

**The effects of land-use on biodiversity and ecological
functioning in a multi-trophic ecosystem (*Coleoptera*)
in Sabah, Northern Borneo.**



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Declaration

The Danum – Maliau Quantitative (DMQI) project collected all beetle samples for this study.

Identification to Family level was originally started by myself however was taken over and mostly performed by Sholto Holdsworth at the Soil Biodiversity Group, Life Sciences Department, Natural History Museum.

All 3044 body length measurements and the assignments into trophic guilds were done by myself using a compound microscope.

All data cleaning and processing, regressions, modelling and statistical analyses was performed by myself in R (version 3.1.2) with guidance of Samraat Pawar. All code was written by myself.

Temperature data was provided by Stephen Hardwick, RapidEye satellite images were provided by Marion Pfieifer but extraction of above ground biomasses values using Arc GIS 2.0 and were performed by myself.

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24th September 2015

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1) ABSTRACT

The effects of habitat alteration on ecosystem functioning remain largely unquantified in the tropics. Logged forests have been shown to maintain relatively high biodiversity, but it remains unclear if this correlates with ecological functioning. This study used metabolic theory to model energy flux in Coleopteran (beetle) food webs in primary and secondary habitats in Malaysia. It was found that across heterogeneous habitat types, ecological functioning is maintained along a land-use gradient of intermediate logging. Within primary homogeneous habitat types, ecological functioning is found to be significantly positively correlated to non-beetle above ground biomass. Observed leaf litter beetle biodiversity is highest in areas of intermediate disturbance. In support of previous in situ experiments, I provide evidence of a real world example of a significant correlation between biodiversity and ecological functioning.

2) INTRODUCTION

The increasing intensification of the transformation of natural ecosystems to agricultural land use has far reaching consequences for biodiversity, ecosystem services and holistic ecological functioning of those ecosystems (Edwards *et al.* 2012; Wilcove and Koh, 2010; Wilcove *et al.* 2013). Across the tropics, in the 1980's and 1990's, 55% of new agricultural land came at the expense of undisturbed forests, with another 28% coming from previously logged forests (Gibbs *et al.* 2010). In the paleotropics, recently observed land transformation has been primarily driven by the proliferation of the cash crop oil palm (*Elaeis guineensis*). Current global estimates total plantation area of oil palm to be over 15 million hectares, it is the most rapidly expanding crop globally (Carter *et al.* 2007). Between 1990 and 2005, the area of oil palm in Malaysia increased by 1.8 million hectares. With this expansion an estimated 1.1 million hectares of forest was lost, such destruction was facilitated by the reclassification of multiple protected forest reserves (Fitzherbert *et al.* 2008). The effect of land use change in Malaysia is important to understand because of the continuous deforestation and habitat change in Borneo. The highest losses were recorded in Sabah, Borneo, Malaysia with 39.5% of its total forest becoming non-forest in the last 30 years (Gaveau *et al.* 2014). This is predicted to have decreased dramatically again to 23% by 2020 (Sha *et al.* 2011). The drivers of this relentless deforestation were historically illegal logging, susceptibility of logged forest to wild fires and the timber industry. However in recent years there has been a dramatic shift and such habitat change is now predominantly driven by the expansion of the oil palm industry. Given that more than 85% of forests in Sabah have been logged, and that the palm oil industry in Malaysia is growing at annual rate of nearly 7% (Sodhi *et al.* 2010) and 9% globally (Clay, 2004) the rapid expansion on such a global scale of land alteration highlights the importance for emerging research to question the impending implications of such on biodiversity, ecosystems responses and functionality in fragmented and degraded habitats.

Although primary forests remain irreplaceable for conservation of the natural habitat types and tropical biodiversity (Gibson *et al.* 2011), the value of logged forest as a conservation tool must be not neglected, previous studies have shown depending on the intensity of logging, logged forests can maintain high biodiversity value (Burivalova *et al.* 2014; Edwards *et al.* 2012; Struebig *et al.* 2013; Wearn *et al.* 2013). That noted, an ecosystem is more than just the sum of its constituent species, and the complex network of species interactions and ecosystem processes which maintain ecological functioning is what needs to be evaluated in order to assess the value of logged forests (Ewers *et al.* 2015). Due to inherent difficulties in quantifying ecological functioning empirically and a lack of

consensus in how this should be done, tropical ecosystem responses to anthropogenic perturbations remains unsatisfactorily characterised and understood.

In recent years there have been progressive advances in the literature towards multi-trophic approaches to this emerging research area. Despite this shift away from single-trophic-level investigation which negates the complex interactions between food webs and whole community responses, there is still an apparent lack of agreement between studies on approaches to quantify a single measure of multi-trophic ecosystem functioning that can be directly compared between studies and ecosystems (Ives and Cardinale, 2004). A novel approach to address this was recently proposed, using total energy flux, whereby the amount of energy flowing through a particular system is a proxy for ecological functioning (Barnes *et al.* 2014). Although the idea that process rates could be an adequate proxy for ecological functioning has been present in the literature for some time it has only recently been applied to the concept of land use transformation utilising energy fluxes (Duffy, 2002; Foster *et al.* 2005; Barnes *et al.* 2014). Energy flux is superlative to general process rates due to the ability to directly relate fluxes to ecosystem services such as decomposition, plant biomass production and predation depending on the resource pool (Cardinale *et al.* 2003; Enquist *et al.* 2007; Handa *et al.* 2014).

Energy flux calculations can be made by combining metabolic scaling theory with information on food-web (feeding interaction network) links (Brown *et al.* 2004). Prior investigations that have attempted to calculate energy flux have used individual metabolic rate calculations derived from individual mass, phylogenetic clade and environmental temperature (Ehnes *et al.* 2011). Currently such calculations in combination with assimilation efficiencies, feeding preferences and loss to predation have been presented as a unified measure for multi-trophic ecosystem functioning (Barnes *et al.* 2014). Although this approach arguably improves upon the previous trends in the literature that relied solely on biomass as a measure of ecosystem functioning. It still neglects the effects of consumer resource interactions such search rate and consumption rate (Duffy *et al.* 2007; Dell *et al.* 2014). This approach also unsatisfactorily characterises basal resources and calculates flux at each node rather than at each link, a less realistic representation of the natural system (Rueman and Cohen, 2005).

Thus this investigation will compare the model of flux used by Barnes *et al.* 2014 (here after referred to as metabolic flux) in comparison with a new quantification of flux incorporating these previously discounted factors (here after referred to as consumption flux), in an attempt to present a more comprehensive and accurate measure of ecosystem functioning that can be utilised for assessing ecosystem health and relationships at any trophic level or taxonomic group (See Fig 2).

Both metabolic rate and consumption rate are intrinsically linked with body size with related scaling power laws (Ehnes *et al.* 2011; Pawar *et al.* 2012; Woodward *et al.* 2005). Body size is one of the most integral aspects of any organism, this is because size is directly related to almost every aspect of an organism's life history and ecology and can be utilised to infer resource demands, interactions and ecological partitioning (White *et al.* 2007).

As I intend to quantify the effectiveness of total flux as a proxy for ecological functioning it is necessary to compare flux with a previously established assessment of ecosystem health such as biodiversity. Species and family richness are the most commonly used measures of biodiversity and because of this I will use family richness as our metric. However it is important to note it is not the only measurement of biodiversity; others include genotypic, functional and habitat diversity (Woodward, 2009). As biodiversity assessments typically suffer from under-sampling and the relationship between sample size and species richness (Gotelli and Colwell, 2001). Therefore observed family richness will be compared against extrapolated estimated family richness in order to determine the appropriateness of our sampling effort and whether observed species richness realistically reflects actual patterns of total species diversity across land-use gradients (Colwell *et al.* 2004).

Despite a general consensus that ecosystem functioning is significantly correlated with biodiversity in controlled experiments (Cardinale *et al.* 2006; Foster *et al.* 2011; Hooper *et al.* 2005), there is currently a distinct lack of *in situ* examples of such a relationship (Otto *et al.* 2008). Knowledge of how perturbations in species richness, composition, abundance and biodiversity influence ecosystem functioning demands an understanding of functional traits of species in the system. Functional traits refer to traits that effect ecosystem properties or responses to change (Petchey, 2000; Petchey, 2004). Species are often grouped according to such traits in order to further understand mechanisms behind a system or to make investigations of more complex systems more manageable (Hooper and Dukes, 2004). There are two current hypotheses persisting in the literature for the mechanism that dictates the link between biodiversity and ecosystem functioning.

- 1) Only a very minimal number of species have a large effect on ecosystem function by the services that they provide and increasing species richness increases the likelihood they such integral species will be present (Loreau, 2000).
- 2) Functional or species richness increases ecosystem functioning through species interactions and niche partitioning. Using different resources or the same resources at different points in time or space result in more of the total available resources being utilised by a community (Vandermeer, 1998).

I will attempt to test the correlation between ecosystem functioning and biodiversity to test the two hypotheses in Coleoptera in Sabah, Borneo using family richness as a metric of biodiversity and total flux as a proxy of ecological functioning.

Previous studies have primarily compared the effects of land use within discrete habitat types; typically categorising forest degradation into various stages (Barnes *et al.* 2014; Fayle *et al.* 2010; Gillespie *et al.* 2012). Such grouping is sufficient to highlight general trends and the necessity to conserve natural habitat types but is impractical in assessing the relationship between habitat quality and complex ecological processes that do not respond in a categorical fashion. Utilising a scale of disturbance based on continuous measurements (e.g. average above ground biomass (Kg/m)) enables the observation of the ecological transitions accompanying land-use modification and also promotes direct comparison between studies, removing the subjective nature of categorisation (Pfeifer *et al.* In Press).

I hypothesize that:

- Ecological functioning will significantly decrease as habitat degradation increases, i.e. higher in both Danum and Maliau when compared with SAFE and higher within plots of higher above ground biomass.
- Biodiversity will be significantly higher in pristine forest sites, and therefore higher in Danum and Maliau compared with SAFE.
- Biodiversity and ecological functioning are intrinsically linked and will be significantly correlated.

3) METHODS

i) Study site

This project was conducted at three study sites in Sabah, Borneo: Danum Valley, Maliau Basin and the Stability of Altered Forest Ecosystems (SAFE) Project. SAFE is an experimental landscape situated in the North-East Malaysian state of Sabah (Ewers *et al.* 2011). The SAFE project is based in a 7,200 hectare landscape that is currently being converted from logged forest into oil palm plantation by Benta Wawasan (Turner *et al.* 2012), experimentally setting the size and location of remnant forest fragments to monitor the effect of forest fragmentation. The landscape has undergone one rotation of selective logging (removing 113 m³ ha⁻¹) during the 1970s (Fisher *et al.* 2011) and an additional rotation of salvage logging (removing 66 m³ ha⁻¹) occurred between 2000 and 2008 (Struebig *et al.* 2013). Danum Valley Conservation Area (DVCA) (4055'N,

117040'E) is a 43,800 hectare area of pristine lowland forest, and accounts for approximately 50% of Sabah's total remaining undisturbed forest (Reynolds *et al.* 2011). Maliau Basin Conservation Area (MBCA) (4049'N, 116054'E) is a 58,840 hectare area of primary forest, the outskirts of which have undergone low intensity selective logging once (Marsh and Greer, 1992). Both DVCA and MBCA are considered Class 1 Forest Reserves. In order to quantify quality of forest in each plot we utilised RapidEye™ satellite images acquired over the study sites in 2012 for which above ground biomass values were extracted by using Raster in ArcGIS 2.0 (Hijman & Etten, 2012; Pfeifer *et al.* In Press). For instances when clouds covered sampling sites in the images, the nearest available points were used and a mean value was taken.

ii) Study group

Insects are suitable subjects for investigating ecological paradigms because their inherent high abundance provides sufficient statistical power. This in combination with ease of sampling through a variety of economical standardised methodologies makes them an ideal focal taxa (Wilson, 1987). Beetles (*Coleoptera*) are particularly well suited due their intrinsic high diversity, approximately 4,000,000 described species (Nilsson-Ortman and Nilsson, 2010) and ubiquity across terrestrial habitats. The extensive radiation of beetles into practically all ecological niches and the presence of the majority of basal trophic guilds makes them viable for examining flux in a particular system. Beetles previously established sensitivity to environmental perturbations makes them particularly valuable when evaluating the impacts of habitat modification (Ewers and Didham, 2008). This is exemplified by their utilisation in a plethora of systems and studies (Ewers *et al.* 2015; Fagundes *et al.* 2011; Stokstad, 2004; Susilo, 2009).

iii) Sampling methods

Sampling was undertaken from September 2012 – October 2012, Danum and Maliau had 8 plots respectively and SAFE had 6 plots due to constraints of the sites experimental design. Coleopteran leaf litter communities were censused in each 1 hectare plot along 100m transects with 15 sampling points every 7m. At every sampling point 1m² of leaf litter was sifted through a 13mm wire mesh sieve and the contents put into Winkler bag extractors, which were left to hang for 3 days. Such a method was utilised as it has been found most effective for collecting quantitative data on ground-dwelling arthropods (Sabu *et al.* 2011). In total 3044 beetles were hand collected from Winkler bags, stored in 80% ethanol and transported back to the UK. Soil temperature data from SAFE and Maliau was collated using Thermochron iButtons (Maxim Integrated Systems, temperature accuracy ± 0.5 °C) buried at a depth of 10 cm. Sensors recorded instantaneous temperature readings every 3 hours in Celsius, starting at midnight each day and a mean temperature reading was taken for the study period and

converted into Kelvin (Hardwick *et al.* 2015). This data was not available for Danum and soil temperature data was recorded using a bi-metal thermometer when sampled.

iv) Lab methods

Each of the 3,044 beetles were identified to Family level and sub-family level where possible and assigned to one of five feeding guilds: predator, omnivore, herbivore, detritivore or fungivore based on phylogeny and the literature (Chung, 2003). All specimens' body lengths were then measured to an accuracy of 0.01 mm using a compound microscope with a maximum magnification of 50x.

v) Data processing and calculation of response variables

As all beetles were stored in 80% ethanol and therefore, length – mass regressions were performed in order to discern dry weight of individuals (mg). Multiple length – mass regressions were available for certain families, in such situations the regression with the most appropriate minimum and maximum values were selected. In instances where family specific calculations were not available, a general coleopteran inferred equation was used. See Appendix for all length mass regressions used (Table 9).

To obtain individual metabolic rates a liner equation based on the metabolic theory of ecology (MTE) was utilised without fixed values (Downs *et al.* 2008).

$$I = i_0 M_a e^{-\frac{E}{kT}}$$

I is metabolic rate, i_0 a normalisation factor, M is mass, a is the allometric exponent, E the activation energy (eV), k is Boltzmanns constant ($8.62 \times 10^{-5} K^{-1}$) and T temperature in Kelvin. Values for i_0 , a and E values were taken from Ehnes *et al.* 2011's coleopteran phylogenetic model.

Search rate was obtained using the 2D size scaling model (Pawar *et al.* 2012; Dell *et al.* 2014) based on mass of individuals to obtain per gram search rate:

$$a = a_0 M_c^p e^{-\frac{E}{kT}}$$

a is search rate, a_0 is allometric scaling factor, M is mass of individual and p is mass based scaling exponent, k is Boltzmanns constant ($8.62 \times 10^{-5} K^{-1}$) and T temperature in Kelvin.

vi) Modelling

All modelling was carried out in R (version 3.1.2) by creating my own functions based on the formula below.

Metabolic flux:

$$F = \left(\frac{1}{e}\right) \times \left(\sum MR_r + L\right)$$

To compare metabolic flux I utilised the Barnes *et al.* 2014 model for energy flux on the dataset, where F is flux, e is assimilation efficiency, MR_r is individual metabolic rate of resources and L is loss. Metabolic flux was calculated at every trophic node ($n = 5$), i.e. Predators, herbivores etc. These were then summed together to get total metabolic flux ((see Figure 1).

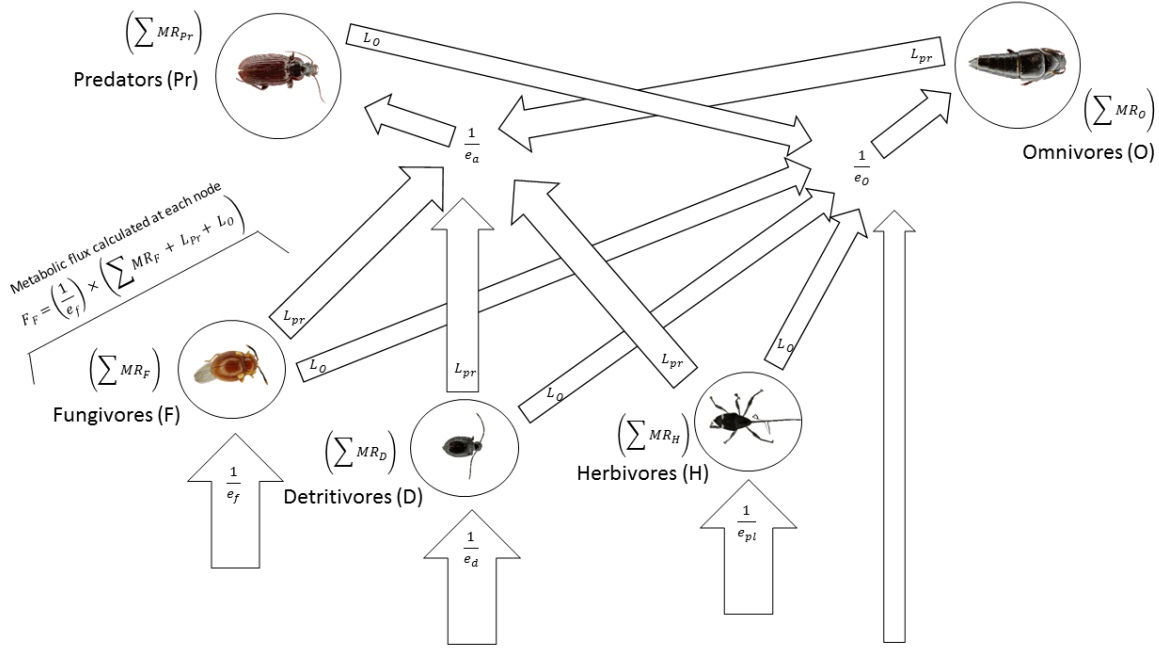


Figure 1: Diagrammatic representation of Barnes *et al.* (2014) model for metabolic energy flux, MR is metabolic rate, e is assimilation efficiency, L is loss. Metabolic flux is calculated at each trophic node, one divided by the assimilation efficiency is multiplied with the community metabolic rate of that trophic group (the sum of all individual metabolic rates) and loss is added on to obtain metabolic flux at each node. Loss is calculated from the metabolic rate of consumers multiplied by their preference for that trophic group.

Consumption flux:

$$C = e \times \left(p \times \left(\sum a\right)\right) \times \left(\sum M_r\right) \times \left(\sum M_c\right)$$

C is consumption flux, e is assimilation efficiency, p is preference, a is the search rate (per gram of beetles), and M is mass. Subscript r and c refer to resources and consumers. Preference of consumers was based on the simple assumption that predators fed equally from the 4 other beetle trophic guilds

($p_{pr} = 0.25$) while omnivores fed equally from all 5 guilds, including plant resources based on above ground biomass data ($p_o = 0.2$). Assimilation efficiencies were taken from the literature and were based on the resource being consumed (de Ruiter *et al.* 1993); if from another animal $e_a = 0.6$ if from plant matter $e_{pl} = 0.45$. Preference was manually altered to check the robustness of models. Consumption flux was calculated between every link in the food web ($n = 10$), i.e. resources – herbivores, herbivores – predators, predators – omnivores etc. Each links flux was then summed together to obtain total consumption flux (see Figure 2).

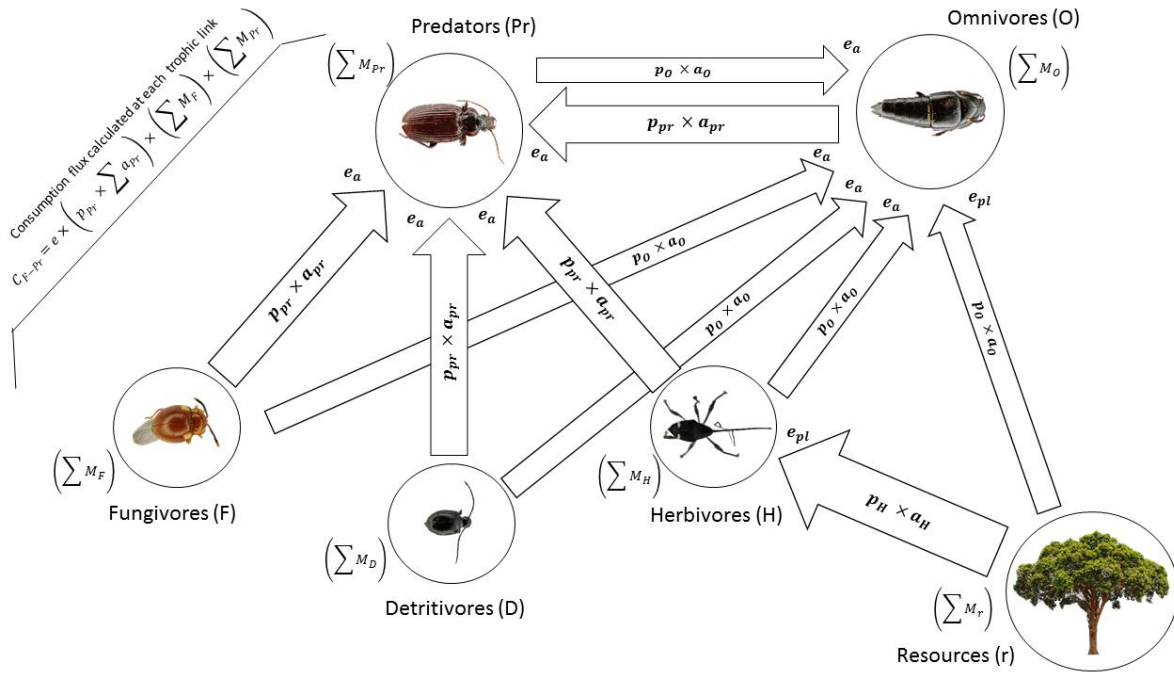


Figure 2: A diagrammatic representation of our proposed model of consumption based flux. p = preference of a consumer towards a certain group, a = search rate of that consumer, e = assimilation efficiency and M = mass. Width of arrows between nodes is weighted by preference. Consumption flux is calculated at each link, preference of the consumer is multiplied by the sum of the search rate of the consumer group to get the per capita proportion of search rate used in that link. This is multiplied with assimilation efficiency and the community biomass of the resources (the sum of individual masses) to obtain per capita consumption rate. This is then multiplied by the community biomass of consumers (the sum of individual masses) to give the consumption flux of that particular link.

vii) Statistical analysis

All statistical analysis was performed in R (version 3.1.2), extrapolated family richness was generated using rarefied, bootstrap, chao, jackknife 1.0 and jackknife 2.0 in the package *vegan* (Oksanen *et al.* 2015). These tests are widely used to estimate the number of undetected families in biodiversity assessments (Colwell *et al.* 2004). Packages *car* and *permute* were also used in this part of the analysis (Fox and Weisberg, 2011; Simpson, 2014) (See appendix, table 10 for respective equations for each estimated family richness test). For family richness analysis one way ANOVAs with welch correction were utilised to test for significance since variance was deemed to be non-homogenous from histograms. Data was cleaned and organised using *dplyr* and *reshape2* (Wickham and Francois, 2015; Wickham, 2007). Gaussian Generalised linear models (GLMs) were used to test for differences in variance of observed family richness, community biomass, consumption flux and metabolic flux. Overdispersion in the data was tested by comparing residual deviance to the degrees of freedom, however there was no presence of overdispersion. The data was also checked for normality and heteroscedasticity utilising quantile – quantile plots to ensure that residuals were equally varied. AIC values were used to compare robustness of models. All figures were made in *ggplot2* and lattices were made using *GridExtra* (Wickham, 2009; Auguie, 2015).

4) RESULTS

i) Biodiversity and abundance

A total of 48 different beetle families were found in the 3044 individuals across 22 line transects from 3 sampling sites.

A Gaussian GLM of observed family richness against sampling site shows that SAFE's observed family richness is significantly higher than other sites, Maliau is not significantly different from the other sites and Danum is significantly lower (See Table 1). SAFE displays the highest observed family richness and Danum the lowest. (See Figure 3). One way ANOVAs of expected family estimates extrapolated from bootstrap, chao, jackknife 1.0 and jackknife 2.0 show that observed family richness is significantly lower than expected at all sites (See Table 2). This demonstrates that sampling effort was inadequate at all sites (See Figures 4). Above ground biomass is not significantly correlated to absolute abundance of beetles across sites, or within sites (See Table 4); except for SAFE where it is significant (See Figure 5).

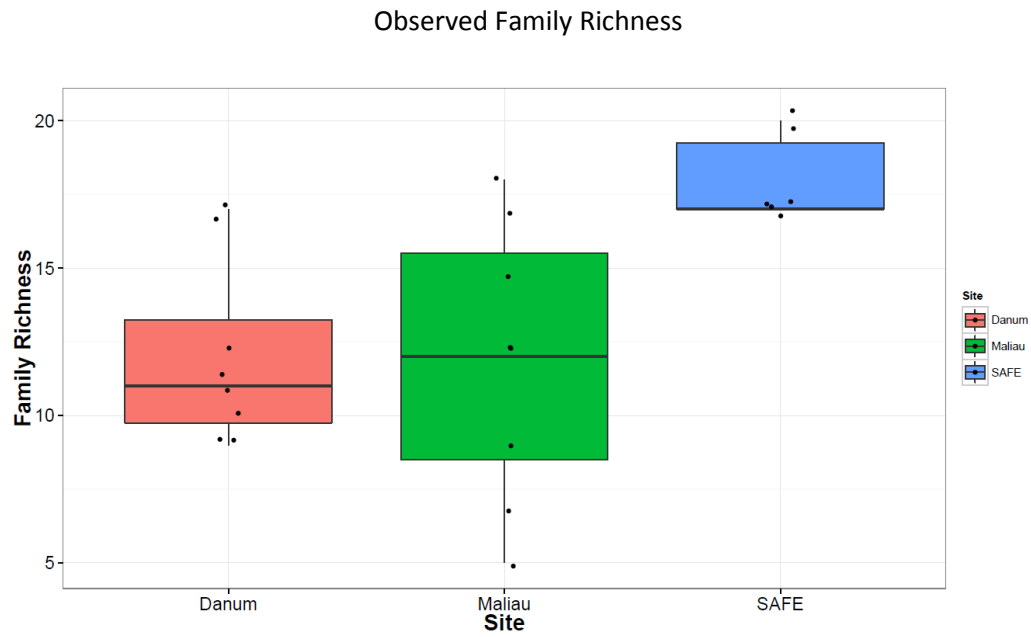


Figure 3: Boxplot plot showing the number of different families recorded at different sampling sites.

Table 1: Table displaying results of Gaussian GLM (Observed family richness ~ Site).

Site	Degrees of freedom	t value	<i>P value</i>
Danum	19	9.572	<0.001
Maliau	19	-0.071	0.945
SAFE	19	3.137	0.005

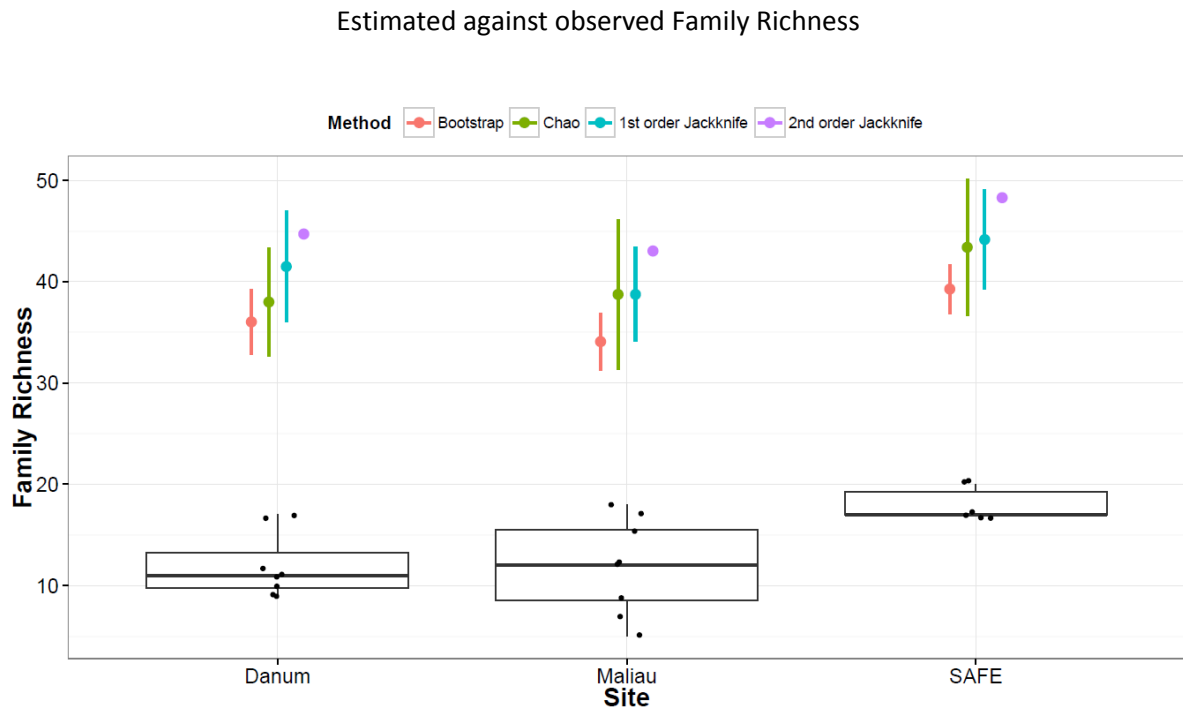


Figure 4: Boxplots displaying observed family richness of sampling sites and estimated species richness extrapolated from bootstrap, chao, jackknife 1.0 and jackknife 2.0 tests, suggesting that the sampling effort was inadequate and that although none of the observed family richness levels are realistic to the natural system SAFE was the closest.

Table 2: Results of one way ANOVAs on proportion of observed to estimated site richness ~ site.

Test	Degrees of freedom numerator	Degrees of freedom Denominator	F statistic	<i>P value</i>
Bootstrap	2.00	11.619	7.21296	0.009
Chao	2.00	11.569	6.0123	0.016
Jackknife 1.0	2.00	11.67	8.2026	0.006
Jackknife 2.0	2.00	11.66	7.8446	0.007

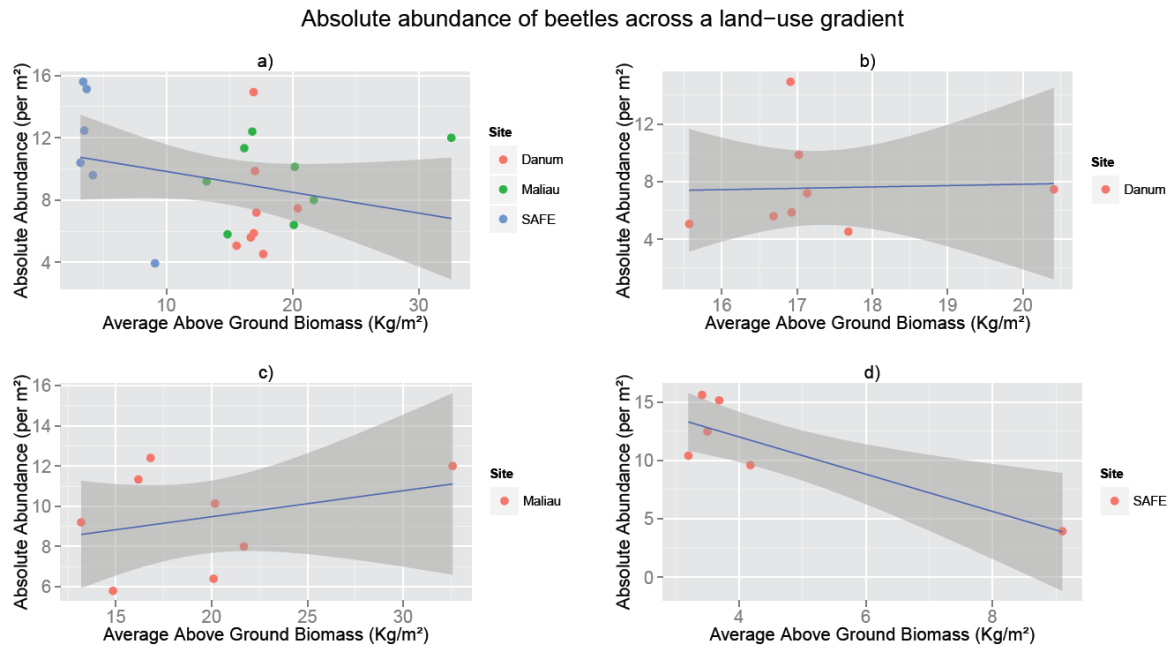


Figure 5: Scatterplots showing the relationship between absolute abundance of beetles and above ground biomass, plotted with a Gaussian GLM regression and 95% confidence intervals. A) All sites, b) Danum, c) Maliau, d) SAFE. Above ground biomass is not significant in explaining the variance observed in absolute abundance of beetles across sites, and within sampling sites is only significant at SAFE. (See Table 3).

Table 3: Displays results of Gaussian GLM Absolute abundance ~ Above ground biomass at all sites and within sites.

Site	Degrees of freedom	t value	<i>P value</i>
All	20	-1.303	0.207
Danum	6	0.093	0.929
Maliau	6	0.805	0.452
SAFE	4	-3.122	0.035

ii) Consumption Flux

Variance in consumption flux is significantly explained by the observed family richness across sampling sites and within Danum and Maliau (See Table 4). Consumption flux is significantly higher with increased family richness (See Figure 6). Total consumption flux variance is not significantly explained by above ground biomass across all of the sites however it is significant within all sites (See Figure 7). This shows that ecological functioning is maintained in heterogeneous logged forests but within homogenous habitat types variance is significantly explained by forest quality. Total consumption flux is also significantly explained by absolute abundance of beetles across all of the sites (See Table 6) however within sites this trend is only observed at SAFE (See Figure 8).

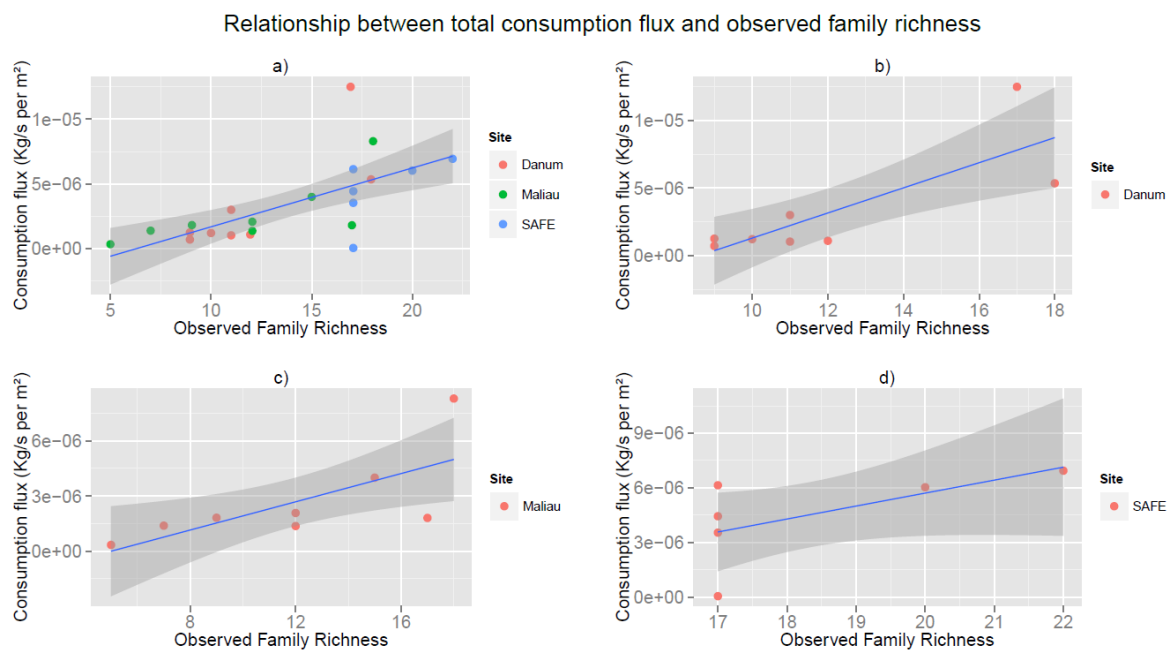


Figure 6: Scatterplot showing the relationship between consumption rate and observed family richness, plotted with a Gaussian GLM regression and 95% confidence intervals. a) All sites, b) Danum, c) Maliau, d) SAFE. Variance in consumption flux is significantly explained by family richness across all sites and within all sites apart from SAFE.

Table 4: Displays results of Gaussian GLM (Consumption flux ~ Family Richness) at all sites and within sites.

Site	Degrees of freedom	t value	<i>P</i> value
All	20	4.009	<0.001
Danum	6	3.293	0.017
Maliau	6	2.508	0.046
SAFE	4	1.542	0.198

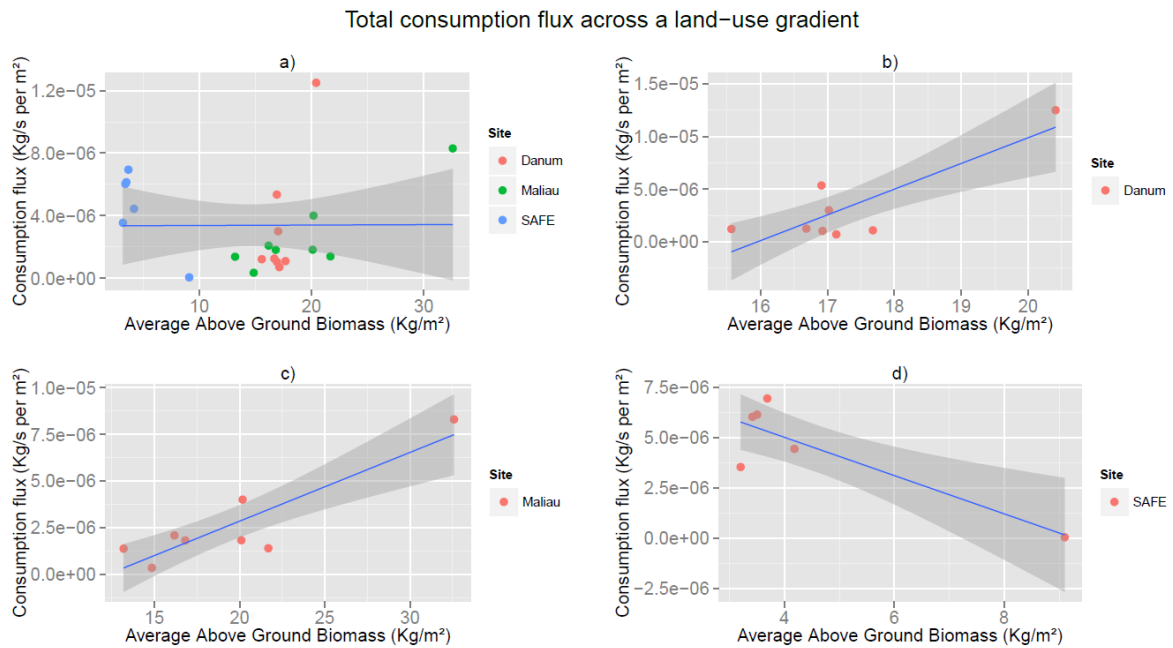


Figure 7: Total consumption rate across land-use gradients with GLM regression and 95% confidence intervals. A) All sites, b) Danum, c) Maliau, d) SAFE. Above ground biomass was significant in explaining variance within all sites; positively correlated in old growth sites (Danum and Maliau) and negatively correlated at SAFE. Above ground biomass was not significant in explaining variation in consumption flux across all sites suggesting consumption flux is maintained across heterogeneous land-use types (See Table 7). The GLM for total consumption flux ~ to above ground biomass has an AIC value of -490.64.

Table 5: Displays results of Gaussian GLM Total consumption flux ~ Above ground biomass at all sites and within sites

Site	Degrees of freedom	t value	<i>P value</i>
Total	20	0.027	0.979
Danum	6	3.835	0.008
Maliau	6	4.776	0.003
SAFE	4	-3.316	0.029

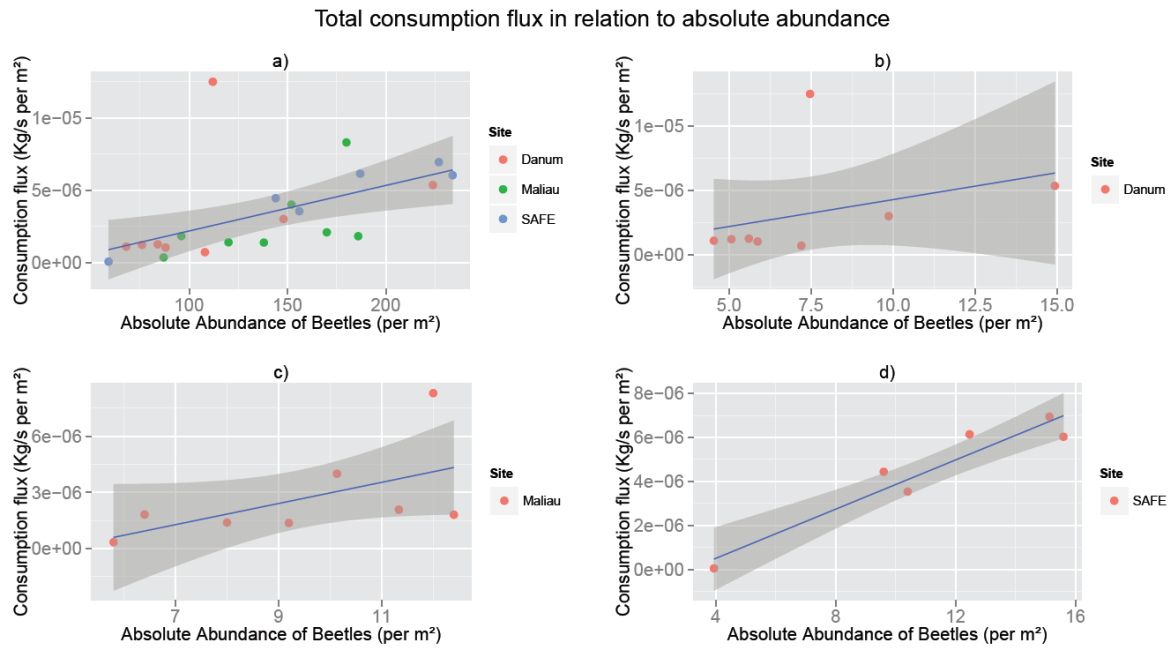


Figure 8: Scatterplot showing relationship between consumption rate and observed absolute abundance, plotted with a Gaussian GLM regression and 95% confidence intervals, a) All sites, b) Danum, c) Maliau, d) SAFE.

Table 6: Displays results of Gaussian GLM Total consumption flux ~ Absolute abundance at all sites and within sites.

Site	Degrees of freedom	t value	<i>P value</i>
All	20	2.865	0.009
Danum	6	0.928	0.389
Maliau	6	1.679	0.144
SAFE	4	6.309	0.003

iii) Metabolic Flux

Metabolic flux is significantly higher in sites with higher observed family richness, variance in flux is significantly explained by family richness across all sites (Gaussian GLM, $df = 20$, $t = 4.360$, $p = <0.001$).

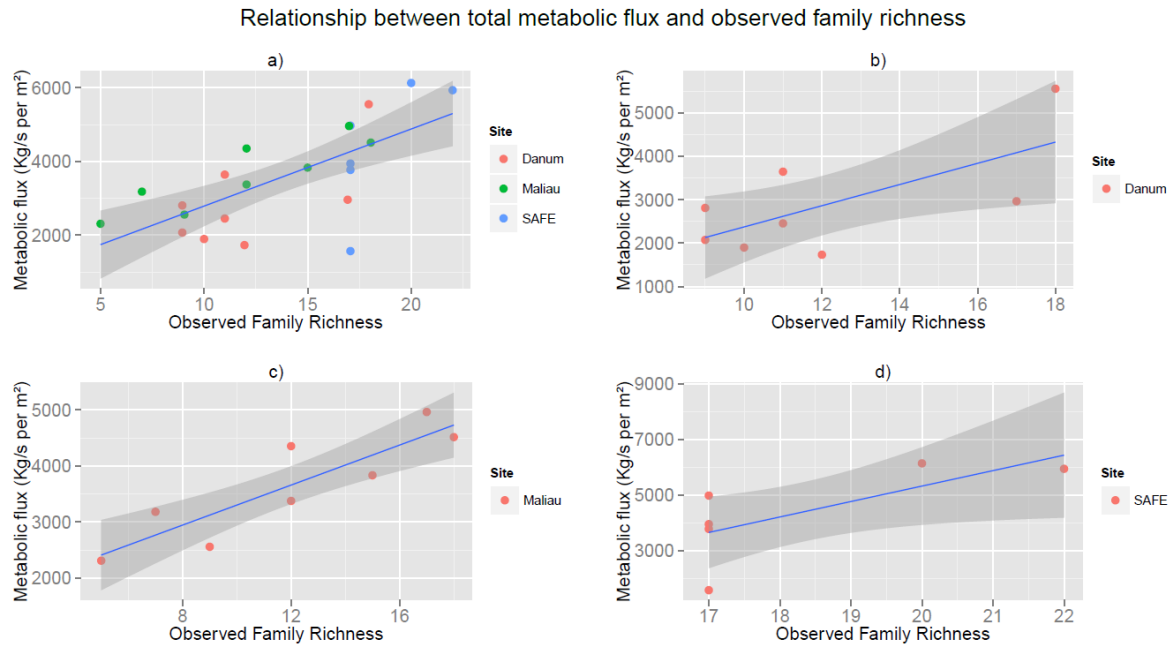


Figure 9: Lattice of scatter plots showing relationships between metabolic flux and observed family richness, plotted with Gaussian GLM regressions with 95% confidence intervals. These show a significant positive correlation between observed family richness and metabolic flux across all of the sites. However when comparing within sites at Danum the correlation was weakly significant, at Maliau it was significant and at SAFE was not significant (See Table 7).

Table 7: Displays results of Gaussian GLM Total metabolic flux ~ observed family richness at all sites and within sites.

Site	Degrees of freedom	t value	<i>P</i> value
All	20	4.360	<0.001
Danum	6	2.286	0.0623
Maliau	6	4.550	0.004
SAFE	4	2.017	0.114

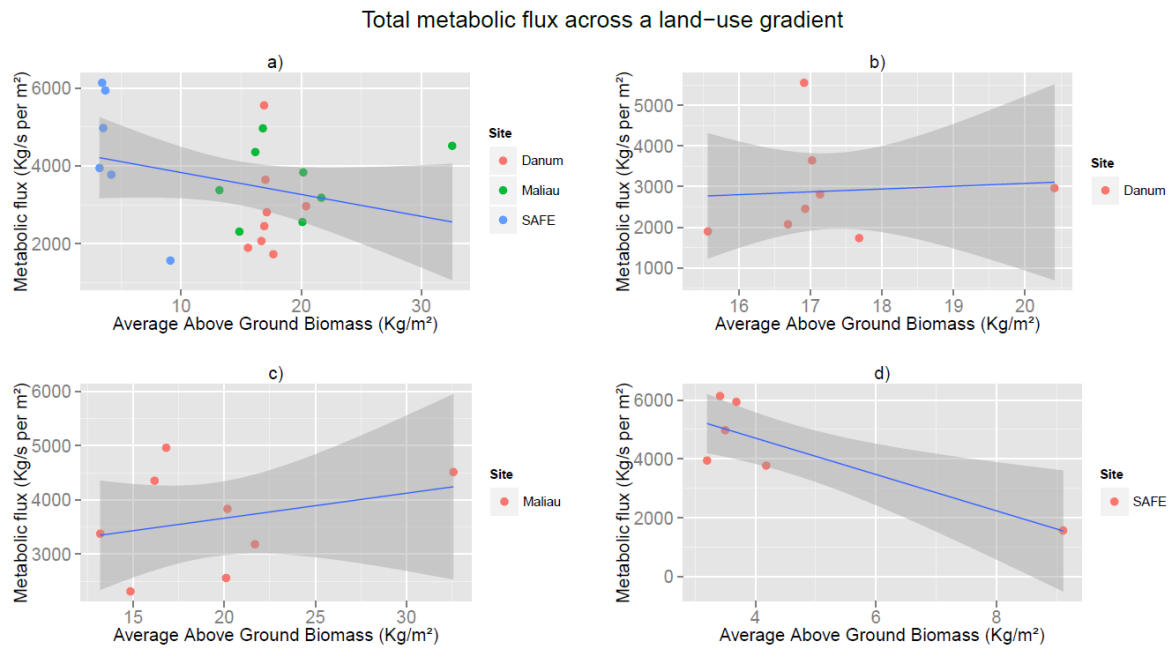


Figure 10: Lattice of scatter plots showing the relationships between metabolic flux and above ground biomass plotted with Gaussian GLM regressions with 95% confidence intervals. These demonstrate no significant correlation between total metabolic flux and above ground biomass across all sites. Within sites the relationship was also no significant at Danum and Maliau, however it was negatively significant at SAFE (See Table 8).

Table 8: Displays results of Gaussian GLM Total metabolic flux ~ Above ground biomass at all sites and within sites

Site	Degrees of freedom	t value	<i>P value</i>
All	20	-1.430	0.168
Danum	6	0.191	0.855
Maliau	6	0.756	0.479
SAFE	4	-2.971	0.041

5) DISCUSSION

Anthropogenic pressures are increasingly changing natural habitats, these alterations have many direct and indirect effects on biodiversity, flux and ecological functioning. Here, I provide evidence that ecological functioning within homogenous primary habitat types is significantly positively correlated with above ground biomass, suggesting that an increase in forest quality will indirectly result in an increase in ecological functioning; inferred from consumption flux (See Figures. 7b; 7c). These results are consistent with other studies documenting significant shifts in levels of ecological functioning across land use gradients (Barnes *et al.* 2014), which showed the same correlation across more extreme types of land-use which may explain the increased significance of their results. We also present evidence that ecological functioning is maintained across degraded heterogeneous habitat types (consumption flux; See Figure. 7a). This is due to a plethora of factors; increased abundance of beetles (see Figure. 8), increased family richness (see Figure. 6), net primary production in logged forest is reported to be higher than old growth (T. Riutta, pers comms) and could in part be explained by the intermediate disturbance hypothesis (Connell, 1978). This suggests that although there may be loss of environmentally sensitive species these are compensated for by robust disturbance tolerant counterparts (Larsen *et al.* 2005). This demographic response to disturbance indicates that the tropical forests of Sabah represent a resilient ecosystem up to an undiscerned threshold of logging (Walker, 1992). This is a key observation when trying to predict human induced impacts of land use on ecosystem functioning. It is especially important when considering a recent estimate which suggests that 46% of tropical forests globally are fragmented and another 30% are degraded (Lewis *et al.* 2015). The wider implications of this result require validation on a larger scale. If ecological functioning is maintained in logged forests ubiquitously this highlights the importance of degraded forests as a valuable conservation tool globally.

Furthermore these results demonstrate a significant relationship between biodiversity (family richness) and ecological functioning (See Figure. 6). As previously mentioned although this relationship has been established previously *in situ* (Hooper *et al.* 2005; Foster *et al.* 2011), it has been rarely assessed using a natural ecosystem. The results of a significant relationship family richness and ecological functioning could be used to lend support to the hypothesis that the mechanism driving the association between biodiversity and ecological functioning is that species richness increases ecosystem functioning through species interactions. This would create more links in the food-web, utilisation of different resources, spatial or temporal separation of resource use which results in an increased use of total available resources (Vandermeer, 1998).

Surprisingly, there was a significantly higher observed biodiversity at SAFE (twice logged forest) in comparison to either of our primary forest sites (See Figure 3). This is in consensus with Connell's intermediate disturbance hypothesis (Connell, 1978). The significantly higher species richness in logged forest could have been due to the ability of disturbance tolerant species to colonise logged forest rapidly. Furthermore, leaf litter in disturbed forests is dominated by increased proportions of grasses and herbaceous species which have decreased quantitative chemical defences (i.e. tanins) in comparison to woody species characteristic of primary forests (Coley and Barone, 1996). This decrease in chemical defences may make resources available in logged forests higher quality as a source of nutrients for invertebrates (Hassall and Rushton, 1984), therefore explaining the significantly higher species richness of logged sites in comparison to old growth. On the contrary, previous investigations in the same study sites which have repeatedly shown a decrease in biodiversity and functional response of beetles with intensifying land-use. Ewers *et al.* (2015) demonstrated that the functional abundance of predatory beetles decreased by up to half in logged sites. However, this disparity may be explained by the fact that the basal species of food webs are expected to follow the intermediate disturbance hypothesis (Wootton, 1998), whereas top consumers within Coleoptera do not (Lovei and Sunderland, 1996). Another investigation into the beta and gamma diversity of beetles at the same study sites showed a similar decrease in biodiversity across land-use gradients (Sharpe *et al.* Unpublished). The disparity in results could be due to different trapping methodologies, whilst this investigation sampled 1m² leaf litter collecting all beetles, their methodologies used modified flight intercept/pitfall traps which targeted only mobile beetles. The differing results may have been due therefore to the fact the beetles being targeted have completely different life histories, and evidently different responses to disturbance.

Another study which compared Danum to logged forest found no significant difference between abundance and species richness however found a significant increase in abundance and species richness of disturbance tolerant species in agricultural land (Hassall *et al.* 2006). Such results may suggest that this investigation was constrained by its lack of agricultural land use type, patterns may be more easily observable over more extreme land-use type comparisons. This considered extrapolated family richness tests have demonstrated that there was significant difference between observed family richness and expected family richness for every test used (See Figure. 4). This result suggests that sampling effort was inadequate and observed family richness was not representative of the true system. Biodiversity levels may in actual fact be very different to the results reported in this investigation. This notion is loosely supported by the fact that a meta-analysis found that higher trapping effort is needed in the tropics for catching all or at least a representative proportion of the

fauna (Rainio and Niemela, 2003). This study suffers from its lack of true repeats, an increased sampling effort may compensate for the disparity between observed and actual family richness.

These constraints could have far reaching implications on the resulting models and conclusions; perhaps a maintenance of ecological functioning in degraded heterogeneous habitat types was due to unobserved higher biodiversity in old growth sites which other studies have reported but was not represented in our primary data (Ewers *et al.* 2015; Sharpe, Unpublished).

i) Model comparison and limitations

Until this point the consumption flux model has been utilised as the proxy of ecological functioning rather than the metabolic flux model. This is primarily due to the AIC values which demonstrate that our consumption model was the more robust model (Consumption flux = -490.64; Metabolic flux = 382.94). Although using metabolic rate may give more insight into energy requirements and demands of individuals or a group it negates consumer resource interactions and fails to determine how often consumers and resources encounter each other, which is imperative when modelling a system and how energy flows through it (Benedetti-Cecchi, 2000; Pawar *et al.* 2012). The main differences between the models stem from our quantification of primary resources and the location of calculations; at links or nodes. In a review of models calculating flux the model to emerge as the most robust was the metabolic action model (MA) (Rueman and Cohen, 2005). This model is most similar to our consumption rate model as despite its name it utilises the consumption rate of predators and the population production of prey. This model also calculates flux between links. To calculate flux at nodes is intuitively nonsensical because when calculating flux it is necessary to determine how much energy is flowing through a system, not how much energy is at each node, by calculating efficiency at each node and it reduces the validity of assimilation energies. It is important to consider that our assumptions on preferences of consumers (based on simple fractions of how many other trophic groups it was feeding on) may produce inaccuracies in the model as it does not take into account the ratio of predator – prey body sizes (Emmerson and Raffaelli, 2004). This may be especially true when considering our data set, for example the most abundant predator subfamily present were the Pselaphines. These are relatively small bodied (highest recorded length <3mm) and are myrmeceophiles that predominantly feed on ants (Chung, 2003), and therefore realistically would obtain minimal energy from other beetles. However, this is not reflected in the model as the model concentrates on just one taxa and certain assumptions had to be made.

Further investigation would benefit from calculating and discerning appropriate body size ratios for predator-prey relationships that could physically feed on each other. In addition to this it would be more accurate to select validated feeding pairs, rather than just all individuals in one trophic group feed on all individuals of another group. This raises the issue that modelling flux for just one taxa is an

unrealistic assessment of any system; it ignores varied and complex species interactions outside of the focal taxa. It also negates the effect of trophic cascades of higher trophic orders (Berger *et al.* 2008; Woodward *et al.* 2008). It may in fact be that ecological functioning is lost in higher orders with logging. Evidence suggests that mammals are particularly sensitive to anthropogenic processes, due to inherent biological traits such as large body size which increases probability of hunting and is also indicative of a slower reproductive cycle (Cardillo *et al.* 2005). Extirpation of apex organisms in a system would have huge effects on flux, but this is not represented when examining just one taxa. Temperature is also an important consideration when calculating flux, because it effects the rates of species interaction and metabolic demands in a systematic nature (Dell *et al.* 2014). It effects the ecological and physiological traits of organisms (encounter rate and metabolic rate) which has direct impacts on resultant flux. This highlights the possible adverse effect of utilising different methods of collecting temperature data. In the future, investigation methods should be standardised, however it was not possible in this instance.

ii) Conclusions

Despite the above mentioned limitations, I still provide sufficient evidence that ecological functioning within homogenous habitat types is significantly correlated with disturbance (above ground biomass). In addition to this, I have shown that across heterogeneous land use gradients, ecological functioning within Coleoptera is maintained, which indicates that this taxa in Bornean tropical forests is resilient to logging based disturbance. This highlights the importance of logged forests as a valuable conservation tool. I provide a comprehensive model that can be used for assessing ecological functioning in any multi-trophic group in any system globally. In addition to suggestions for model improvement, I have also presented a real world example that ecological functioning is directly linked with biodiversity and although a forests level of ecological functioning is more than the sum of its species composition and abundance. When used in conjunction with each other biodiversity and abundance are suitable as loose indicators of ecosystems functioning.

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7) REFERENCES

- Auguie, B., & RGraphics, S. Package 'gridExtra'. (2012).
- Barnes, A. D., Jochum, M., Mumme, S., Haneda, N. F., Farajallah, A., Widarto, T. H. and Brose, U. Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. *Nature communications*, **5**: (2014).
- Benedetti-Cecchi, L. Variance in ecological consumer-resource interactions. *Nature*. **407**: 370-374. (2000)
- Berger, K. M., Gese, E. M. and Berger, J. Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. *Ecology* **89**: 818-828 (2008).
- Burivalova, Z., Şekercioğlu, Ç. H. and Koh, L. P. Thresholds of logging intensity to maintain tropical forest biodiversity. *Current biology* **24**: 1893-1898 (2014)..
- Brown, T. J., Hall, B. L., and Westerling, A. L. The impact of twenty-first century climate change on wildland fire danger in the western United States: an applications perspective. *Climatic change* **62**, 365-388 (2004).
- Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R., Sechrest, W., Orme, C.D.L and Purvis, A. Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239-1241 (2005).
- Cardinale, B. J., Harvey, C. T., Gross, K., and Ives, A. R. Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters* **6**, 857-865 (2003).
- Cardinale, B. J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M. and Jouseau, C. Effects of biodiversity on the functioning of trophic groups and ecosystems. – *Nature* **443**, 989–992 (2006).
- Carter, C., Finley, W., Fry, J., Jackson, D. and Willis, L. Palm oil markets and future supply. *European Journal of Lipid Science and Technology* **109**, 307-314 (2007).
- Chung, A.Y.C. Manual for bornean beetle (Coleoptera) family identification. *The course on tools for monitoring soil biodiversity in the ASEAN region at University Malaysia SABAH, Kota Kinabulu* (2003).

- Clay, J. World agriculture and the environment: A commodity-by-commodity guide to impacts and practices. Island Press, Washington, D.C (2004).
- Coley, P. D. & Barone, J. A. Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* **27**, 305–335 (1996).
- Colwell, R. K., Mao, C. X. and Chang, J. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* **85**, 2717-2727 (2004).
- Connell, J. H. Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302-1310 (1978).
- Dell, A. I., Pawar, S., and Savage, V. M. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology* **83**, 70-84 (2014).
- De Ruiter, P. C., Van Veen, J. A., Moore, J. C., Brussaard, L. and Hunt, H. W. Calculation of nitrogen mineralization in soil food webs. *Plant and Soil* **157**, 263-273 (1993).
- Downs, C. J., Hayes, J. P., & Tracy, C. R. Scaling metabolic rate with body mass and inverse body temperature: a test of the Arrhenius fractal supply model. *Functional Ecology* **22**, 239-244 (2008).
- Duffy, J. E. Biodiversity and ecosystem function: the consumer connection. *Oikos* **99**, 201-219 (2002).
- Duffy, J. E., Cardinale, B. J., France, K. E., McIntyre, P. B., Thébault, E. and Loreau, M. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology letters* **10**, 522-538 (2007).
- Edwards, D. P., Woodcock, P., Edwards, F. A., Larsen, T. H., Hsu, W. W., Benedick, S. and Wilcove, D. S. Reduced-impact logging and biodiversity conservation: a case study from Borneo. *Ecological Applications* **22**, 561-571 (2012)
- Ehnes, R. B., Rall, B. C. and Brose, U. Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates. *Ecology Letters* **14**, 993-1000 (2011).
- Emmerson, M. C. and Raffaelli, D. Predator–prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology* **73**, 399-409 (2004).
- Enquist, B. J., Kerkhoff, A. J., Stark, S. C., Swenson, N. G., McCarthy, M. C. and Price, C. A. A general integrative model for scaling plant growth, carbon flux, and functional trait spectra. *Nature* **449**, 218-222 (2007).

- Ewers, R. M. and Didham, R. K. Pervasive impact of large-scale edge effects on a beetle community. *Proceedings of the National Academy of Sciences* **105**, 5426-5429 (2008).
- 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 of London B: Biological Sciences*, **366**, 3292-3302.
- Ewers, R. M., Boyle, M. J., Gleave, R. A., Plowman, N. S., Benedick, S., Bernard, H., Bishop, T.R., Bakhtiar, E.Y., Chey, V.K., Chung, A.Y.C., Davies, R.G., Edwards, D.P., Eggleton, P., Fayle, T.M., Hardwick, S.R., Homathevi, R., Kitching, R..L., Khoo, M.S., Luke, S.H., March, J.J., Nilus, R., Pfeifer, M., Rao, S.V., Sharp, A.C., Snaddon, J.L., Stork, N.E., Struebig, M.J., Wearn, O.R., Yusah, K.M., Yusah, K.M. Turner, E. C. Logging cuts the functional importance of invertebrates in tropical rainforest. *Nature communications*, **6** (2015).
- Fagundes, C. K., Di Mare, R. A., Wink, C., and Manfio, D. 2011. Diversity of the families of Coleoptera captured with pitfall traps in five different environments in Santa Maria, RS, Brazil. *Brazilian Journal of Biology* **71**, 381-390.
- Fayle, T. M., Turner, E. C., Snaddon, J. L., Chey, V. K., Chung, A. Y., Eggleton, P. and Foster, W. A. Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. *Basic and Applied Ecology* **11**, 337-345 (2010).
- Fisher, B., Edwards, D.P., Giam, X. and Wilcove, D.S. The high costs of conserving Southeast Asia's lowland rainforests. *Front. Ecol. Environ.* **9**, 329–334 (2011).
- Fitzherbert, E. B. *et al.* How will oil palm expansion affect biodiversity? *Trends Ecol. Evol.* **23**, 538–545 (2008).
- 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. Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **366**, 3277–3291 (2011).
- Fox, J., and Weisberg, S. (2011). Car: companion to applied regression Available at: <http://CRAN.R-project.org/package=car> Accessed, 2015 (2011).
- Gaveau, D. A., Sloan, E. Molidena, D. Sheil, N. J. Abram, M. Ancrenaz, R. Nasi, M. Quinones, N. Wielaard, and E. Meijaard. Four decades of forest persistence, clearance and logging on Borneo. *PLoS ONE* **9**:e101654 (2014).

- Gibbs, H. K. *et al.* Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proc. Natl Acad. Sci. USA* **107**, 16732–16737 (2010).
- Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J. and Sodhi, N. S. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* **478**, 378–381 (2011).
- Gilbert, N. Palm-oil boom raises conservation concerns. *Nature* **487**, 14–15 (2012).
- Gillespie, R. G., Baldwin, B. G., Waters, J. M., Fraser, C. I., Nikula, R. and Roderick, G. K. (Long-distance dispersal: a framework for hypothesis testing. *Trends in Ecology & Evolution* **27**, 47–56 (2012).
- Gotelli, N. J. and Colwell, R. K. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology letters* **4**, 379–391 (2001).
- Handa, I. T., Aerts, R., Berendse, F., Berg, M. P., Bruder, A., Butenschoen, O., Chauvet, E., Gessner, M.O., Jabiol, J., Makkonen, M., Mckie, B.g., Malmqvist, B., Peeters, E.T.H., Scheu, S., Schmid, B., Ruijven, J., Veronique, C.A. and Hättenschwiler, S. Consequences of biodiversity loss for litter decomposition across biomes. *Nature* **509**, 218–221 (2014).
- Hassall, M. and Rushton, S.P. Feeding behaviour of the terrestrial isopods in relation to plant defences and microbial decay S.L. Sutton, D. Holdich (Eds.), Proceedings of the Zoological Society of London Symposium No. 53. The Biology of Terrestrial Isopods pp. 487–505 (1984).
- Hassall, M., Jones, D. T., Taiti, S., Latipi, Z., Sutton, S. L. and Mohammed, M. Biodiversity and abundance of terrestrial isopods along a gradient of disturbance in Sabah, East Malaysia. *European Journal of Soil Biology* **42**, S197–S207 (2006)
- Hijman, R.J. & Etten, J.V. (2012). Raster: Geographic analysis and modelling with raster data. R package version 2.0-12. <http://CRAN.R-project.org/package=raster>.
- Hooper, D. U. and Dukes, J.S. Overyielding among plant functional groups in a long-term experiment. *Ecology Letters* **7**, 95–105(2004).
- 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., Setela, H., Symstad, A.J., Vandermeer, J. and Wardle, D. A. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* **75**, 3–35 (2005).

Ives, A. R. and Cardinale, B. J. Food-web interactions govern the resistance of communities after non-random extinctions. *Nature* **429**, 174-177 (2004).

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

Larsen, T. H., Williams, N. M., & Kremen, C. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology letters* **8**, 538-547 (2005).

Lewis, S.L., Edwards, D.P. and Galbraith, D. (2015). Increasing human dominance of tropical forests. *Science*. **349**: 827 - 832

Loreau, M. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**, 3-17 (2000).

Lövei, G. L. and Sunderland, K. D. Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual review of entomology* **41**, 231-256 (1996).

Marsh, C. W. and Greer, A. G. Forest land-use in Sabah, Malaysia: an introduction to Danum Valley. *Philosophical Transactions of the Royal Society B: Biological Sciences* **335**, 331-339 (1992).

Nilsson-Örtman, V., and A. N. Nilsson. 2010. Using taxonomic revision data to estimate the global species richness and characteristics of undescribed species of diving beetles (Coleoptera: Dytiscidae). *Biodiversity Informatics* **7**:1–16

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B. and Oksanen, M. J. Package 'vegan'. *Community ecology package, version, 2-2* (2015).

Pawar, S., Dell, A. I. and Savage, V. M. Dimensionality of consumer search space drives trophic interaction strengths. *Nature* **486**, 485-489 (2012).

Petchey, O. L. Species diversity, species extinction, and ecosystem function. *The American Naturalist* **155**, 696-702 (2000).

Petchey, O. L., Hector, A. and Gaston, K.J. How do different measures of functional diversity perform? *Ecology* **85**, 3:847-857 (2004).

Pfeifer, M., Kor, L., Nilus, R., Turner, E., Khen, C.V., Cusack, J., Lysenko, I., Chung, A., Ewers, R.M. Satellites map the structure of Borneo's tropical forests across a degradation gradient. In Press.

Rainio, J. and Niemelä, J. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity & Conservation* **12**, 487-506 (2003).

- Riutta, Tehri. (2015). Personal Communication. University of Oxford.
- Reuman, D. C., and Cohen, J. E. Estimating relative energy fluxes using the food web, species abundance, and body size. *Advances in ecological research* **36**, 137-182 (2005).
- Reynolds, G., Payne, J., Sinun, W., Mosigil, G. and Walsh, R. P. Changes in forest land use and management in Sabah, Malaysian Borneo, 1990–2010, with a focus on the Danum Valley region. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 3168-3176 (2011).
- Sabu, T. K., Shiju, R. T., Vinod, K. V. and Nithya, S. A comparison of the pitfall trap, Winkler extractor and Berlese funnel for sampling ground-dwelling arthropods in tropical montane cloud forests. *Journal of Insect Science* **11**, 28 (2011).
- Sha, J.C.M., Matsuda, I. & Bernard, H. The Natural History of the Proboscis Monkey. *Natural History Publications (Borneo) Sdn. Bhd.* **126** (2011).
- Sharpe, A.C., (Unpublished). Relating beta-diversity to distance and disturbance in Borneo's disturbed tropical forests. A thesis submitted for the partial fulfilment of the requirements for the degree of Master of Science/Research at Imperial College London. 2014.
- Simpson, G. L. permute: Functions for generating restricted permutations of data. R package version 0.8–3. (2014).
- Sodhi, N.S., Koh, L.P., Clements, R., Wanger, T.C., Hill, J.K., Hamer, K.C., Clough, Y., Tschardtke, T., Posa, M.R.C. & Lee, T.M. Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biol. Conserv.* **143**, 2375–2384 (2010).
- Stokstad, E. Loss of dung beetles puts ecosystems in deep doo-doo. *Science*, **305** 1230-1230 (2004).
- Struebig, M. J., Turner, A., Giles, E., Lasmana, F., Tollington, S., Bernard, H., and Bell, D. Quantifying the biodiversity value of repeatedly logged rainforests: gradient and comparative approaches from Borneo. *Adv. Ecol. Res.* **48**, 183–224 (2013).
- Susilo, F. X. and Indriyati, S. H. Diversity and Abundance of Beetle (Coleoptera) Functional Groups in a Range of Land Use System in Jambi, Sumatra. *Biodiversitas* **10**, 195-200 (2009).
- Turner E.C., Abidin Y.Z., Barlow H., Fayle T.M., Jaafar M.H.H., Chey V.K., Larenus J., Nainar A., Reynolds G., Yusof Y.B., Khoo M.S. and Ewers R.M. The Stability of Altered Forest Ecosystems

Project: Investigating The Design Of Human-Modified Landscapes For Productivity And Conservation. *The Planter, Kuala Lumpur* **88**, 453-46 (2012).

Otto, S. B., Berlow, E.L., Rank, N.E., Smiley, J. and Brose, U. 2008. Predator diversity and identity drive interaction strength and trophic cascades in a food web. *Ecology* **89**, 888 – 888 (2008).

Vandermeer, J., van Noordwijk, M., Anderson, J., Ong, C. and Perfecto, I. Global change and multi-species agroecosystems: concepts and issues. *Agriculture, Ecosystems & Environment* **67**, 1-22 (1998).

Walker, B. H. Biodiversity and ecological redundancy. *Conserv. Biol.* **6**, 18–23 (1992).

Wearn, O. R., Rowcliffe, J. M., Carbone, C., Bernard, H. and Ewers, R. M. Assessing the status of wild felids in a highly-disturbed commercial forest reserve in Borneo and the implications for camera trap survey design. *PLOS ONE* *e77598* (2013).

Wilcove, D. S., Giam, X., Edwards, D. P., Fisher, B. & Koh, L. P. Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends Ecol. Evol.* **28**,531–540 (2013).

Wilcove, D. S. & Koh, L. P. Addressing the threats to biodiversity from oil-palm agriculture. *Biodivers. Conserv.* **19**: 999–1007 (2010).

White, E. P., Ernest, S. M., Kerkhoff, A. J. and Enquist, B. J. Relationships between body size and abundance in ecology. *Trends in ecology & evolution* **22**, 323-330 (2007).

Wickham, H. Reshaping data with the reshape package. *Journal of Statistical Software*, **21**, 1-20 (2007).

Wickham, H., & Chang, W. ggplot2: An implementation of the Grammar of Graphics. R package version 0.8. 3. (2009).

Wickham, H. and Francois, R. dplyr: A Grammar of Data Manipulation. URL <http://CRAN.Rproject.org/package=dplyr>. R package version 0.4.2 (2015).

Wilson, D. S., & Knollenberg, W. G. (1987). Adaptive indirect effects: the fitness of burying beetles with and without their phoretic mites. *Evolutionary Ecology* **1**, 139-159 (1987).

Woodward, G., Ebenham, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. and Warren, P.H. Body size in ecological networks. *Trends in Ecology and Evolution* **20**, 402-409 (2005).

Woodward, G., Papantoniou, G., Edwards, F. and Lauridsen, R. B. Trophic trickles and cascades in a complex food web: impacts of a keystone predator on stream community structure and ecosystem processes. *Oikos* **117**, 683–692 (2008).

Woodward, G. Biodiversity, ecosystem functioning and food webs in fresh waters: assembling the jigsaw puzzle. *Freshwater Biology* **54**, 2171-2187 (2009).

Wootton, J. T. Effects of disturbance on species diversity: a multitrophic perspective. *The American Naturalist* **152**, 803-825 (1998).

8) APPENDIX

Table 9: Table displaying all length mass regressions used for different families, a and b parameters are presented as well as minimum and maximum values.

Family	Length Mass Regression	a	b	Min (mm)	Max (mm)	Reference
Aderidae	$M = a * L^b$	0.0134	2.26	3.34	7.84	(Lang, Krooss & Stumpf, 1997)
Anobiidae	$M = a * L^b$	0.008	3.463	3.35	4.45	(Grunner, 2003)
Anthicidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Anthribidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Biphyllidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Brentidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Carabidae	$M = a * L^b$	0.0237	2.7054	2.88	24.00	(Lang, Krooss & Stumpf, 1997)
Cerambycidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Cerylonidae	$M = a * L^b$	0.007	2.91	2.65	3.79	(Benke <i>et al.</i> 1999)
Chrysomelidae	$M = a * L^b$	3.11	0.039	2.65	3.79	(Benke <i>et al.</i> 1999)
Ciidae	$M = a * L^b$	0.0247	3.102	1.45	2.45	(Grunner, 2003)
Clambidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Coccinellidae	$M = a * L^b$	0.343	1.5	2.74	16.40	(Sabo, Bastow and Power, 2002)
Colydiidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Corylophidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Cryptophagidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Curculionidae	$M = a * L^b$	0.0607	2.315	2.50	17.60	(Grunner, 2003)
Dermestidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Discolomatidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Dryopidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Dytiscidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Elateridae	$M = a * L^b$	0.0138	2.595	1.65	10.30	(Grunner, 2003)
Elmidae	$M = a * L^b$	2.879	0.0074	2.65	3.79	(Benke <i>et al.</i> 1999)
Endomychidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Georissidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)

Histeridae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Hydraenidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Hydrophilidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Laemophloeidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Languriidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Leiodidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Limnichidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Lucanidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Melandryidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Nitidulidae	$M = a * L^b$	0.0679	1.308	3.00	4.50	(Grunner, 2003)
Pedilidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Phalacridae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Ptiliidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Ptilodactylidae	$M = a * L^b$	3.1	0.0012	2.65	3.79	(Benke et al. 1999)
Ptinidae	$M = \exp(a + b * \log(L))$	-3.247	2.492	3.34	34.82	(Sample, Cooper, Greer, & Whitmore, 1993)
Scarabaeidae	$M = \exp(a + b * \log(L))$	-2.448	2.494	4.24	24.79	(Sample, Cooper, Greer, & Whitmore, 1993)
Silvanidae	$M = a * L^b$	0.0138	2.595	1.65	10.30	(Grunner, 2003)
Staphylinidae	$M = a * L^b$	0.0134	- 2.26	2.20	13.60	(Lang, Krooss & Stumpf, 1997)
Tenebrionidae	$M = \exp(a + b * \log(L))$	-0.043	1.2	5.65	13.39	(Sample, Cooper, Greer, & Whitmore, 1993)

Table 10: Table displaying equations used in estimated family richness calculations, where q^0 is the number of undetected species (species present in the assemblage but not included in the set of samples), q^1 is the number of unique species, q^2 is the number of duplicate species. m is the total number of species.

Test	Equation
Bootstrap	$S = D + \sum_{i=1}^S (1 - p_i)$
Chao	$var(S_{Chao2}=q_2 \left[\frac{1}{2} \left(\frac{q_1}{q_2} \right)^2 + \left(\frac{q_1}{q_2} \right)^3 + \frac{1}{4} \left(\frac{q_1}{q_2} \right)^4 \right]$
Jackknife 1.0	$S_{jackknife1} = S_{abs} + q_1 \left(\frac{m-1}{m} \right)$
Jackknife 2.0	$S_{jackknife2} = S_{abs} + \left[\frac{q_1 (2m-3)}{m} - \frac{q_2 (m-2)}{m (m-1)} \right]$

Consumption flux at each trophic link across a land-use gradient

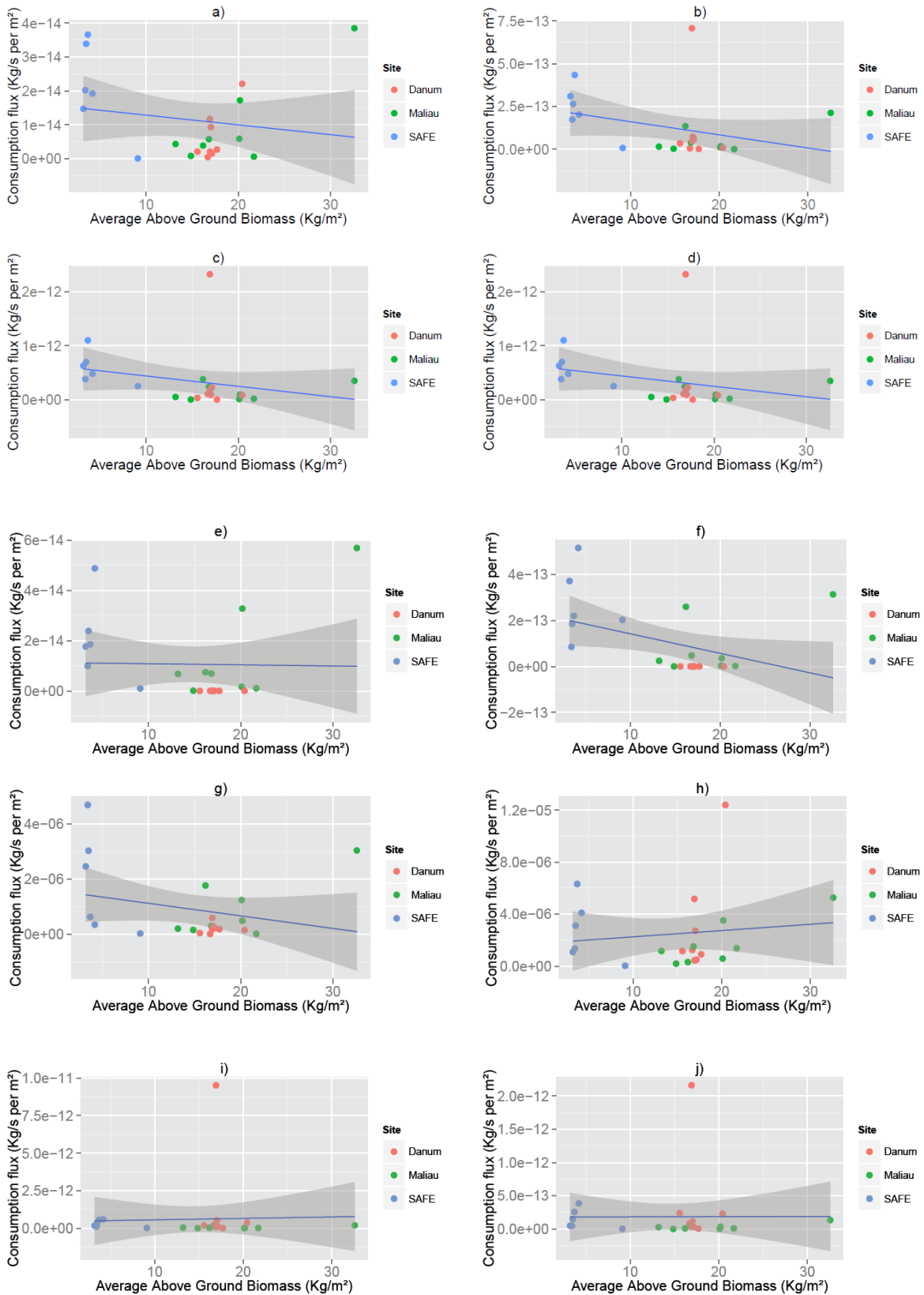


Figure 11: Lattice of scatter plots showing relationships between consumption flux and above ground biomass plotted with Gaussian GLM regressions with 95% confidence intervals. Each plot represents a different link in the system. a) Herbivores – Omnivores, b) Herbivores – Predators, c) Detritivores – Omnivores, d) Detritivores – Predators, e) Fungivores – Omnivores, f) Fungivores – Predators, g) Resources – Herbivores , h) Resources – Omnivores, i) Omnivores – Predators j) Predators – Omnivores.

Table 11: Displays results of Gaussian GLM, Consumption flux ~ Above ground biomass at each link

Link	Degrees of freedom	t value	<i>P value</i>
Herbivores – Omnivores	20	-0.788	0.440
Herbivores – Predators	20	-1.516	0.145
Detritivores – Omnivores	20	-0.78	0.938
Detritivores – Predators	20	-1.273	0.218
Fungivores – Omnivores	20	0.089	0.930
Fungivores – Predators	20	-2.063	0.523
Resources – Omnivores	20	0.561	0.581
Resources – Herbivores	20	-1.224	0.2353
Omnivores – Predators	20	0.161	0.874
Predators – Omnivores	20	0.024	0.981

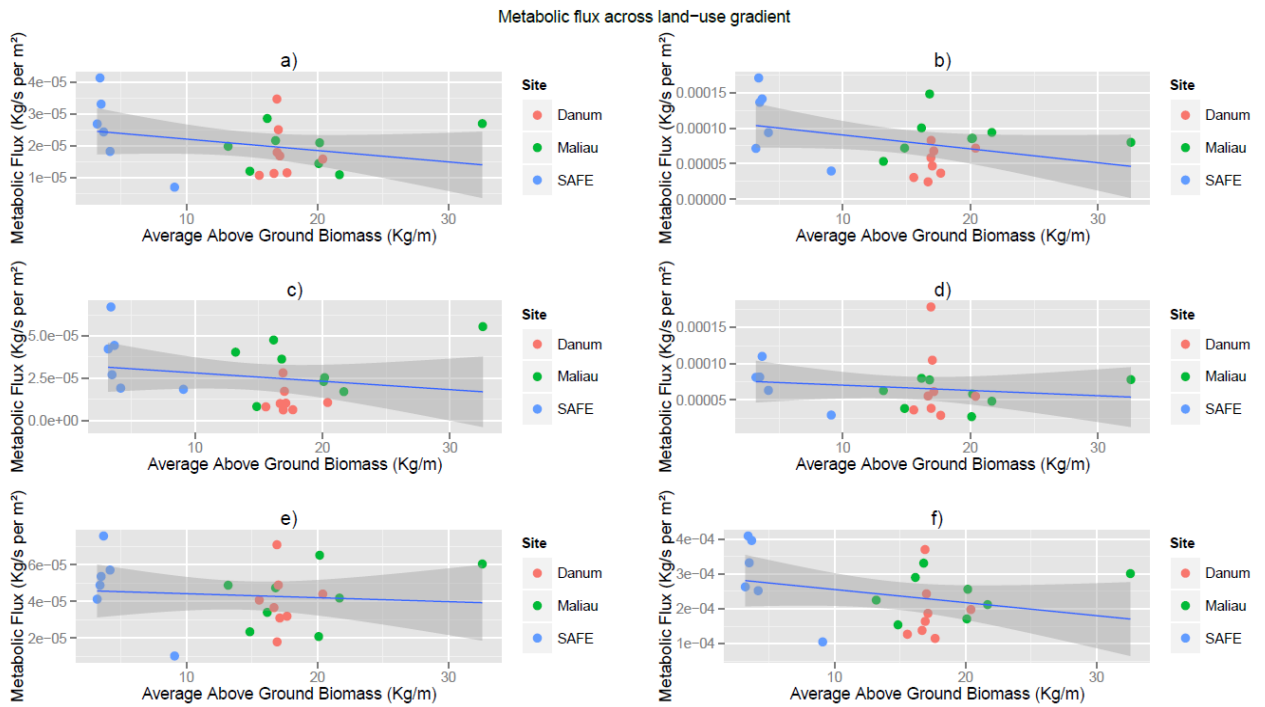


Figure 12: A lattice of scatterplots presenting the relationship between metabolic flux and above ground biomass in different trophic groups of beetles plotted with Gaussian GLM regressions: a) Herbivores, b) Detritivores, c) Fungivores, d) Predators, e) Omnivores, f) Total flux. The GLM for total metabolic flux \sim above ground biomass has an AIC value of 382.94.

Table 12: Displays results of Gaussian GLM, Metabolic flux \sim Above ground biomass at each trophic node

Node	Degrees of freedom	t value	<i>P</i> value
Herbivores	20	1.394	0.179
Detritivores	20	-0.1778	0.091
Fungivores	20	-0.960	0.349
Predators	20	-0.713	0.454
Omnivores	20	-0.427	0.674
Total	20	-1.434	0.164

Community Biomass

Above ground biomass (Kg/m) is significant in explaining the variance in total community biomass (Kg/m) between sampling sites (Gaussian GLM, $df=3042$, $t=2.291$, $p=0.022$). Above ground biomass was also significant in explaining variance in community biomass of omnivores ($df=730$, $t=-3.546$, $p=0.000415$), however it was not significant in any of the other trophic guilds (see Table X for GLM results.).

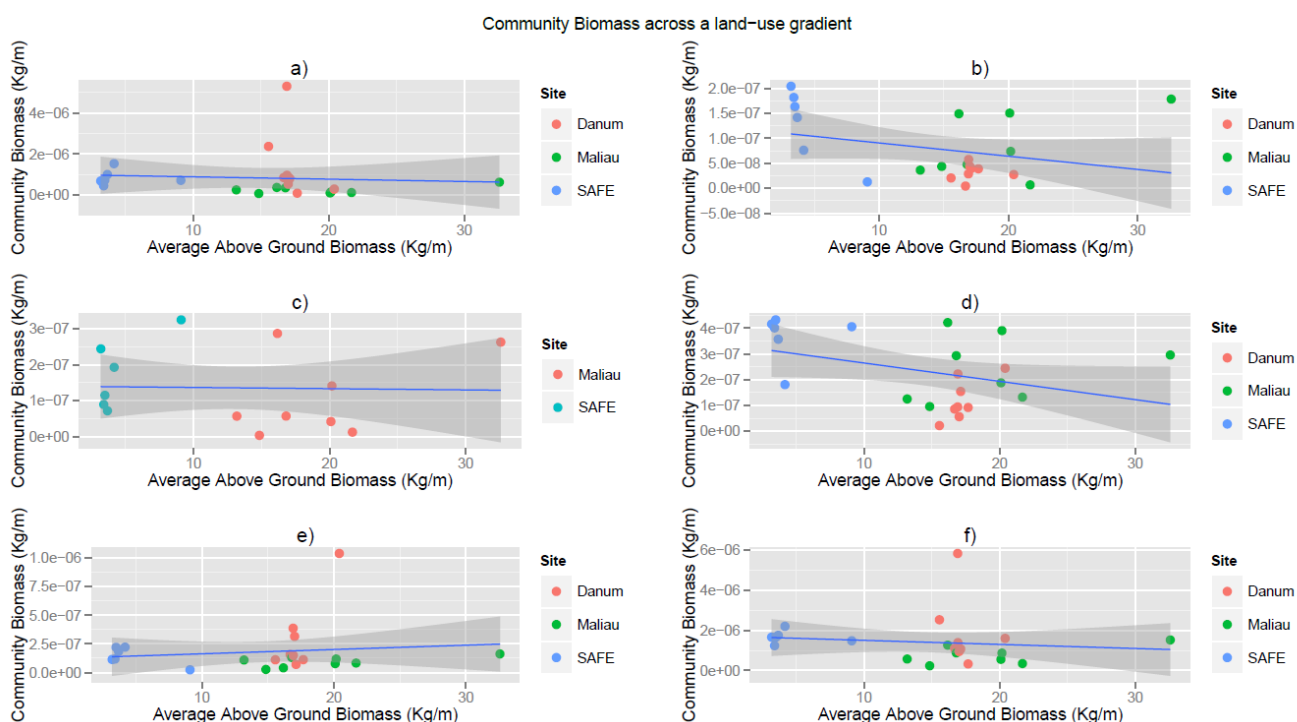


Figure 13: Scatterplots showing relationship between community biomass and above ground biomass in different trophic groups plotted with a Gaussian GLM regression and 95% confidence intervals; a) Predators, b) Herbivores, c) Fungivores, d) Detritivores, e) Omnivores, f) Total community biomass.

Table 13: Results of Gaussian GLM of Community Biomass ~ Average above ground biomass

Guild	Degrees of freedom	t value	<i>P</i> value
Predators	1305	0.218	0.828
Herbivores	139	1.371	0.172
Fungivores	200	0.422	0.632
Detritivores	659	-1.213	0.275

Omnivores	730	-3.546	<0.001
Total	3042	2.291	0.022