	0.2230
Trees	0.292	0.782	-0.423	0.690	0.804	0.458	0.691	0.492	-0.0400	0.968

* = significant at p<0.05

Species richness and abundance, vs. environment data

A significant negative relationship was found between air temperature and both species richness and abundance (p < 0.05, t = -2.11, and p < 0.05, t = -2.07, respectively). A significant negative relationship was also found between low vegetation cover and species richness (p < 0.05, t = -2.14). These results are illustrated by **Fig. 7.** No other significant relationships were found between the environment data and species richness or abundance, see **Table 3.**
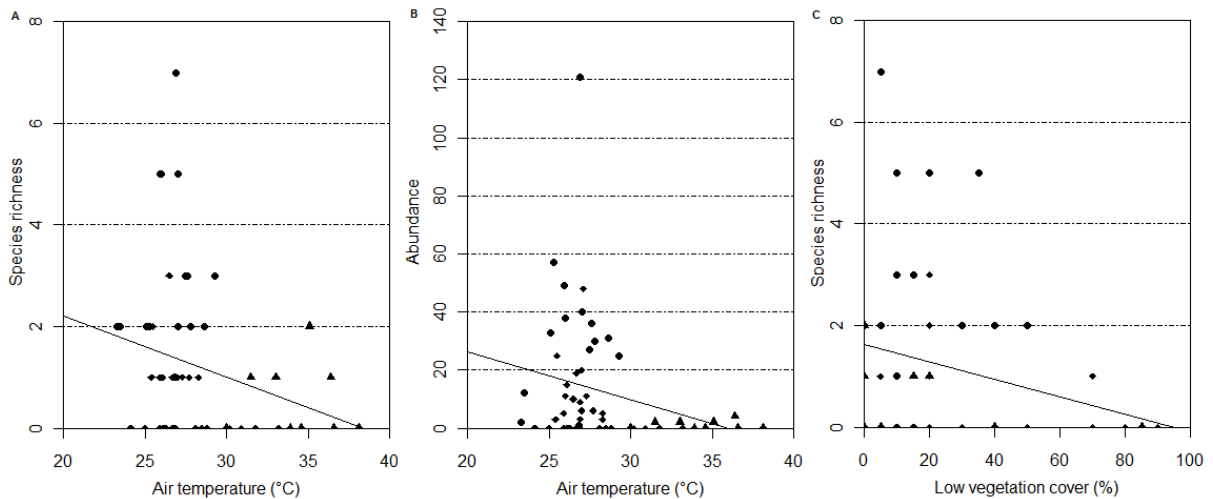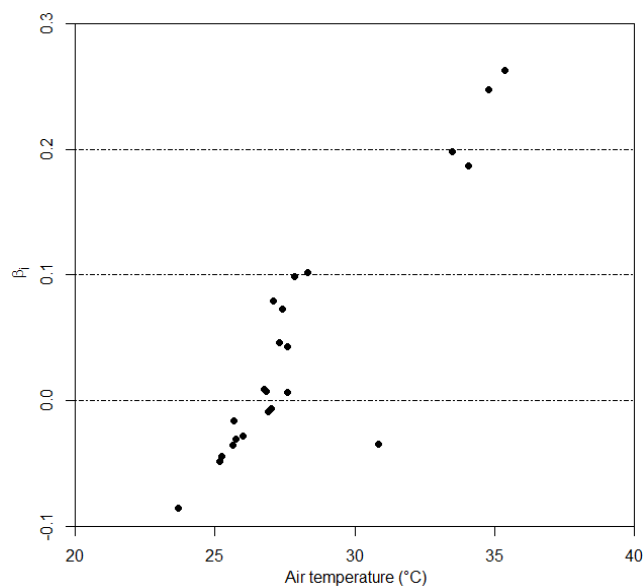
Figure 7. *The relationship between air temperature and species richness (**A**), air temperature and abundance (**B**), and percentage cover of low vegetation and species richness (**C**), 2nd order survey point for each habitat type. ● = OG, ◆ = SF and ▲ = OP sites. All of these statistically significant relationships are illustrated with linear regression lines. N = 18 survey points for OG, 32 for SF and 9 for OP for each graph.*

Unimodal relationships

Regression analysis showed a negative linear relationship between air temperature and both species richness and abundance, as illustrated by the regression lines in **Figs. 7. A** and **B**. However, the spread of the points in both plots suggest that species richness and abundance both have an optimum temperature of around 27°C. When this apparent unimodal relationship was investigated for species richness, an ANOVA test showed the alternative quadratic GLMM to fit the data significantly better than the linear null GLMM (F = 102.54, p <0.001) (**Fig. 8.**).

***Figure 8.*** *The unimodal relationship between species richness and air temperature. The y axis ($β_i$) represents species richness decreasing either side of the optimum temperature. Maximum species richness ($β_i$ = 0.0) is at approximately 27°C.The apparent linear relationship between air temperature and $β_i$ lends support to the hypothesis that species richness has a unimodal relationship with air temperature.*

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As already explained, this method is not suitable for analysing abundance data, so the apparent unimodal relationship between abundance and air temperature is not explored.

Relationship between functional richness and species richness

Linear regression analysis also showed a very significant positive relationship between species richness and FRic ($p < 0.01$, $t = 6.00$), see **Fig. 9.**
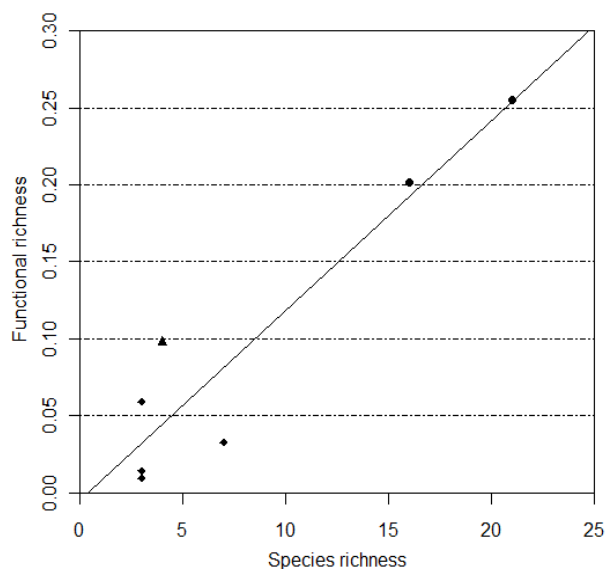
Figure 9. *The significant positive relationship between species richness and FRic for each site. ● = OG, ◆ = SF and ▲ = OP sites.*

Discussion

Effects of habitat disturbance on termite diversity

The above results illustrate various effects of habitat disturbance on termite diversity in Sabah, Malaysia. First of all, functional richness is shown to be significantly higher in old growth forest than in secondary forests or in oil palm plantation. No significant difference was found between secondary forest and oil palm. Such findings are unsurprising, as species richness follows the same pattern (i.e. significantly higher in OG than in other habitats, no difference between SF and OP), and functional richness and species richness have been shown to correlate (Villéger *et al.,* 2008, and see **Fig. 9**). Seeing as species richness has been shown to decrease with habitat disturbance (Eggleton *et al.,* 1995, Jones *et al.,* 2003, Donovan *et al.,* 2007), it is not surprising that these results also show functional richness to decrease.

Whereas one would expect species richness and functional richness to be significantly higher in secondary forest than in oil palm, this was not found to be the case (see **Fig. 4. A** and **B.**). In fact, functional richness was slightly (but not significantly) lower in secondary forest. Species richness was not significantly higher in secondary forest than in oil palm. There are a

couple of possible explanations for this. Firstly, it could be that the forest quality in secondary forest is not much better than in oil palm plantation (given that it has undergone two rounds of logging). This is supported by the fact that when species richness is plotted against SAFE forest quality rather than habitat type, a significant positive relationship is found (see **Fig. 6.A**). A positive, but non-significant trend is also found between functional richness and forest quality (**Fig. 5.A**).

Another reason for the lack of significance could be due to the fact that there are not enough replicates for the analysis of functional diversity (e.g. only one replicate for oil palm). This will be explored further in a later section, but it could explain why the regression analysis of species richness against forest quality is significant, whereas functional richness against quality is not. Species richness is analysed at second-order survey point level giving a total of 59 values (18 OG, 32 SF and 9 OP), whereas functional richness was analysed by grouping 8 or 9 neighbouring survey points into 7 sites (2 OG, 4 SF and 1 OP). Such a major loss of information makes it difficult for a comparison to achieve statistical significance. This major loss of information is represented by such a low value for the quality of the reduced space representation (0.319). Furthermore, the oil palm site contained 9 survey points, whereas the secondary forest sites contained 8, meaning there is a slight bias towards higher functional richness oil palm over secondary forest.

Of course, it is also possible, that despite having higher scores on the SAFE project forest quality scale, secondary forest is in fact no better a habitat for many termite species than oil palm. For example, logging disrupts the structured soils required by termite species (Donovan *et al.,* 2007). Disturbance causes lasting damage to a forest, and logged secondary forests may not attain the same levels of diversity as old growth (Morris, 2010). For these reasons, secondary forest will have to undergo a long period of regeneration before disturbance begins to lose its effect. This may explain why there is not much difference in species richness or functional richness between the secondary forest and oil palm sites.

In addition, despite having a wider plant diversity than oil palm, secondary forest may have a more open canopy than some oil palm sites. Canopy is important in buffering many climate conditions such as temperature, sunlight, wind and humidity (Szarzynski and Anhuf, 2001), and thus isolating ground level from extreme conditions. As canopy cover decreases, termite species become more exposed to these extreme conditions (Hassal *et al.,* 2006). Disturbed areas with near-complete canopy have been shown to have similar diversity to primary growth (Eggleton *et al.,* 2002). To summarise, where oil palm sites have a more complete canopy than secondary forest sites, a higher termite diversity might be expected. Having said that, this study did not find any correlation between canopy openness and any of the functional diversity indices, species or abundance.

A significant negative correlation was found between percentage of low vegetation cover and species richness. Low vegetation cover is higher in oil palm and secondary forest sites

than in old growth sites. This is probably due two smaller opportunist plant species taking advantage of the removal of tall dominant tree species, a well-documented phenomenon (Denslow, 1980). Thus the negative correlation observed here is probably not because of some detrimental effect that low vegetation has on species richness, but more likely a product of the relationship that both these variables have with habitat disturbance. The significant result from this regression analysis should be viewed with caution, as it was run alongside 34 other regression analyses, only three of which were significant, and this small degree of significance may have occurred by chance. This relationship should be explored further in future studies.

In contrast to functional richness and species richness, the other two functional diversity indices show no significant relationship with habitat disturbance at all. No significant difference was found in functional evenness between old growth, secondary forest or oil palm. The same was found when the functional divergence results were analysed. Furthermore, the slight negative relationship found between functional evenness and forest quality was not significant, and no significant relationship was found between functional divergence and forest quality (see **Fig. 5.B** and **C**). Finally, neither of these indices showed any significant relationship with any environmental variables.

Functional richness describes the range of traits exhibited by the assemblage of species. Functional evenness illustrates how evenly this range of traits is spread between species abundances. Functional divergence determines whether abundant or rare species have the most extreme traits values. Functional richness decreases in response to logging and conversion to oil palm, because the reduced species richness results in a reduced range of traits. In contrast, functional evenness was (non-significantly) lowest in old growth sites, potentially due to the trait space being unbalanced towards soil feeding traits. By being especially detrimental to soil feeders (Eggleton *et al.,* 1997 and Eggleton *et al.,* 2002), habitat disturbance may serve to balance the relative spread of wood to soil feeding traits. This would explain why functional evenness and functional richness are affected differently by habitat disturbance. Functional divergence seems almost unaffected by habitat disturbance, suggesting that the traits of abundant species get no more or less extreme in response to logging or conversion of old growth to oil palm. At all sites, functional divergence was relatively high (much nearer to 1 than 0), suggesting that the more abundant species of termite are those with the more extreme traits.

Comparison with ants

Bishop (2012) used a very similar methodology to assess the effect of habitat disturbance on functional diversity in ants. The ants were collected at the same time, in the same plots, and by exactly the same method as the termites in this study. The functional diversity indices were calculated from five functional traits, for 836 individuals from 260 species.

The effects of habitat disturbance on functional diversity in ants contrast with the results for termites found in this study. Bishop (2012) found that functional richness and species richness were not significantly affected by habitat disturbance, whereas functional evenness and functional divergence were. Oil palm had significantly lower functional evenness than both old growth and secondary forest. Old growth had the highest functional evenness (although this was not significantly higher than secondary forest). Old growth also had highest functional divergence, significantly higher than secondary forest. Oil palm was intermediate with respect to functional divergence, being neither significantly different from secondary forest nor old growth.

Differing results for ants and termites were also found in the original analysis (Luke 2010) of the data. Ant genus richness was highest in secondary forest, and high in oil palm, whereas termite genus richness was negatively affected by conversion from old growth to secondary forest or oil palm.

Thus the results of this study, combined with those of Luke (2010) and Bishop (2012), suggest that ants are more resistant to habitat disturbance in tropical forests than termites, with respect to genus richness, species richness and functional richness. A likely reason for this is that ants and termites are affected by different conditions. The most important stress factor in ants is low temperature (Anderson, 1995), which can be influenced by vegetation structure. In addition, high leaf litter levels are also an impediment for ants as they slow down movement, and thus foraging speed (Anderson, 1995). Disturbed forests are less shady, and have less leaf litter than old growth forests, providing favourable conditions for ant species. However, full habitat clearing has been shown to reduce ant species richness much more than partial clearing (Watt *et al.,* 2002), suggesting an intermediate disturbance level is the optimum condition for ant species. This would explain why ants were found to have higher genus richness (Luke, 2010) in secondary forest than in the other habitats.

In contrast, the main stress factors in termites are high temperatures, low humidity and poor soil structure. High temperatures and low humidity can cause desiccation in termites. This is an especially strong stress in soil feeding termites, whose energy-poor diet does not allow them to form the high levels of sclerotisation required to withstand desiccation (Eggleton *et al.,* 1997 and Eggleton *et al.,* 2002). Well-structured soils are also particularly important for soil feeders, which rely on organic materials in the soil for food (Eggleton *et al.,* 1997). Old growth forest provides more shade, thus reducing risk of desiccation, and contains more leaf litter, which leads to a higher organic content in the soil. Buffered, predictable conditions are important for termites, and termites in old growth forests are less subject to fluctuations in temperature and humidity, and more protected from rainstorms (Davies, Eggleton *et al.,* 2003). On this basis old growth should provide a better environment for termites than either secondary growth of oil palm. In sum, habitat conversion will have a much more negative effect on termite species than on ant species, which may benefit from disturbance to a degree.

The results of this study only partially support the above conjecture. Old growth was found to have a higher termite functional richness, species richness, and abundance than the other habitat types.

Furthermore, there was a significant negative correlation between temperature and both species richness and abundance (see **Figs. 6. A** and **B.**), with old growth sites being coolest and oil palm sites the hottest. When this was explored further, a unimodal relationship was found between air temperature and species richness, with an apparent optimum temperature found in old growth forest. This would suggest the influence of canopy in reducing temperature. However, the functional diversity indices, species richness, and abundance were all found to have no significant relationship with canopy openness. In addition, the functional diversity indices, species richness, and abundance were found to have no significant relationship with percentage leaf litter cover, despite expectations to the contrary (as leaf litter may contribute to more organic material in soils).

Limitations and improvements for future study

Many more species of ant were sampled than termites (260 compared with 36), which allowed the functional diversity indices to be analysed at a finer scale for ants than termites. In the ant analysis, groups of 3 survey points were assembled into 20 replicate communities (6 OG, 11 SF and 3 OP). In the termite analysis, groups of 8 or 9 survey points were assembled into 7 replicate sites. This in turn meant that there were more replicates for the ant communities than there were for the termite sites.

This created a number of advantages in the study of functional diversity in ants over the study for termites. First, by grouping the survey points into communities of 3 points for the ants, all of the groups were identical sizes, whereas the secondary forest sites for the termites were slightly smaller than the oil palm and old growth sites. This will have added some slight bias into the termite analysis, which is not present in the ant analysis.Second, by grouping the survey points into smaller communities in the ant analysis, less information is likely to have been lost than in the termite analysis. Lastly, lumping survey points into larger groups for termites meant that there were less replicates than for ants, thus decreasing the chances of a statistically significance result. Bishop (2012) uses the functional evenness and divergence indices to investigate assembly patterns in ants. Such an analysis is not possible with the termite data because there were so few replicates.

The low number of replicate sites is a major drawback, and the primary limitation of this study. The results do provide a useful idea of how functional diversity is affected by habitat disturbance, but do not, for example allow for the analysis of community assembly patterns. Therefore, future studies of the response of termite functional diversity to habitat disturbance must be both more intensive, and more extensive. This would allow for more species to be sampled, leading to more replicates analysed, and thus more informative results.

Future studies in this field could also benefit from a close analysis of the environmental variables (e.g. temperature, humidity, canopy cover, soil quality etc.) that are also affected by habitat disturbance, and which in turn may affect termite diversity. This would shed light on the underlying ways in which habitat disturbance effects ecosystem functioning. Moreover, this would help to separate those variables that cause increases or decreases in diversity from those which simply correlate with habitat disturbance. This has valuable applications, for example priority setting in conservation.

Implications for conservation

There is currently an inadequate understanding of soil biodiversity, and how it effects the provision of ecosystem services (Barrios, 2007). However, it is clear that, in their role as soil ecosystem engineers, termites play an important part in the functioning of tropical soil ecosystems. They facilitate the return of nutrients to the soil by breaking organic matter into smaller pieces, which then undergoes further decomposition by various microfauna. They are an essential step in the mineralisation of organic nutrients into inorganic forms, which are important for plant growth (Barrios, 2007), and play a direct role in facilitating plant growth. For example, many vegetation types that are observed on large mounds built by termites are not found in the surrounding landscape (Jouquet *et al.,* 2011). Finally, Termites have been shown to play a major role in the maintaining soil water balance (Mando, 1997).

Termite nests are carefully engineered environments in which a level of homeostasis is maintained that is not present in many other soil macrofauna. This allows the termite inhabitants to remain active, and to carry on contributing to ecosystem functioning, in harsh conditions whilst other soil organisms are inactive, or eradicated (Jouquet *et al.,* 2011).

The more diverse and abundant a termite population, the more significant is its role in ecosystem functioning (Ueckert *et al.,* 1976). This study suggests that disturbance of old growth habitats has a marked effect on both diversity and abundance. As the human global population increases, so does the need for resources, such as palm oil and wood. If primary forest is cleared to supply these resources, then termite numbers and diversity will decrease thus reducing ecosystem functioning and soil sustainability. There is a danger of creating a vicious circle; agricultural systems, such as oil palm plantations, also rely on soil ecosystem services and, if these are denuded, then more primary forest needs to be cleared in order to supply yet more unsustainable oil palm plantations. Thus a careful a balance must be struck to retain these self-renewing services (Jouquet *et al.,* 2011).

Oil palm is an important crop, both for the economies of the areas where it is grown, but also as sustainable biofuel (Fitzherbert *et al*., 2008). It is a renewable resource if managed intelligently. For oil palm planting purposes, already disturbed secondary forest sites should be prioritised, as this study suggests that this will have no significant effect on termite diversity or abundance. However, this needs to be explored further.

Conclusions

The results of this investigation and its sister study in ants suggest that habitat disturbance has a negative effect on functional diversity in both termites and ants, but that these effects manifest themselves differently in both groups. Habitat disturbance primarily decreases functional richness in termites, whereas in ants it is functional evenness and divergence that are reduced.

Termites are ecosystem engineers and play a key role in the natural functioning of soil ecosystems, and the provision of ecosystem services. Thus it is important to conserve their habitat, and both logging and conversion of primary forest to oil palm must be carefully managed.

Acknowledgements

References

Aerts, R., and Honnay, O. (2011). Forest restoration, biodiversity and ecosystem functioning. *BMC ecology*, **11**: 29.

Andersen, A. N. (1995). A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography*, **22**: 15-29.

Barrios, E. (2007). Soil biota, ecosystem services and land productivity. *Ecological Economics*, **64**: 269-285.

Bates, D., Maechler, M. and Bolker, B. (2011). lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-42.

Bishop, T. R. (2012). Functional diversity and community assembly patterns in ant (Hymenoptera: Formicidae) communities across a forest disturbance gradient in Sabah, Malaysia. *MSc thesis, Imperial College London.*

Boyd, J., and Banzhaf, S. (2007). What are ecosystem services? The need for standardized environmental accounting units. *Ecological Economics*, **63**: 616-626.

Cornwell, W. K., Schwilk, D. W., and Ackerly, D. D. (2006). A trait-based test for habitat filtering: convex hull volume. *Ecology*, **87**: 1465-1471.

Costanza, R., d'Arge, R., de Groot, R., Farberk, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., and van den Belt, M. (1997). The value of the world's ecosystem services and natural capital. *Nature,* **387**: 253-260.

Davies, R. G., Eggleton, P., Jones, D. T., Gathorne-Hardy, F. J., & Hernández, L. M. (2003). Evolution of termite functional diversity: analysis and synthesis of local ecological and regional influences on local species richness. *Journal of Biogeography*, *30*(6), 847-877.

Davies, R.G., Hernandez, L.M., Eggleton, P., Didham, R.K., Fagan, L.L. and Winchester, N.N. 2003. Environmental and spatial influences upon species composition of a termite assemblage across Neotropical forest islands. *Journal of Tropical Ecology* **19**: 509-524

Denslow, J. S. (1980). Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia*, **46**: 18-21.

Díaz, S., and Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, **16**: 646-655.

Donovan, S. E., Eggleton, P., and Bignell, D. E. (2001). Gut content analysis and a new feeding group classification of termites. *Ecological Entomology*, **26**: 356-366.

Donovan, S. E., Griffiths, G. J., Homathevi, R., and Winder, L. (2007). The spatial pattern of soil-dwelling termites in primary and logged forest in Sabah, Malaysia. *Ecological Entomology*, **32**: 1-10.

Eggleton, P. (2011). An introduction to termites: biology, taxonomy and functional morphology. In Bignell, D. E., Roisin, Y., and Lo, N. (Eds.), *Biology of termites: a modern synthesis* (pp. 1-26). Springer Netherlands.

Eggleton, P., and Tayasu, I. (2001). Feeding groups, lifetypes and the global ecology of termites. *Ecological Research*, **16**: 941-960.

Eggleton, P., Bignell, D. E., Hauser, S., Dibog, L., Norgrove, L., and Madong, B. (2002). Termite diversity across an anthropogenic disturbance gradient in the humid forest zone of West Africa. *Agriculture, ecosystems & environment*, **90**: 189-202.

Eggleton, P., Bignell, D. E., Sands, W. A., Mawdsley, N. A., Lawton, J. H., Wood, T. G., and Bignell, N. C. (1996). The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Philosophical Transactions of the Royal Society of London, Biological Sciences*, **351**: 51-68.

Eggleton, P., Bignell, D. E., Sands, W. A., Waite, B., Wood, T. G., and Lawton, J. H. (1995). The species richness of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Journal of Tropical Ecology*, 85-98.

Eggleton, P., Homathevi, R., Jeeva, D., Jones, D. T., Davies, R. G., and Maryati, M. (1997). The species richness and composition of termites (Isoptera) in primary and regenerating lowland dipterocarp forest in Sabah, East Malaysia. *Ecotropica*, **3**: 119-28.

Ewers, R. M., Didham, R. K., Fahrig, L., Ferraz, G., Hector, A., Holt, R. D., Kapos, V., Reynolds, G., Sinun, W., Snaddon, J.L., and Turner, E. C. (2011). A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**: 3292-3302.

Fitzherbert, E. B., Struebig, M. J., Morel, A., Danielsen, F., Brühl, C. A., Donald, P. F., and Phalan, B. (2008). How will oil palm expansion affect biodiversity? *Trends in ecology & evolution*, **23**, 538-545.

Foster, W. A., Snaddon, J. L., Turner, E. C., Fayle, T. M., Cockerill, T. D., Ellwood, M. F., Broad, G.R., Chung, A.Y.C., Eggleton, P., Khen, C.V., and Yusah, K. M. (2011). Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**: 3277-3291.

Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., and Sodhi, N. S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, **12**: 561-582.

Gathorne-Hardy, F. J. (2004). The termites of Sundaland: a taxonomic review. *Sarawak Museum Journal*, **60**, 89-133.

Hooper, D. U., Chapin Iii, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., and Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological monographs*, **75**: 3-35.

Jamil, T., and ter Braak, C. J. (2013). Generalized linear mixed models can detect unimodal species-environment relationships. *PeerJ*, **1**: e95.

Jones, D. T., and Eggleton, P. (2000). Sampling termite assemblages in tropical forests: testing a rapid biodiversity assessment protocol. *Journal of Applied Ecology*, **37**: 191-203.

Jones, D. T., Susilo, F. X., Bignell, D. E., Hardiwinoto, S., Gillison, A. N., and Eggleton, P. (2003). Termite assemblage collapse along a land-use intensification gradient in lowland central Sumatra, Indonesia. *Journal of Applied Ecology*, **40**: 380-391.

Jouquet, P., Traoré, S., Choosai, C., Hartmann, C., and Bignell, D. (2011). Influence of termites on ecosystem functioning. Ecosystem services provided by termites. *European Journal of Soil Biology*, **47**: 215-222.

Kaspari, M., and Weiser, M. D. (1999). The size–grain hypothesis and interspecific scaling in ants. *Functional Ecology*, **13**: 530-538.

Koh, L. P., and Wilcove, D. S. (2007). Cashing in palm oil for conservation. *Nature*, **448**: 993-994.

Koh, L. P., and Wilcove, D. S. (2008). Is oil palm agriculture really destroying tropical biodiversity? *Conservation Letters*, **1**: 60-64.

Laliberté, E. and Shipley, B. (2011). FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-11.

Laliberté, E., and P. Legendre (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**: 299-305.

Lavelle, P., Blanchart, E., Martin, A., Martin, S., and Spain, A. (1993). A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. *Biotropica*, 130-150.

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., and Rossi, J. P. (2006). Soil invertebrates and ecosystem services. *European Journal of Soil Biology*, **42**: S3-S15.

Luke, S. H. (2010) Ant and termite assemblages along a tropical forest disturbance gradient in Sabah, Malaysia: a study of co-variation and trophic interactions. *MSc thesis, University of East Anglia.*

Mando, A. (1997). The impact of termites and mulch on the water balance of crusted Sahelian soil. *Soil technology*, **11**: 121-138.

Mason, N. W., Mouillot, D., Lee, W. G., and Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, **111**: 112-118.

Morris, R. J. (2010). Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**: 3709-3718.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, **403**: 853-858.

Pakeman, R. J. (2011). Functional diversity indices reveal the impacts of land use intensification on plant community assembly. *Journal of Ecology*, **99**: 1143-1151.

R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Ruiz-Jaen, M. C., and Potvin, C. (2010). Tree diversity explains variation in ecosystem function in a neotropical forest in Panama. *Biotropica,* **42**: 638-646.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., and Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, **287**: 1770-1774.

Szarzynski, J., and Anhuf, D. (2001). Micrometeorological conditions and canopy energy exchanges of a neotropical rain forest (Surumoni-Crane Project, Venezuela). *Plant Ecology*, **153**: 231-239.

Thapa, R. S. (1982). Termites of Sabah. *Sabah Forest Record*, **12**.

Tilman, D. (1997). Biodiversity and ecosystem functioning. In Daily, G.C. (Ed.), *Nature's Services: societal dependence on natural ecosystems*, 93-112. Washington: Island.

Ueckert, D. N., Bodine, M. C., and Spears, B. M. (1976). Population density and biomass of the desert termite Gnathamitermes tubiformans (Isoptera: Termitidae) in a shortgrass prairie: relationship to temperature and moisture. *Ecology*, 1273-1280.

Villéger, S., Mason, N. W., and Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**: 2290-2301.

Villéger, S., Miranda, J. R., Hernández, D. F., and Mouillot, D. (2010). Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, **20**: 1512-1522.

Wright, S. J. (2005). Tropical forests in a changing environment. *Trends in Ecology & Evolution*, **20**: 553-560.