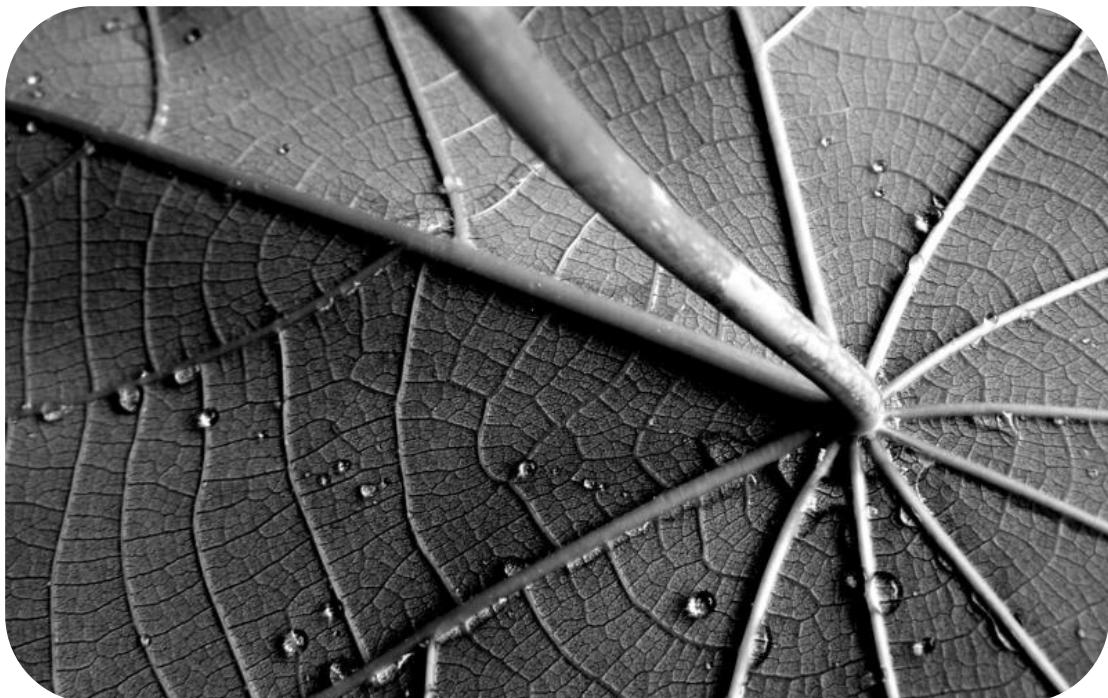


**Impact of invertebrates and fungi on leaf litter decomposition across a  
forest modification gradient in Sabah, Malaysia**

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## **Abstract**

Tropical forests are some of the most species rich biomes on the planet yet are being converted to agricultural landscapes at an alarming rate. The problem is particularly acute in South East Asia and, with the rapid expansion of the oil palm industry Malaysia is one of the top global exporters of palm oil. Since this trend of habitat modification looks unlikely to decelerate in the near future, rapid assessment of existing diversity and its biological consequences is essential. Decomposition is an important ecosystem function for the redistribution of nutrients in forest soils and is performed in a large part by forest biota. This study investigates the role of leaf litter invertebrates and fungi in early stage decomposition across a range of habitat degradation; old growth, secondary forest and mature oil palm plantation. A litterbag exclusion experiment was carried out to determine the relative impacts and interaction of macro-invertebrates and fungi in the first 40 days of decomposition. The experiment excluded (a) macro-invertebrates (>1mm), (b) fungi, and (c) both macro-invertebrates and fungi. In oil palm, excluding fungi inhibited leaf litter decomposition when macro-invertebrates were allowed access but not when they were excluded, suggesting that macro-invertebrates can inhibit decomposition processes in the absence of fungi in this habitat. In old growth, only the combination of excluding macro-invertebrates and fungi caused a decrease in decomposition rate, suggesting that interactions between them are key to normal function in the system. There appears to be a degree of functional redundancy found in every habitat but the mechanisms differ between them. This result illustrates how removing certain guilds can disrupt the complex interactions of decomposer communities. More work is necessary to identify guild and species interactions in order to predict the effect of non-random species loss on the functioning of forest and agricultural ecosystems after habitat modification.

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## **1. Introduction**

Tropical forest ecosystems are important strongholds of biodiversity and carbon storage (Berry et al, 2010) yet are increasingly threatened by anthropogenic factors such as climate change, overexploitation and land use change (Morris, 2010).

Land use change is the major driver of biodiversity loss in the tropics (Sala et al, 2000) Since 2000, over 40million hectares of primary forest have been cleared (FAO, 2010) and 5.8million hectares of tropical forest are converted annually for agricultural purposes (Mayaux et al, 2005). Oil palm, *Elaeis guineensis*, has become one of the most important crops in equatorial regions due to increasing global demand for a cheap source of oil for food products and biofuel (FAO, 2009).

The centre of oil palm production is South East Asia, one of the most diverse regions worldwide spanning four biodiversity hotspots and home to a great number of endemic species (Sodhi et al, 2010 – “The state and conserv...”). The rapid expansion of this industry can now be considered the biggest immediate threat to the region’s diversity because annually millions of hectares of irreplaceable forest habitat are logged and degraded (Fitzherbert et al, 2008; Wilcove & Koh, 2010). Current projections show that South East Asia could lose 3/4 of its forests and 42% of its diversity by 2100 (Sodhi et al, 2004).

Malaysia and Indonesia are the biggest global exporters of palm oil (Koh et al, 2011) and their economies have become more reliant on this industry since the reduction of timber yields following the intensive logging of high value dipterocarp timber (Gardinen et al, 2003). The result is a gradient of habitat degradation from primary forest logged for these high value timbers through to secondary forest, which becomes degraded, fragmented and cleared for agriculture, primarily to become monocultures of oil palm. Between 1990 and 2005, conversion of forest to oil palm accounted for 94% of deforestation in Malaysia (FAO, 2009). There is already much evidence of an overall negative impact on diversity not only in oil palm plantations which support only a fraction of primary forest species (Fitzherbert et al, 2008;

Berry, 2010) but also across a range of habitat degradations within neighbouring secondary forest (Didham et al, 1998; Brühl et al, 2003; Schulze et al, 2004; Turner & Foster, 2009). It is worth noting however that the response to habitat degradation can differ between and within taxa (Didham et al 1998; Schulze et al, 2004).

Despite the irrefutable value of primary forest habitat there is mounting evidence for the conservation value of secondary forest (Schulze et al, 2004; Berry et al, 2010; Woodcock et al, 2011). Berry et al (2010) found that over 90% of primary forest species were still present in logged forest and that species richness typically differed by less than 10%. Secondary forests were also found to accumulate carbon five times faster than natural forest and this could increase even further with appropriate regeneration programmes. However, broad species diversity and richness indices may be misleading when determining the health of an ecosystem since disturbance opens up new niches for more generalist species whilst increasingly marginalizing rarer, more specialist species (Lewis, 2009). Even intact secondary forest is at risk of decay in its original diversity due to edge effects and fragmentation (Laurance et al, 2002) when placed in a disconnected matrix of oil palm so it is essential to look at the biological processes and how they compare with undisturbed forests

There has been much discussion of the effects of land use change on species diversity and richness and increasing debate over its subsequent effects on ecosystem functioning (Wardle et al, 1997; Schwartz et al 2000; Duffy 2002). Ecosystem function can be defined as biogeochemical processes that involve energy flow or nutrient cycling (Naeem, 2009). Most studies investigating the relationship of diversity and function have been based on temperate plant productivity so there is a need for more experimental work on the influence of biota higher trophic levels (Lewis, 2009).

Invertebrates play a crucial role in many ecosystem processes including the decomposition of organic matter (Folgarait, 1998; Jouquet et al, 2006; Lavelle et al, 2006). The presence of invertebrates greatly accelerates litter decomposition and nutrient release in tropical forests worldwide (Meyer et al, 2011; Schädler & Brandl,

2005) but their impact can differ from site to site depending on litter chemistry and decomposer community (Powers et al, 2009). Recent studies have shown the importance of invertebrate diversity to function such as carbon flux being linked to termite and nematode diversity (Lawton, 1996) and a positive relationship between ant species richness and nutrient redistribution (Fayle, 2011).

Decomposition plays an essential part in nutrient cycling and carbon flux. Although annual litter fall in tropical forests is much higher than in temperate zones, there is little accumulation of organic matter as it is accompanied by a high decay rate (Olson, 1963). In the lowland tropics most forest litter is broken down within a year (Sampaio et al 1993). The three major factors influencing decomposition are climate, litter quality and soil and litter biota (Swift et al, 1979; Coûteaux et al, 1995). Climate and litter quality are considered the most important regulators of decomposition on a global scale, but more locally soil fauna becomes important, especially where temperature and moisture are not limiting factors (Wall et al 2008). Biotic factors, especially the presence of arthropods and fungi, are much more important in the humid tropics (Lavelle et al, 1993; Seastedt & Gonzales, 2001). Fungi are likely more important than bacteria in surface litter decomposition because they are physiologically better adapted to invading coarse litter with hyphae and withstanding dessication whereas bacteria potentially perform better with finer litter fragments with greater surface area and increased water retention (Beare et al, 1992).

Habitat modification has ramifications for all three of these factors. Reduced structural complexity will affect humidity, light intensity, and the soil's ability to retain water which in turn affects the species that can tolerate the different abiotic conditions. Changes in plant communities will affect the abundance and diversity of litter and its associated chemistry. For example, habitat modification in Amazonia leads to the proliferation of successional species and leaves of successional tree species decompose more slowly due to high phenolic content and low nitrogen content (Vasconcelos & Laurance, 2005). It can be predicted that these changes along with disturbance will have major effects on the organisms associated with

decomposition. Conversion to oil palm is detrimental to invertebrates in all forest niches (Turner & Foster, 2009) and taxonomic richness has been found to be important in decomposition processes (Wall et al, 2008). Will decomposition processes be impaired across a gradient of habitat modification following the same patterns of general biodiversity decline or will variable responses of different taxa to forest modification modulate the response of ecosystem functionality?

### **1.1 Project aims and objectives**

Few studies have investigated the relative impacts of the biotic drivers of decomposition and how they interact in tropical terrestrial systems. Fungal and invertebrate exclusion could be expected to have a significant impact on the decomposition process considering their major roles in the break down of litter. Invertebrate communiton of coarse litter into smaller particles thereby increasing surface area for other soil microbiota such as bacteria and nematodes (Seastedt, 1984) could encourage decomposition, whereas overgrazing of decomposer microbiota by invertebrates may actually inhibit decay rates (Newell, 1984). Fungal exclusion may have an even greater impact. A study by Beare et al (1992) found that fungal exclusion led to a 36% reduction in surface litter decomposition.

In this study we use litterbags with a fine mesh to exclude macro-invertebrates (>1mm), and a broad-spectrum fungicide to inhibit fungal growth from leaf litter in old growth, secondary forest and oil palm plantation and determine the decomposition rate to address the following questions:

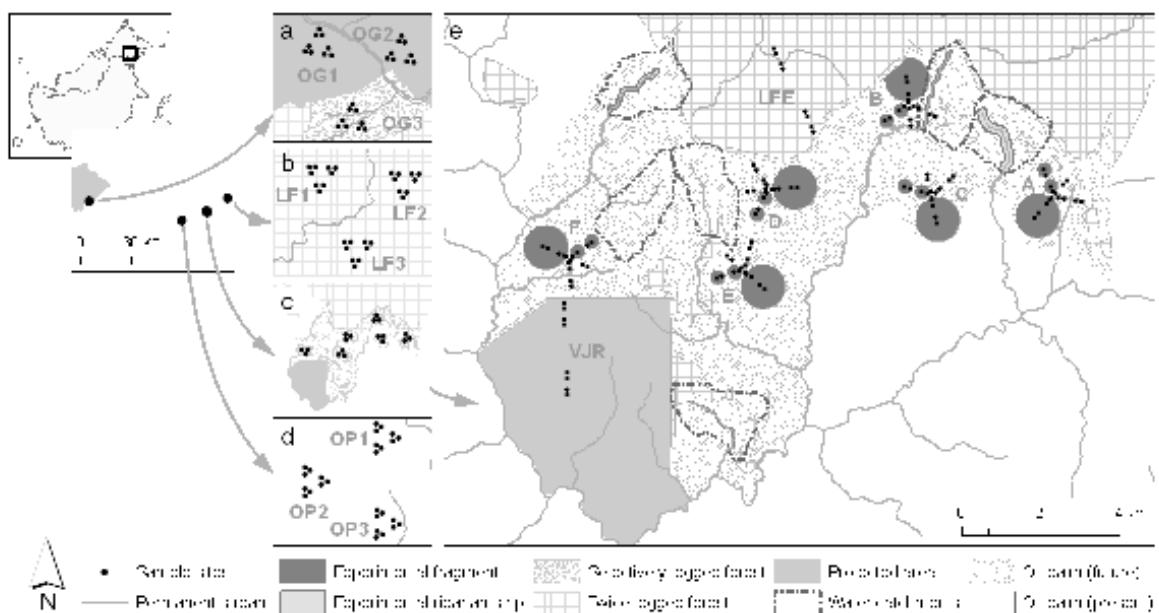
- 1) Do decomposition rates differ across a range of habitat degradation?
- 2) What is the relative contribution of invertebrates and fungi to the decomposition process and does it differ across habitats?
- 3) To what extent do fungi and invertebrates interact in decomposition, and does this change according to the degree of habitat modification?

## **2. Materials and methods**

### *2.1 Study site*

The study was conducted as part of the Stability of Altered Forest Ecosystems (SAFE) project in lowland dipterocarp forest in Sabah, Malaysia. The SAFE project aims to understand the impacts of forest modification on diversity and ecosystem function, using a hierarchical sampling design based on a fractal pattern (Ewers et al, 2011). The SAFE experimental area lies between two protected forest reserves, Danum Valley and Maliau Basin.

Data were collected from May to July 2012 in established SAFE project 2<sup>nd</sup> order points (figure 1) in old growth (hereafter referred to as OG), secondary forest (SF) and oil palm plantation (OP). The old growth block OG3 is a continuous stretch of primary forest in the water catchment for the Maliau Basin Research Centre (N4.74471, E116.95711), consisting of nine 2<sup>nd</sup> order sampling points arranged in three sets of three triangles. Though selectively logged in the 1970s and 1990s it can still be considered representative of high quality forest due to its vegetation structure and composition (Ewers et al, 2011). The twice logged forest block E, located in Benta Wawasan Plantation (N4.64612, E117.44934), consists of sixteen 2<sup>nd</sup> order sampling points arranged in a crow's foot array of four transects (figure 1e). Although not yet cleared, logging outside the areas designated as fragments began shortly after the end of this study. The mature oil palm plantation block OP3 was planted in 2000, has a closed canopy and is 1km from forest. The *E.guineensis* monoculture dominates and ground vegetation is sparse. Like OG3 it consists of nine sampling points.



**Figure 1.** Map of SAFE Project experimental area in Sabah, Malaysia (from Ewers et al, 2011). The area includes a) old growth control in Maliau Basin b) logged forest control c) secondary forest assigned to become fragmented in a matrix of oil palm plantation d) oil palm plantation. The current study was carried out in mature oil palm plantation block OP3 (OP), secondary forest block E (SF) and old growth block OG2 (OG). The sampling points are represented by black circles of which there are 9 in OG and OP and 16 in SF.

## 2.2 Litter preparation

Naturally senesced whole leaves of a common *Macaranga* morphospecies were collected from raised sheets of tarpaulin within twenty-four hours of their falling and subsequently air dried in closed 1mm mesh bags, to minimise further decomposition. They were then cut into roughly  $2\text{cm}^2$  pieces and any large veins or petioles were discarded. Finally the leaves were dried to a constant weight in a basic field oven. Litter pieces were weighed with a microbalance accurate to 0.01g and 4g placed in  $10\text{cm}^2$  nylon bags with 1mm mesh.

## 2.3 Experimental design

The study includes a control and three experimental treatments:

- macro-invertebrate exclusion;
- fungus exclusion; and
- macro-invertebrate and fungus exclusion.

The control bags allowed access to invertebrates and fungi through five 1cm<sup>2</sup> perforations made in each side of bag. Bags excluding macro-invertebrates were not perforated, thus preventing access to anything larger than the 1mm mesh width. Fungi were excluded by treating the filled litterbags with the broad-spectrum fungicide chlorothalonil (as in Sayer et al, 2006). The product used was an emulsifiable concentrate containing 40% w/w chlorothalonil. As per the recommended dose for spraying on fruit crops to provide protection for 12 months, 3ml of fungicide was diluted in 2L of water, previously boiled to purify. Fungal exclusion bags were soaked in fungicide solution for 1 minute immediately prior to being taken to the field. Treatments not excluding fungi were similarly drenched in water purified by boiling, and care was taken to keep them separate from treated bags.

In each sampling point twelve bags, three of each treatment and the control, were set in a circle around the centre of the 2<sup>nd</sup> order points. The position of treatments relative to each other was randomised and bags were set at least 3m apart to prevent the influence of exclusion treatment.

#### *2.4 Litter bag retrieval and processing*

One bag from each treatment was collected after 14 days, 27 days and 40 days (+/- 2 days) in order to construct a decomposition curve for the data from each 2<sup>nd</sup> order point. In addition, 5-6 handling controls were taken to each site on the day of setting and taken back to be oven dried and weighed to calculate the average handling loss for each site.

Bags collected were oven-dried in a field oven to a constant weight, and the contents weighed and corrected for handling loss. Any mud or other debris was gently brushed off before weighing and any bags that were completely spoiled by mud were excluded from the data set.

## *2.5 Abiotic measurements*

Standing litter depth and soil pH were recorded directly adjacent to each litterbag in the field. Canopy openness for each 2<sup>nd</sup> order point was estimated using a spherical densiometer as part of the core SAFE project work.

## *2.6 Statistical analyses*

Samples that weighed more than their initial weight after collection were assigned to 0% weight loss (n=76 out of 743) to minimise the effect of error due to weight gain caused by undetected mud spoiled litter or over-correction for handling loss.

To reduce spatial pseudoreplication, 2<sup>nd</sup> order points were grouped into clusters of neighbouring points (eight clusters of two for SF and three clusters of three for OP and OG).

Using the statistical package R (R Development Core Team, 2011) an ANOVA was performed on decomposition rate as a function of habitat followed by a Tukey test to determine any differences between habitats. A linear regression was fitted to untransformed percentage weight loss data as a function of time for each treatment in each 2<sup>nd</sup> order point. Decomposition rate was then calculated from the average slope estimates per cluster. The maximal explanatory model, decomposition rate ~ block \* treatment \* pH, was fitted in a linear model then simplified and an ANOVA performed on the minimal explanatory model. The environmental variables canopy cover and litter depth were removed from the model as they were highly correlated with pH. Separate linear regressions were then fitted to each habitat to detect any habitat-specific effect of treatment.

Modelling decomposition rate as a function of habitat masks the variability of the forest within SF. As part of the SAFE core data collection, all 2<sup>nd</sup> order points have been assigned a forest quality score from 0 to 5, 0 being oil palm and 5 being completely closed canopy. OP sites all score 0, OG sites are all 5 whereas SF has a range of scores from 1-4. To account for this, forest quality (averaged by 2<sup>nd</sup> order clusters) was fitted to the following minimal linear model:

$$\text{Decomposition rate} \sim \text{forest quality} + \text{treatment}$$

### **3. Results**

#### *3.1 Abiotic measurements*

There was marked environmental variation between the different habitats, following the forest modification gradient. OG typically had the most closed canopy with a mean canopy openness score of 7% (SE=0.22). The canopy in SF was three times more open than OG with an average score of 26% (SE=4.90). Unsurprisingly, OP had the most open canopy, on average 36% (SE=11.8). Correspondingly, mean litter depth was greatest in OG with an average of 48mm (SE=4.62), followed by 36mm (SE=2.91) in SF, and 9mm (SE=2.33) in OP which had very little standing litter. OP has the most acidic soils which on average were pH 5.4 (SE=0.05), whilst SF had a greater range of pH but a mean of pH 5.9 (0.07) and OG had the most neutral soils with a mean of pH 6.2 (SE=0.31).

#### *3.2 Litter loss*

There was much variation in the mass of litter lost from litterbags within habitats and treatments (figure 2). After 40 days in the field leaf litter in OG lost on average 10.3% of its original weight (SE=1.10), in SF they lost 10.5% (SE=1.01) and in OP they lost a much lower 4.7% (SE=0.97). The difference in litter mass loss between treatments was less evident. The control lost an average of 10.4% of its original weight (SE=1.46). When macro-invertebrates were excluded, litter lost an average of 12.0% (SE=1.63). When fungi were excluded the loss of leaf mass was marginally less, with a mean loss of 6.4% when excluding just fungi (SE=1.23), and 8.2% when both macro-invertebrates and fungi were excluded (SE=1.12).

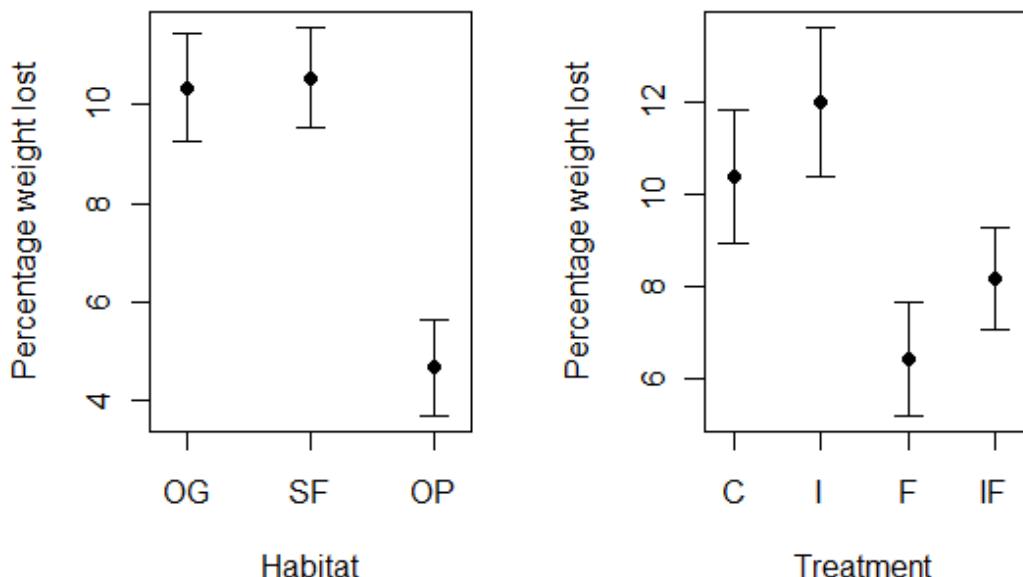


Figure 2. Percentage weight loss of leaf litter after 40 days in old growth (OG), secondary forest (SF) and oil palm plantation (OP) averaged by clusters of 2<sup>nd</sup> order points (n=14). A) Comparison of weight loss between habitats; litter in OG and SF lost on average 10 and 11% of their original weight, while litter in oil palm plantation lost only 5% on average. B) Comparison of weight loss between treatments: control (C); macro-invertebrate exclusion (I); fungal exclusion (F); and macro-invertebrate and fungal (IF) exclusion. There was no marked difference in litter mass loss between the treatments when pooling data from all habitats.

### 3.3 Modelling the effects of habitat, treatment and pH

There were marked differences in decomposition rate across the gradient of forest modification ( $F_{2,53}=5.6$ ,  $p<0.01$ ). Decomposition rates were slower in OP than in OG (Tukey's HSD,  $p=0.04$ ) and in SF (Tukey's HSD,  $p<0.01$ ) (figure 3).

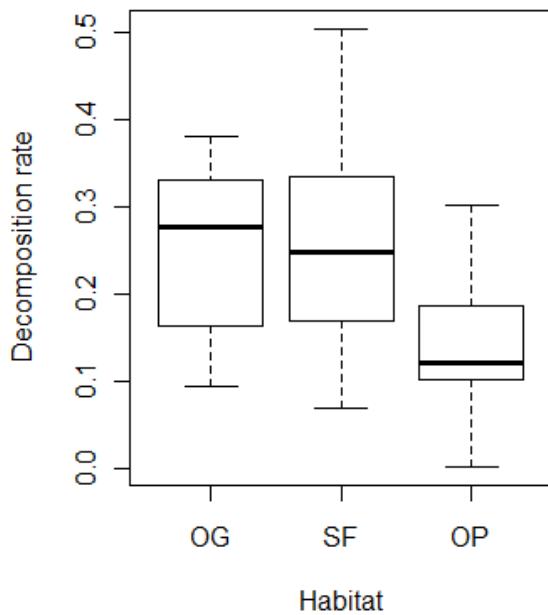


Figure 3. Decomposition rates across the clustered 2<sup>nd</sup> order points (n=14) in three habitats: old growth (OG), secondary forest (SF), oil palm plantation (OP). Decomposition rates are significantly lower in OP than the other habitats.

Model simplification resulted in the following minimal explanatory model:

$$\text{Decomposition rate} \sim \text{habitat} + \text{exclusion treatment} + \text{pH} + \text{habitat: pH}$$

Decomposition rate differed significantly between habitats ( $F_{2,45}=10.2$ ,  $p<0.01$ ) and treatment ( $F_{3,45}=5.25$ ,  $p<0.01$ ) (figure 4). There was also highly significant interaction of habitat and pH ( $F_{3,45}=7.90$ ,  $p<0.01$ ). Soil pH had a highly significant effect on decomposition ( $t=3.24$ ,  $F_{8,45}=7.47$ ,  $R^2=0.494$ ,  $p<0.01$ ) and a significant interaction effect in SF ( $t=-4.86$ ,  $F_{8,45}=7.47$ ,  $R^2=0.494$ ,  $p<0.01$ ). Decomposition rates were significantly faster in SF than OG ( $t=4.89$ ,  $F_{8,45}=7.47$ ,  $R^2=0.49$ ,  $p<0.01$ ). Fungal exclusion was the only treatment found to differ significantly from the control ( $t=-2.53$ ,  $F_{8,45}=7.47$ ,  $R^2=0.49$ ,  $p<0.05$ ).

### *3.4 The effect of treatment within each habitat*

Modelling decomposition rate as a function of treatment, with pH as a main effect, detected a significant decrease in decomposition in OG when excluding both invertebrates and fungi ( $t=-4.79$ ,  $F_{4,7}=47.7$ ,  $R^2=0.94$ ,  $p<0.01$ ) and soil pH in OG was highly correlated with faster rates of decay ( $t=12.7$ ,  $F_{4,7}=47.7$ ,  $R^2=0.94$ ,  $p<0.01$ ).

In SF pH was found to be negatively correlated with decomposition rates ( $t=-2.77$ ,  $F_{4,25}=5.32$ ,  $R^2=0.37$ ,  $p<0.05$ ) but there was no detectable effect of any of the treatments, including fungal exclusion ( $t=-1.95$ ,  $F_{4,25}=5.32$ ,  $R^2=0.37$ ,  $p=0.06$ ). When soil pH is removed from the model, decomposition rates in the fungal exclusion treatments are significantly reduced ( $t=-2.38$ ,  $F_{3,28}=3.94$ ,  $R^2=0.22$ ,  $p=0.02$ ). In OP, pH had no detectable effect so was removed from the model, and fungal exclusion was found to be weakly correlated with a decrease in decomposition rate ( $F_{3,8}=1.87$ ,  $R^2=0.19$ ,  $p=0.05$ ).

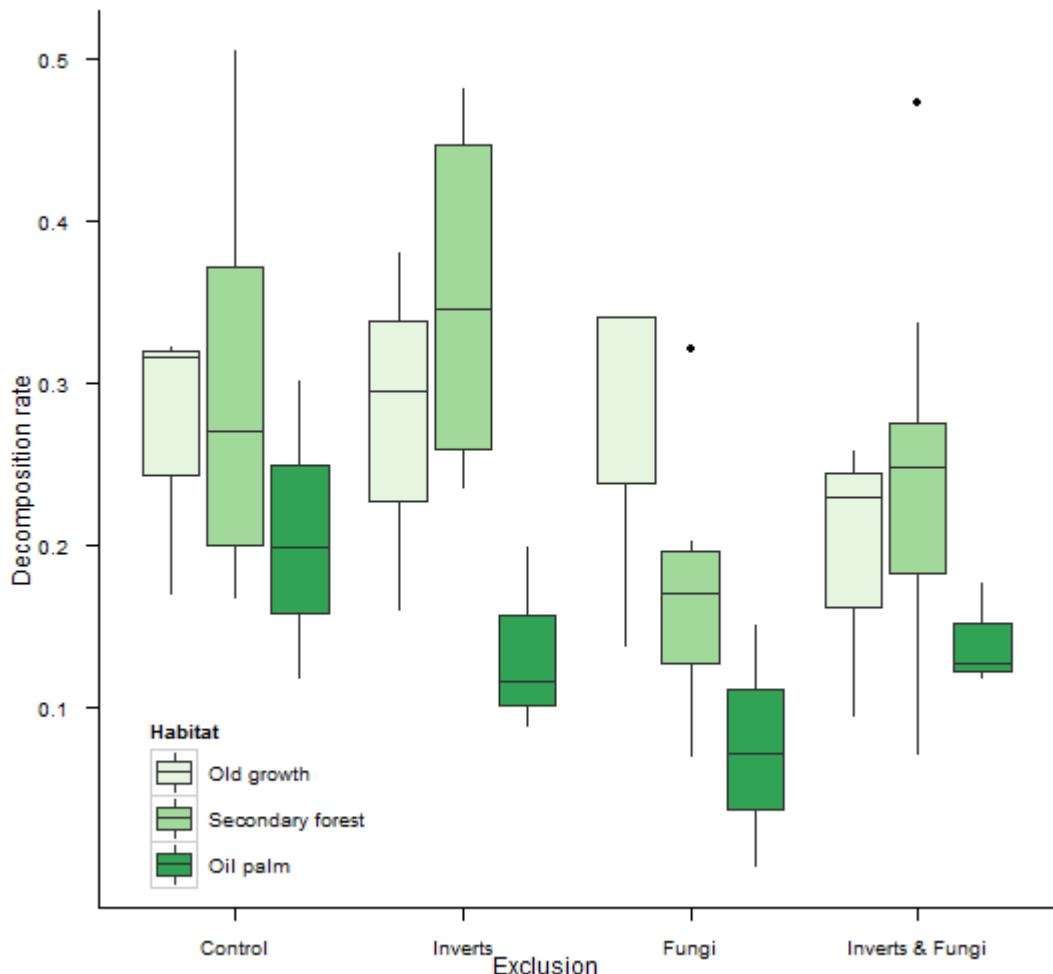


Figure 4. Decomposition rate of *Macaranga* leaf litter between 0 and 40 days in old growth (OG), secondary forest (SF) and oil palm plantation (OP) when excluding macro-invertebrates, fungi and both macro-invertebrates and fungi. Decomposition rates are slowest in OP and in OP and SF rates of decay are inhibited by the fungal exclusion treatment. In OG excluding both macro-invertebrates and fungi reduced the rate of decay.

Figure 5 illustrates the relationship between decomposition rate and soil pH in each habitat. In OP average soil pH is relatively low for all of the clusters of 2<sup>nd</sup> order points, and there is no relationship between pH and decomposition rate ( $t=-0.39$ ,  $F_{1,10}=0.15$ ,  $R^2=0.08$ ,  $p=0.71$ ) although this could be due to the restricted range of pH present. OG shows a much wider range of soil pH, where decomposition rate decreases with increased acidity ( $t=6.25$ ,  $F_{1,10}=39.0$ ,  $R^2=0.78$ ,  $p<0.01$ ). In SF, however, the opposite trend can be seen - pH is negatively correlated with decomposition rate( $t=-3.53$ ,  $F_{1,28}=12.5$ ,  $R^2=0.28$ ,  $p<0.01$ ).

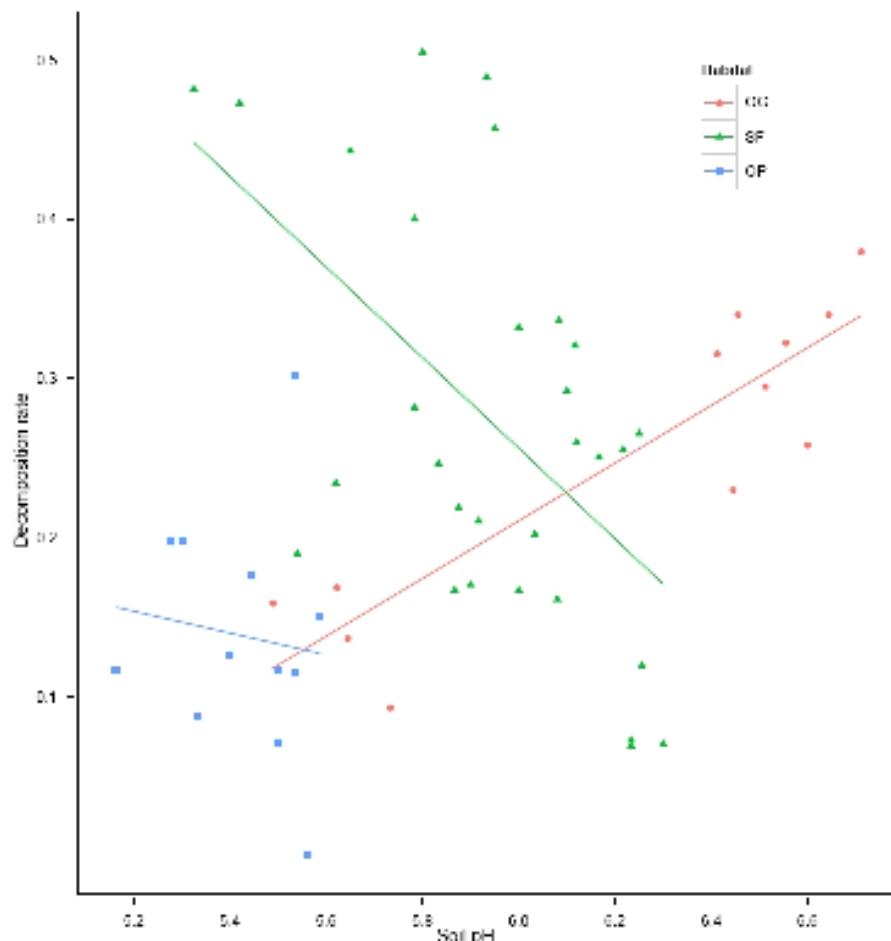


Figure 5. The range of soil pH and its effects on decomposition rate in old growth (OG), secondary forest (SF) and oil palm plantation (OP). OP sites tend to be the most acidic and generally experience lower decomposition rates. Decomposition rate decreases with acidity in OG, but increases with acidity in SF suggesting a shift in decomposer communities and their environmental preferences between the two habitats.

When decomposition rate is modelled as a function of forest quality rather than habitat the minimal explanatory model was:

$$\text{Decomposition rate} \sim \text{forest quality} + \text{treatment}$$

Using forest quality as a continuous explanatory variable takes account of the differences in pH between sampling points. This model found that higher forest quality had a positive effect on decomposition rates ( $t=2.68$ ,  $F_{4,51}=4.59$ ,  $R^2=0.20$ ,  $p=0.01$ ) and a significant decrease in decomposition rates was observed in the fungal exclusion treatment only ( $t=-2.55$ ,  $F_{4,51}=4.59$ ,  $R^2=0.20$ ,  $p=0.01$ ). When grouped into

categories of forest quality (High=5, Good=2-4, Low=1-2, Poor=0) only poor quality (aka OP) rates differed from those in the high quality forest (aka OG) ( $F_{6,49}=4.15$ ,  $R^2=0.26$ ,  $p=0.01$ ).

## 4. Discussion

### 4.1 Possible sources of error

OP and SF tended to be much muddier habitats so more litter samples spoiled by mud had to be excluded from the data set. Mass increase from undetected mud however could remain a potential source of error. It was decided not to wash leaf samples after collection because loss of litter mass would occur. Samples may also have gained fungal mass which would have been undetectable in this study, and though there are methods of estimating fungal growth (eg. Sayer et al, 2006) they were not within the scope of this project. In bounding the data that gained weight to an upper limit of 100% of their original weight, I hope to present a conservative estimate of relative decomposition rates.

Across the different sampling points microclimates varied, and some bags were markedly wet or dry upon collection suggesting that some were subject to more favourable conditions for decomposition than others. The mesh bag design compounds this problem, as the invertebrate exclusion litter could possibly retain more moisture by being less exposed than litter in perforated bags. It is possible that the more humid conditions in the invertebrate exclusions treatments could have favoured different decomposer species.

### 4.2 Main findings

Overall loss of litter mass and decomposition rates varied across the range of forest modification. In OP they were consistently less than in other habitats, a trend that corresponds highly with the lower pH of its soils, increased canopy openness and paucity of standing leaf litter. These and related abiotic factors in oil palm such as soil compaction, nutrient leaching, drier conditions and increased disturbance likely contribute to reducing the efficacy and abundance of decomposer organisms in oil

palm plantations. The lack of standing litter reduces habitat space for arthropods and thus decreases comminution of coarse litter into fine litter by detritivorous arthropods (Sayer, 2006) as well as limiting the nutrients and surface area available for microbial decomposers (Sayer et al, 2006). SF had a greater pH range than OP but on average was slightly less acidic than OP and had a more closed canopy. OG had the most canopy cover, standing litter and the least acidic soils. Despite its lower forest quality, decomposition rates tended to be faster in SF than in OG. This result is somewhat unexpected considering the less favourable abiotic factors for the microbial decomposer community which might be expected to persist better in humid, more neutral soils. A possible explanation is that disturbance has created more micro-niches for decomposing biota than are available in OG, allowing for a higher diversity and abundance. It is also worth considering that the leaf litter used, *Macaranga spp.*, is a common secondary forest species in Malaysia and would not be so common in primary forest. It may be that SF had the fastest decomposition rates due to this choice of leaf litter. Litter from secondary tree species in Puerto Rico has been found to decompose faster than litter of primary or late secondary species (Zou et al, 1995) and leaf decomposing fungi have been shown to have strong host preferences (Cowley, 1970; Cornejo et al, 1994) perhaps due to litter chemistry. If *Macaranga* is more likely to be encountered in secondary forest, it may be broken down more quickly in SF than in other habitats where it is less common due to an increased diversity and abundance of organisms with a preference for its leaf chemistry.

In OG decomposition rates decreased with soil pH whereas the opposite trend was seen in SF where decomposition rates increased with soil acidity. This suggests that decomposer communities differ between habitats, and offer a different range of environmental tolerances and preferences. Changes in plant community structure and composition driven by the abiotic factors accompanying disturbance is likely to play a large role in determining the structure and composition of soil and litter biota through changes in microhabitat structure and nutrient availability (Parmelee et al 1989; Badejo & Tian et al 1999).

With the exception of the fungal exclusion treatment decomposition rates within SF did not differ from the control,. This effect was found to be due to soil pH rather than the experimental inhibition of fungal growth. In OP however, fungal exclusion, independent of soil pH effects, decreased the decomposition rate. Why was this the case in OP and not the other habitats? Inhibition of fungal growth was predicted to have impacts on the wider detritus based food web. The fungicide treatment may reduce the numbers of grazing arthropods due to a reduced food supply as it did in a similar treatment used by Beare et al (1992). At low to moderate densities, grazing by micro-arthropods can stimulate microbial growth (Hanlon, 1981) and micro-invertebrates are known to play a role in spreading microbial propagules (Parkinson, 1979; Visser, 1985). In preventing the fungal colonisation of litter, there will be less direct breakdown of the leaf litter by fungi, and a reduction in food resources for fungivorous arthropods, whose habits indirectly aid in breakdown and mineralisation processes, causing a decrease in their populations. Perhaps in OG and SF this promotes a boost in the populations of bacteria and bacterivorous decomposers now released from competition with fungi and fungivores for resources. This activity by bacteria may compensate for the loss of fungi. In OP this switch to a bacteria-bacterivores food web may not be possible due to the high temperature and low humidity which are beyond the physiological tolerances of many species. Data was collected in the dry season which could mean that the fungi-fungivore based food web was predominant due to better growing conditions for fungi than for bacteria (Cornejo et al, 1994).

Surprisingly, the same effect is not seen when both macro-invertebrates and fungi are excluded, suggesting that the presence of macro-invertebrates may be inhibitory when fungus is absent in OP. In the fungal exclusion, predatory macro-invertebrates may contribute to the population crash of fungi-grazing invertebrates such as collembolans and mites, further compounding the reduction in decomposition rate. Alternatively, if our fungicide was not effective at inhibiting fungal growth, predators' contribution to reducing grazer populations may play a role in preventing overgrazing by micro-invertebrates resulting in an increase of fungal mass, which in this experiment would be indistinguishable from a genuine decrease in

decomposition rate. Beare et al (1992) found that treating litter with insecticide resulted in a decrease in micro-arthropods, allowing an increase in hyphal densities after the reduction in grazing pressure. Highly disturbed habitats are susceptible to colonisation by generalist or invasive invertebrate predators, so in OP they may be acting in the same way as the insecticidal treatment.

In OG the decomposition process was only inhibited when both macro-invertebrates and fungi were excluded. This suggests that the interaction of these two groups is key to maintaining decomposition processes although the mechanism is unclear. Possibly the reduction in fungal growth reduces the population of micro-invertebrate fungivores reducing the further break down of litter. Excluding detritivorous macro-invertebrates further decreases the amount of coarse litter being broken down to fine litter. Bacteria-bacterivore food webs could be limited by reduced surface area normally provided by fine litter.

All the habitats appear to exhibit some flexibility in the functioning of their system, so as other organisms have the potential to fill a functional gap when one group is removed. The degree and mechanism of this functional redundancy appears to be habitat specific since the effect of the treatments varied within each habitat. In OP the roles of macro-invertebrates and of fungi can be replaced but only if macro-invertebrates are not inhibiting the process. In OG the role of invertebrates and of fungi can be replaced unless both are excluded from the system. Perhaps SF has the highest degree of functional redundancy since the treatment did not affect the decomposition rate and it may be that microclimatic factors and variation in forest quality are the main limiting factors for ecosystem functioning. This redundancy should be regarded with caution when considering the conservation implications however, as redundancy of certain taxa or species does not necessarily mean they are expendable. Having a range of species that perform similar function could mean however that the habitat has a greater resilience to environmental change. The results of this study therefore suggest that disturbed habitat could be the least resilient to climatic change since species are already performing at the limits of their physiological tolerances in drier and more acidic soils.

The exclusion treatments of this study are too broad to determine which species interactions are the most important to the decomposition process, and the complex competitive or predatory interactions between macro-invertebrate species and between fungal species are masked. It would be useful to characterise guilds within these groups and to identify the key species regulating the decomposition process. In addition identifying the species most vulnerable to extinction due to anthropogenic disturbances, invasive species and climate change along with their roles will be key to predicting changes in ecosystem functionality. There is mounting evidence that simple indices of species diversity and abundance are not enough to explain differences in decomposition rate (Andren et al, 1995; Wardle et al, 1997) further highlighting the need for more detailed knowledge of species interactions. Current research characterising species by functional traits looks promising in its ability to predict effect of species loss on redundancy and ecosystem function (Diaz et al, 2001; Mouchet et al, 2010).

#### *4.3 Implications for the management of OP and SF*

Forest clearance is often followed by soil acidification (Goh & Hardter 2003), an affect which is compounded by the addition of N fertilisers in OP (Kee et al, 1996 in Nelson et al, 2010). Plant growth is not usually affected directly by pH, unless it is extreme, but by the heavy metals and deficiency of nutritional elements that accompanies unfertile acid soils. Palm oil is mainly grown on the inland acid soils in Borneo (Uexktill & Muter, 1995). To maintain a higher level of soil nutrients, empty fruit bunches, palm oil mill effluent and mineral fertilizers are often applied. Pruned fronds are left on the ground to allow “leaf-wash” where nutrients are leached from the fronds and reenter the soil. (Goh & Härdter). Could the need for fertiliser applications be reduced by better management of oil palm plantations for healthier soils? Improving the structural complexity and integrating other plant species could improve nutrient turnover but the competition with other plants and possible increase in herbivorous enemies may reduce yield and make it unprofitable.

The decrease in decomposition rate after using fungicide is relevant to future disease management strategies in plantations. Currently oil palm suffers little from fungal disease outside of its native range in Africa, but in an increasingly globalised world trade the eventual arrival of a fungal pathogen is inevitable. The consequences of poorly applied broad-spectrum fungicide could disrupt decomposition processes and thus nutrient turnover and potentially decrease yield. Improving yield on land already converted to oil palm should be a priority in order to avoid the need to convert valuable secondary and primary forest to further plantations.

## 5. Conclusion

The difference in decomposition rates between OG, SF and OP habitats is likely driven by both abiotic factors and vegetation community structure. These in turn contribute to the community structure of microbiota and invertebrates that are involved in decomposition processes. There is evidence of functional redundancy in all habitats but the effects of excluding fungi or macro-invertebrates, or both, differ due to complex interactions of guilds within microbial and invertebrate taxa that are impossible to identify in the scale of this study.

The development of the oil palm industry shows no sign of declining in the near future, so informed management of both plantations and neighbouring secondary forest will be necessary to maintain their vital ecosystem functions. A better understanding of interactions between and within multiple trophic levels could be achieved by focussing on functional traits rather than species richness or diversity which would help to direct conservation efforts and improve the resilience of the systems to further anthropogenic driven disturbance.

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