



**The effect of land-use gradients on composition,
efficiency, abundance and phenotypic parameters of
scavenging vertebrates in Sabah, Northern Borneo.**

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Project Declaration

Project design was created by the author with guidance and fine tuning by R.M.E. All data was collected by the author, with a proportion of it being available due to collection by the author prior to commencing MRes, except for RapidEye satellite maps containing Biomass data which were provided by Dr Marion Pfeifer.

All data processing and cleaning was performed by the author with guidance from R.M.E. Dr Igor Lysenko provided tuition on processing and extracting Biomass data from satellite images.

None of the mathematical models or statistical tests utilised were developed by the author or R.M.E. R.M.E. provided discourse, suggestions and fine tuning of analyses presented.

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Table of Contents

Abstract	iii
1) Introduction.....	1
i) Effect of land-use gradients on vertebrate scavenger community composition and effectiveness.	2
ii) Occupancy as a surrogate for relative abundance across land-use gradients.....	3
iii) Effects of disturbance on phenotypic parameters and community health (V. s. <i>macromaculatus</i> specific).	4
2) Methods.....	5
i) Study Site	5
ii) Sampling Method.....	6
iii) Data Analysis	7
3) Results.....	8
i) Scavenger community composition and efficiency	8
ii) Occupancy and relative abundance of scavenger species.....	9
iii) Phenotypic parameters and community health	10
4) Discussion	13
5) Acknowledgments	16
6) References	17

Abstract

Human land-use is continuously altering the natural environment yet the greater ecological implications on many groups that are key to healthy ecosystem functioning remain uncharacterised in the tropics. Scavenging vertebrates provide integral ecosystem services through the removal of carrion; a crucial role in nutrient cycling and disease dynamics. To explore how anthropogenic processes may effect such services we investigated the effects of land use on scavenger community composition, abundance, efficiency and health. Scavenger community composition is altered with increasing land-use pressures, mammalian scavengers are unable to persist in highly degraded habitats and an increased abundance of Water monitors (*V.s. macromaculatus*) to fill the extirpated niche is observed. Contrary to previous research land-use has minimal effect on community efficiency and established areas of disturbance display similar carrion removal rates to areas unaffected by human activity. However active habitat change causes a decrease in biodiversity, abundance and efficiency of scavenger communities, the wider implications of this are yet fully understood.

Key Words: Vertebrate Scavengers, land-use, mesopredator, fragmentation, community composition, carrion, health, habitat change, biodiversity, occupancy.

1) Introduction

Scavenger communities play vital roles in nutrient cycling and redistribution as well as disease dynamics via the removal of carrion from the environment, providing a crucial ecosystem service and are therefore ecologically integral for healthy ecosystem functioning. The disruption of intact scavenger communities has possible far reaching implications and understanding how scavenging communities function and respond to environmental changes has become a subject of increased importance (Selva & Fortuna, 2007). Scavengers are often overlooked in favour of more charismatic study species, it has been suggested this is due to human aversion to rotting substances in combination with the ephemeral nature of carrion has led to a paucity of information on scavenger communities, ecology and dynamics (Houston, 1979). Additionally, previous research on ecology of scavengers has primarily focused on invertebrates due to comparative ease of sampling and ability to achieve higher sample size with minimal effort, however this neglects the fact a high percentage of naturally occurring carrion is utilised and removed by vertebrate scavengers rather than microbes and arthropods (DeVault *et al.* 2003). Even in the minority of studies targeting vertebrate scavengers investigations have been predominantly conducted in relatively pristine environments, and additionally have concentrated on temperate regions (Beasley *et al.* 2011). Due to this, previous studies have failed to address the fact that habitat and human disturbance strongly influences community composition and scavenger dynamics (DeVault *et al.* 2011). Therefore there is an existing gap of knowledge on scavengers in tropical ecosystems dramatically altered by anthropogenic land-use.

This investigation will utilise the experimental landscapes of the Stability of Altered Forest Ecosystems (SAFE) Project, Sabah, Borneo to experimentally examine the effect of deforestation on vertebrate scavenger diversity, abundance and community health in a tropical environment. This is important to understand because of the high rates of deforestation and habitat loss in Borneo, currently estimated to only have 52.8% of natural forest cover remaining from the approximated 75.7% still remaining in 1973. The highest losses were recorded in Sabah with 39.5% of its total forest becoming non-forest in this timeframe (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 are illegal logging, timber industries and susceptibility of logged forest to wild fires but predominantly the proliferation of the oil palm industry. In 2007 the oil palm industry already accounted for 5% of Malaysia's gross national income and has continued to grow rapidly since (Koh & Wilcove, 2007). Such economic incentive puts tremendous pressure on the remaining shrinking forests of Borneo. Worryingly in 2008 oil palm accounted for 60% of vegetable oil production globally, yet it was the topic of only 10% of total research (Turner *et al.* 2008). Such reports highlight the importance for the emerging areas of research

in the wake of this having to concentrate on species ability to persist in degraded and fragmented habitats and the changes such degradation will have on community composition, interspecific interactions and ecosystem functioning. However, because of previously mentioned inherent difficulties in the observing and sampling of vertebrate scavenger species and their populations response to landscape change remains unsatisfactorily characterised and understood.

This project will provide currently lacking information on the effects of tropical land use change on vertebrate scavenger communities by addressing four questions. The first two are a general investigation into the effects of land use change holistically on the scavenger community and its functioning, while the last investigates in detail the population and phenotypic structure of the water monitor (*Varanus salvator macromaculatus*) communities specifically. The study species of this project are all the carnivorous facultative scavengers present in the study area including but not limited to; South-east Asian Water Monitors (*Varanus salvator macromaculatus*), Malay Civets (*Viverra zibetha*), Sun Bears (*Helarctos ussuricus*), Oriental Small-clawed Otters (*Aonyx cinereus*), Smooth-coated Otters (*Lutrogale perspicillata*) and Short-tailed Mongooses (*Herpestes brachyurus*) (Payne *et al.* 1985; Shukor, 1996). The focal species of this investigation will be the South-east Asian Water Monitor (*Varanus salvator macromaculatus*), this is not only due to their presence and expected abundance in all habitat types but primarily because of the ability to capture and process individuals without anaesthesia and the possible long term health effects which come with administering anaesthetics to wild animals. The South-east Asian water monitor (*Varanus salvator macromaculatus*) is one of the largest, and most widely distributed, squamate lizard complexes in the world (Koch *et al.* 2007, Somaweera & Somaweera, 2009, Koch & Bohme, 2010). In Sabah (Borneo, Malaysia) they are mesopredators alongside the numerous carnivorous mammalian species (Payne *et al.* 1985). Little is known about the functional role of monitor lizards in many ecosystems, as their impact has previously been omitted in favour of placental mammals (Sweet & Pianka, 2007). Herpetofaunal community composition and taxonomy as a whole has received little attention in the study area and as a result varanids have largely been ignored (Turner *et al.* 2012, Ewers pers comms. 2013).

- i) Effect of land-use gradients on vertebrate scavenger community composition and effectiveness.

The extirpation of scavenger species from localised ecosystems can disrupt the composition and therefore the efficiency of scavenging communities (Olson *et al.* 2012). Existing evidence suggests that mammals are particularly sensitive to anthropogenic processes, due to inherent biological traits such as large body size which not only increases probability of hunting but also is indicative of a slower

reproductive cycle (Cardillo *et al.* 2005). The inability of a less robust species (I.e. *Helarctus malayanus*) to persist in a degraded environment can not only alter and interrupt the flow of energy in an ecosystem, but also may lead to increased health risks for people and other wildlife through the persistence and spread of disease due to prolonged presence of carrion (DeVault *et al.* 2003). Previous research in temperate zones suggests that with land-use driven habitat transformation mesopredators species may increase in abundance and compensate, maintaining established community functioning and the existing rate of carrion removal, however results were equivocal (Beasley *et al.* 2011). Therefore this investigation will assess scavenger community composition and correlate this to duration of time before carrion is removed from the environment by vertebrates at varying land use levels in an attempt to quantify the effect of disturbance and anthropogenic processes on holistic community composition and functioning.

ii) Occupancy as a surrogate for relative abundance across land-use gradients.

Knowledge of a species habitat preferences and geographical distributions is central to the conservation of any organism (Thorn *et al.* 2009). Assessing abundance of a species across land-use gradients is integral in being able to understand a species ability to persist in degraded habitats. Typically, indirect or direct competition for resources influences the abundance and distribution of a species. However, as the population dynamics of the target species is poorly understood it is not known what influences their abundance and distribution (Smith *et al.* 2009). However generally in areas affected by human disturbance and in the presence of human trophic subsidies (e.g. high calorific and concentrated food sources) it is suggested apex predators (typically mammalian species) will perish while robust mesopredator species (e.g. *V. s. macromaculatus*) can achieve, and sustain, larger densities while occupying a smaller area due to this abundance of food and decreased interspecific competition through expiration of mammalian counterparts. To investigate this pattern occupancy will be modelled for both water monitors (*V. s. macromaculatus*) and Malay civets (*V. tangalunga*). Malay civets were selected due to expected high abundance comparable to other mammalian scavengers and the fact they share the same ecological niche with water monitors both being generalists, typically living sympatrically, separated only temporally, monitors being diurnally active and civets being nocturnal (Traeholt, 1997a; Traeholt, 1997b; Seymour *et al.* 2010). It might be expected that abundance of *V. s. macromaculatus* would be higher in areas of high anthropogenic land-use while abundance of mammalian counterparts decrease. A similar paradigm was observed in water monitors (*Varanus salvator*) on Tinjil Island, Indonesia which showed a significant positive correlation between human disturbance and relative abundance of individuals (Uyeda, 2009), however that study area has a highly truncated scavenger diversity in comparison to Sabah, Borneo. Understanding the proportion of sites occupied by target species is essential for long term monitoring

and being able to model the effects of habitat degradation and deforestation on a community. This is especially true with typically elusive species in which rarity of a species caused by transient nature, low abundance or low detection probabilities inhibits the ability to reach the minimum sample size needed for density estimates or when identification of individuals is implausible (MacKenzie *et al.* 2002). In such a situation occupancy can be used as a surrogate for relative abundance and utilising presence – absence data across sites can be effective for estimating extinction rates. Therefore, to improve our understanding of this we proposed to investigate the factors that influence scavenger species abundance and distribution. This study will investigate the relationship between occupancy of Malay Civets (*Viverra zibellina*) and Water Monitors (*Varanus salvator macromaculatus*) to human land-use.

- iii) Effects of disturbance on phenotypic parameters and community health (*V. s. macromaculatus* specific).

Although the effects of deforestation on factors such as presence / absence of species and relative abundance are becoming more easily attainable through the utilisation of camera trapping and a general movement away from live trapping, this largely ignores equally integral effects on population dynamics, phenotypic trends and community health. The ability to make a priori assessments and accurate predictions of species responses to fragmentation based primarily on its distribution in the landscape, would prove a valuable conservation tool (Gehring & Swihart, 2003). Humans are increasingly altering natural habitats and interfering with natural food webs in disturbed areas such as palm oil plantations, where trophic subsidies such as human refuse and carrion are persistent and concentrated within previously natural habitats. But also in a less obvious way in logged or partially logged forest where disturbance may lead to undesirable conditions for naturally occurring species, increasing localised emigration from an area, altering the natural biotic composition, increasing death rates and therefore indirectly increasing the concentration of carrion in a previously pristine area. Research evaluating the complex effect of such and the far reaching ecological implications of altered population components and phenotypes of wild populations is lacking and thus demands investigation (Polis & Strong, 1996, Jessop *et al.* 2010). In light of this, this investigation will assess the effect of land-use on population dynamics, phenotypic parameters and community health i.e. tendency to larger masses, greater aggregations of males and smaller home ranges in anthropogenically disturbed areas, as observed in Lace Monitors (*Varanus varius*) by Jessop *et al.* (2012). However not all effects are so straightforwardly quantifiable: environmental factors may also have negative effects such as

increasing abundance of parasites and levels of transmission, perturbations to naturally occurring sex ratios and increasing territorial conflict which would have obvious detrimental effects on the health of individuals and communities as a whole (Uyeda, 2009). Consequently this investigation will gather data on all aforementioned points for water monitors (*V. s. macromaculatus*) in an attempt to quantify the relationship between land use and health of localised populations.

2) Methods

i) Study Site

This project was conducted at the Stability of Altered Forest Ecosystems (SAFE) Project: an experimental landscape situated in the North-East Malaysian state of Sabah (Ewers *et al.* 2011). The SAFE project is based in a 7,900 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 and riparian buffers to monitor the effect of forest fragmentation and riverine margin size on a wide range of ecosystem and ecological topics, through a multi-disciplinary approach. There also exists two spatial controls: a 2,200 ha area of Virgin Jungle Reserve (VJR) south of SAFE project area characterised as primary forest by the local government although it has had some illegal logging on the lower slopes, and previously existing Oil Palm (OP) planted in 2006, in the Selangan Batu oil palm estate located further to the southwest of the VJR (Turner *et al.* 2011). The study was carried out at six sampling sites; four sites (0m, 5m, 30m and 120m) are previously marked and existing experimental catchments retaining riparian buffer zones: consisting of three riparian land habitat types; continuous secondary forest (30m), secondary forest surrounded by oil palm (120m), and secondary forest with active logging (0m and 5m) (See Figure 1). These numbers refer to future riparian widths for a future SAFE experiment but are currently irrelevant and are only used to designate different sampling sites. In order to quantify quality of forest we utilised RapidEye™ satellite images acquired over the SAFE landscape in 2012 and 2013 analysed with Raster in ArcMap2.0 to obtain average above ground biomass (AGB) values for each catchment (Hijman & Etten, 2012; Pfeifer *et al.* In Press). It is important to note since these satellite images were taken and this investigation commenced sampling sites 5m and 0m have undergone extensive logging so their values are no longer representative of de facto AGB and no recent satellite images are available. Besides the sites containing riparian buffers there were also 2 control sites in oil palm (OP)

The map displays a landscape with different land use types: Continuous Logged Forest (CLF), Fragmented Logged Forest (FLF), and Oil Palm [Mature]. Various experimental plots are marked, including RR2, RR3, RR16, RR15, RR13, VJR, and OP2. A scale bar at the bottom indicates a distance of 0 to 4 km. The map is titled "Tentative SAFE experimental plots v3 (18/03/14)".

ii) Sampling Method

6

measurements recorded with a number of other life history and dietary notes. Individuals were searched for ectoparasites residing on the scales and endoparasites in the mouth and cloacal opening. Tagged individuals were given a tail crest clippings in order to facilitate identification of re-captures during subsequent trapping days. Any injuries resulting from trap doors and tag injectors were disinfected thoroughly with iodine before releasing animals. Individuals were finally released at the point of capture. Varanids under stress will often flush their stomachs voluntarily (Traeholt, 1994; Gaulke, 1991). Regurgitated prey items of *V. salvator* (other than the bait) was collected and photographed from the interior of traps in order to record digested prey. Initially stomach lavaging was trailed however in consensus with previous research on varanids it was found to be largely ineffective and was therefore discontinued (Auliya, 2003). Bait was randomised on availability including: Fish, Chicken, Pig and other opportunistically discovered carrion, but all bait items were 1kg+ as to remove the effect of ontogenic shifts in feeding preferences observed in water monitors (Traeholt, 1993).



Figure 2: Photo of baited metal cage trap at 0m sampling site, covered with available substrates to provide trapped individuals with shelter.

iii) Data Analysis

Due to the nature of ecological communities in the tropics and specifically the rarity and transience of target species in combination with the large spatial scale of this investigation estimates for occupancy will be made unadjusted from capture rates. As we aim to investigate the effects and the interactions

of environmental factors on populations and communities rather than make an absolute estimate of abundance it is unnecessary to control for detection probabilities (Banks-Leite *et al.* 2014). All statistical analysis was performed in R Version 3.2.1 utilising dplyr and lme4 packages (Bates *et al.* 2014; R Core Team, 2014; Hickman and Francois, 2015). Occupancy was modelled by creating GLMs from the data set and fitting regression lines using binomial models. Phenotypic and community health parameters were analysed for significance using ANOVA tests and the data was plotted as linear regressions.

3) Results

i) Scavenger community composition and efficiency

River	AGB (Tonnes/Hectare)	V. <i>macromaculatus</i>	s. <i>tangalunga</i>	V. <i>familiaris</i>	L. <i>perspicillate</i>	H. <i>semitorquatus</i>	H. <i>brachyurus</i>	H. <i>malayanus</i>
OP	30.47	•	•	•				
120m	54.43	•	•		•			
30m	69.68	•	•			•		
0m	77.12	•	•				•	
5m	81.95		•		•			•
VJR	80.71	•	•	•				•

Table 1: A table displaying the scavenger community composition of different sampling sites, a black dot indicates presence.

The table above displays the recorded presence of scavenger species at the different sampling sites only. It is important to note a lack of a presence does not necessarily indicate that species is definitively absent only that it was not recorded during sampling. Some species have very low detection probabilities due to elusive nature, rarity or transience and may be present and have remained undetected (Mackenzie and Royle, 2002; 2006). Highest species richness was observed in the protected area (VJR, Table 1). All other sampling sites displayed relatively equal species richness of various compositions and there is no significance to note.

Variance in community efficiency in carrion removal between sampling sites was significantly correlated to above ground biomass (AGB) ($P = 0.0261$), with time to carrion removal being lowest in low biomass sites and increasing with increasing biomass however being relatively similar (See Fig 3). After habitat change (logging) in both 5m and 0m the mean carrion removal rate increased notably. 5m increased by 26.9% to 3.51 days and 0m increased by 24.6% to 3.85 days (See Fig 3).

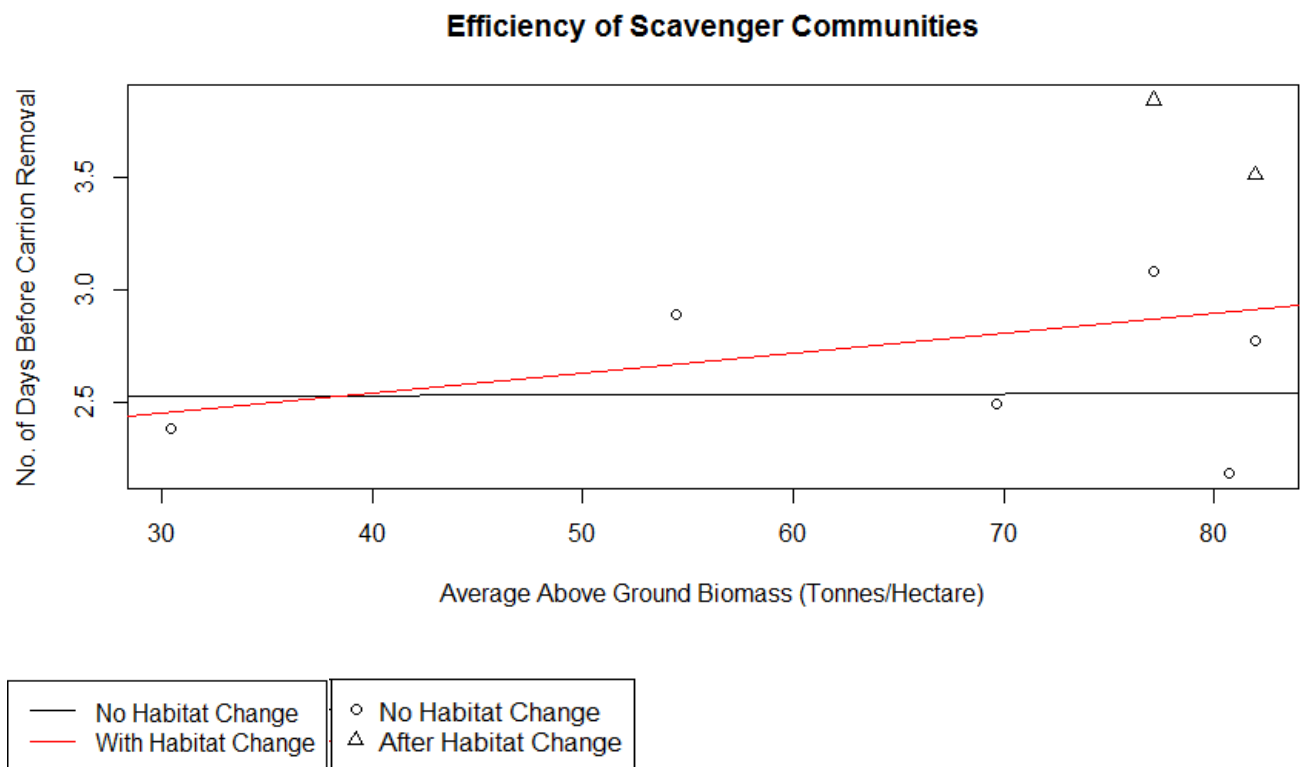


Figure 3: A scatter plot displaying the relationship between average time before removal of carrion from the environment and above ground biomass with two fitted regression lines showing variation before and after habitat change.

ii) Occupancy and relative abundance of scavenger species

AGB of sampling sites was strongly significant in explaining the variance in occupancy of water monitors (*V. s. macromaculatus*) ($P < 0.001$) and of Malay civets (*V. tangalunga*) ($p < 0.001$). Occupancy of monitors was highest in the most disturbed land use areas and decreased with increasing tree biomass. Malay civets occupancy rates demonstrated the reverse of this trend, having the highest occupancy in protected forest (area of high AGB) and the lowest occupancy in Oil Palm (low AGB). See Fig. 4 for details.

Occupancy of Water Monitors (*V.s. macromaculatus*) and Malay Civets (*Viverra tangalunga*)

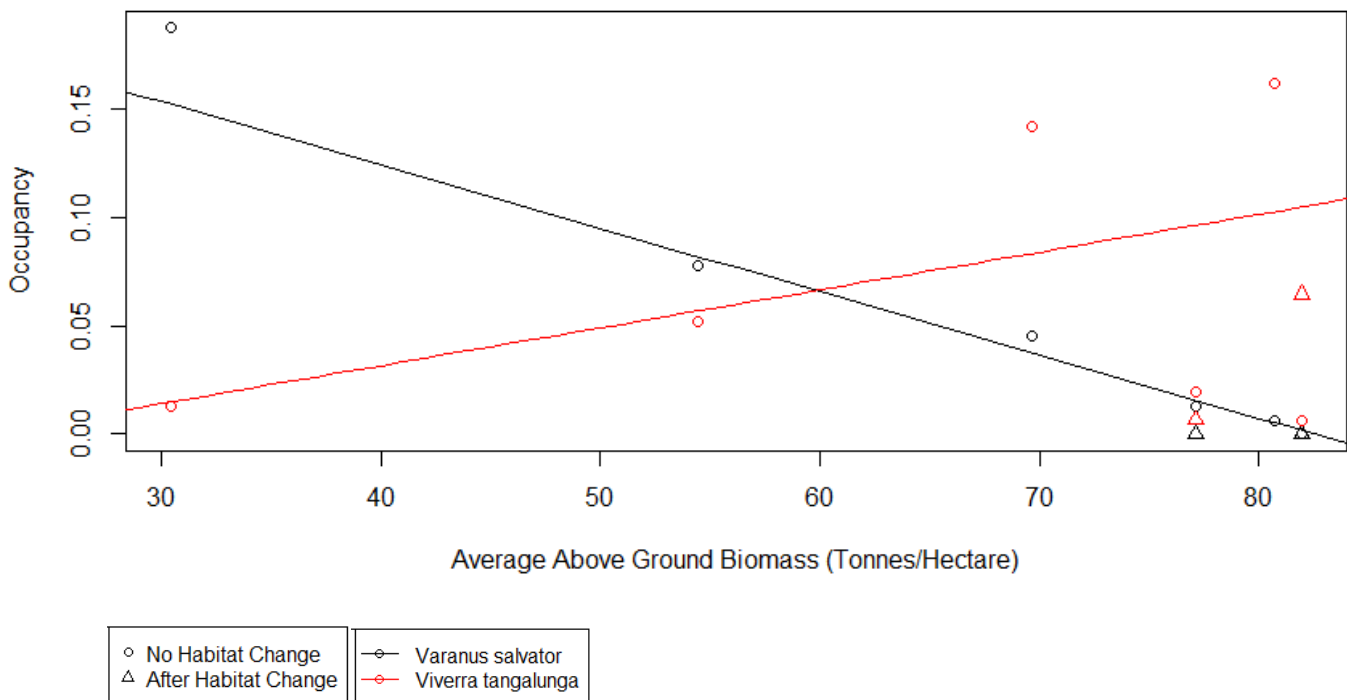


Figure 4: A scatterplot detailing the relationship between occupancy of the two predominant scavenger species (Water monitors (*V.s. macromaculatus*) and Malay civets (*V. tangalunga*)) and biomass at sampling sites, fitted with regression lines for each species.

iii) Phenotypic parameters and community health

Water monitors had a general tendency to be larger in more disturbed sampling sites (OP, 120m) in comparison to less disturbed sites (VJR, 0m, 30m), with significantly negative relationships between above ground tree biomass (AGB) and body mass ($P=0.008$), snout-vent length ($P = 0.01$), body condition residuals (mass (g) / total length (mm)) ($P = 0.003$) and head length ($P = 0.008$). (See Fig. 5 for details)

Phenotypic Parameters of Water Monitors (*V. s. macromaculatus*)

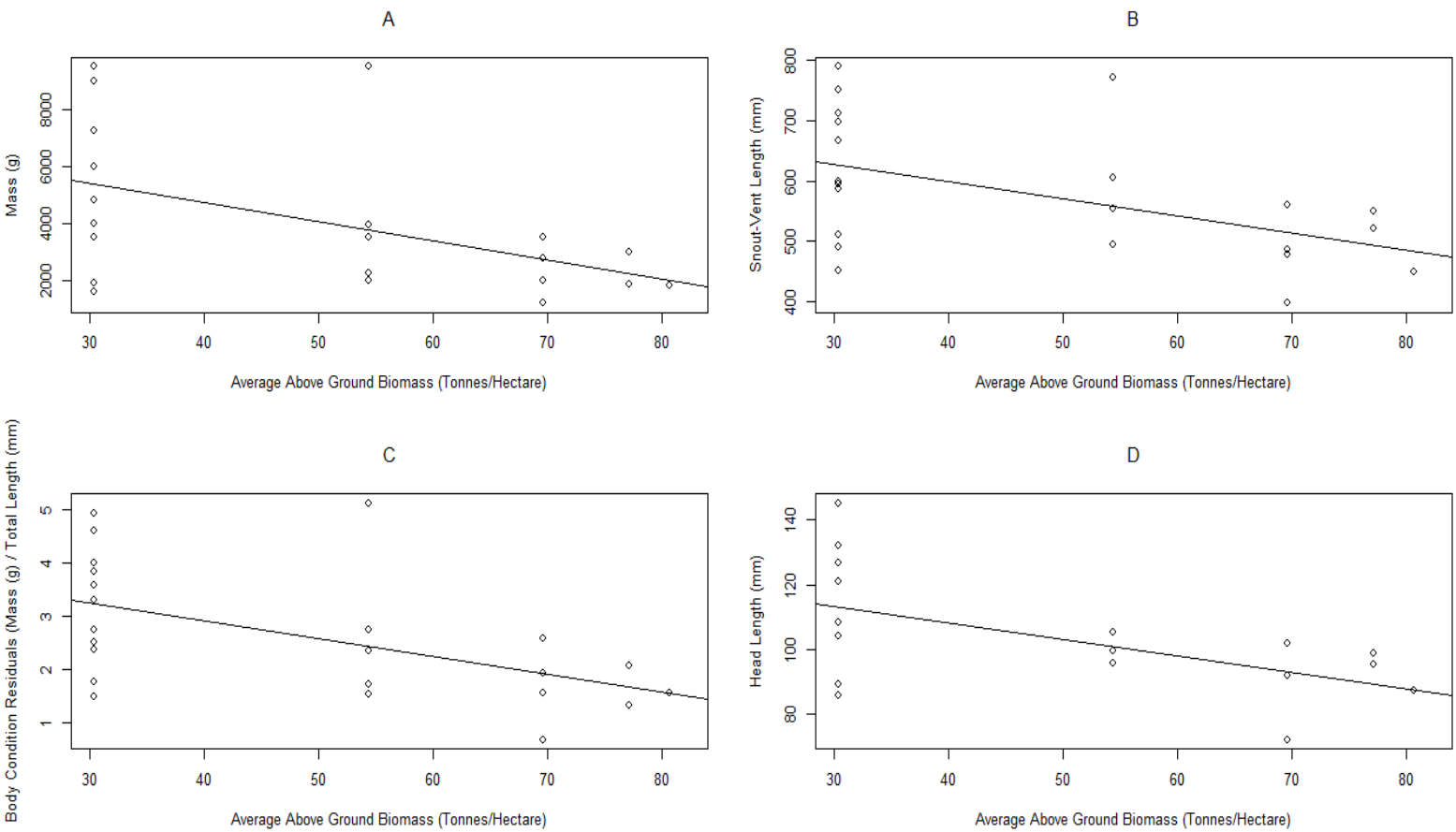


Figure 5: A multi panelled figure with scatterplots fitted with regression lines displaying relationships between above ground biomass and (A) mass, (B) snout-vent length, (C) body condition residuals and (D) head length.

AGB is not highly significant when considering sex ratios of populations of water monitors at our sampling sites ($P = 0.053$). However obvious skewing of sex ratios can be observed from the naturally occurring 1:1 (male:female) ratio in less disturbed secondary forest sites (0m, 30m) to 4:1 (male:female) in 120m and 4.5:1 (male:females) in OP 4:1 (male:female) in 120m (see Fig. 6).

AGB has significance in explaining variance in frequency of scarring in different populations of water monitors (*V. s. macromaculatus*) ($P = 0.0295$). Presence of scarring displays its highest occurrence in sites highly disturbed by anthropogenic processes, in OP (lowest AGB sampling site) scarring was present in 80% of individuals, declining steeply as AGB increases. In areas of high AGB scarring from territorial conflict is almost completely absent (see Fig 6).

AGB is not significant in explaining the variation in parasite abundance between individuals at different sampling sites ($P = 0.0837$). This may be due to sample size, an increased n number may have produced a different result. However generally individuals from sampling sites with low AGB did not have parasites present and a small number of individuals from sampling sites with higher AGB did (See Fig 6).

Population Dynamics and Life History notes of Water Monitors (*V. s. macromaculatus*)

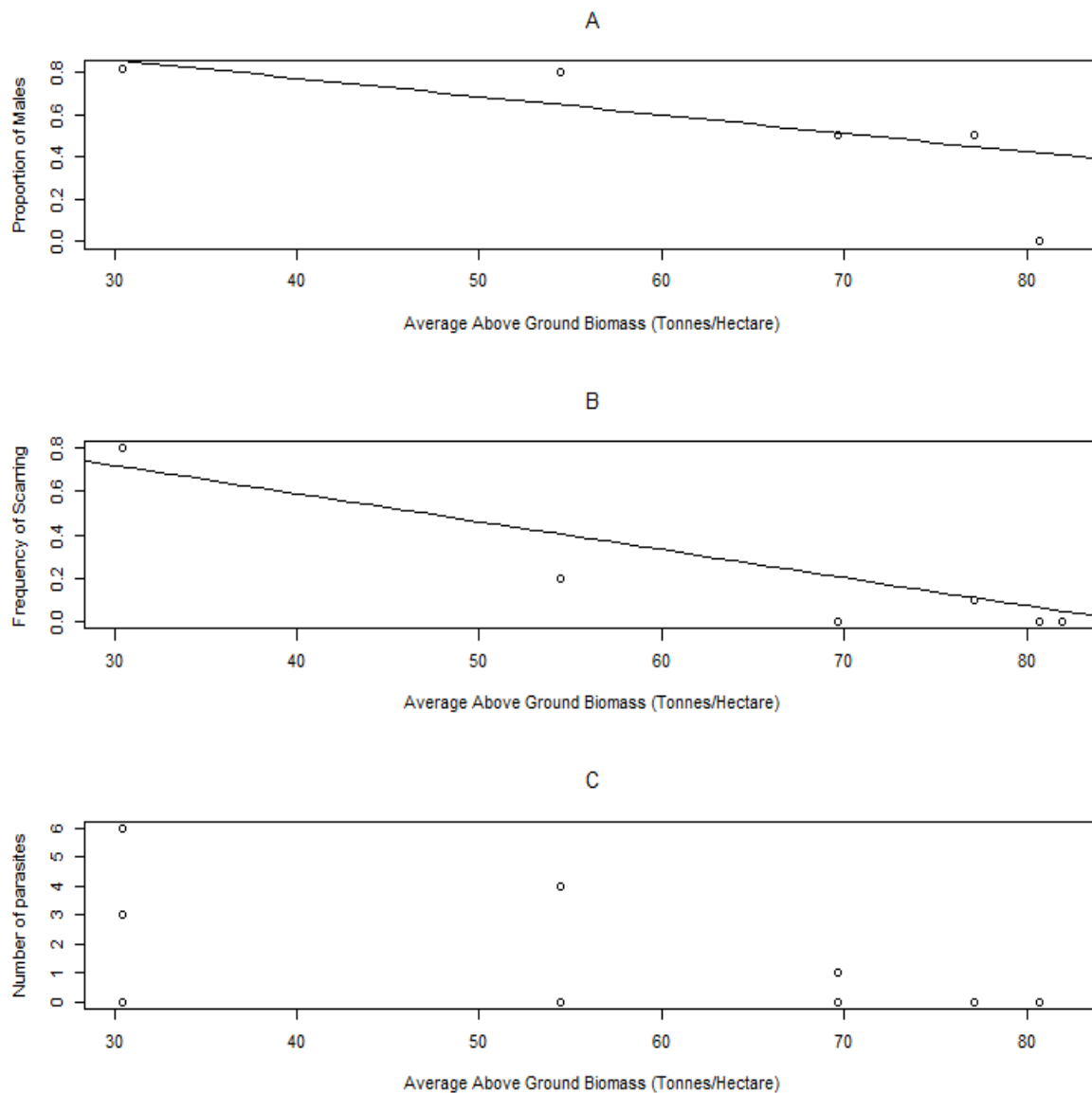


Figure 6: A multi-panelled figure with scatterplots displaying relationships between above ground biomass and (A) sex ratio, (B) presence of scarring and (C) parasite abundance of different sampling sites.

4) Discussion

Anthropogenic land uses are increasingly altering natural habitats, these alterations have multiple direct and indirect effects on the effectiveness, composition, abundance and health of scavenger communities. Here, we provide evidence that disturbance of riverine margins result in a significant shift in community composition, with robust species (e.g. *V.s. macromaculatus*) becoming more abundant, filling the niche created by localised extinctions of dominant apex and meso-predators, Cardillo (2005) notes that mammalian species are typically more susceptible to human processes and land-use changes. These results are consistent with other studies documenting significant shifts in scavenger community composition in fragmented ecosystems in temperate zones as they provide insufficient habitat for the persistence of top trophic level predators while providing increased food resources and decreased interspecific competition for generalist species (Robinson *et al.* 1995; Beasley *et al.* 2011; Brashares *et al.* 2010). This observed higher abundance of robust mesopredator populations in human-modified ecosystems is due to alleviation of top down and bottom up governing mechanisms and increased pressure on localised populations of prey species further than that of the direct effects of fragmentation (Elmhagen & Rushton, 2007; DeVault *et al.* 2011). This observed compositional shift and decrease in biodiversity in an area of established land use (i.e. mature Oil Palm) interestingly has little influence on the effectiveness of the scavenging community, as increasing numbers of disturbance tolerant mesopredators fill the niche left by extirpated species: mean number of days before carrion is removed in VJR (protected area) is 2.18 days while in established Oil Palm it is 2.37 days.

These results are contrary to previous research in temperate zones which found although abundance of mesopredators increased when a dominant scavenger was removed, community efficiency was disrupted by perturbations in composition (Olson *et al.* 2012). Such observed differences in results may be due to the fact that in the previously mentioned study the dominant scavenger was removed artificially through trapping and community efficiency was immediately tested, therefore there may not have been sufficient time for the emptied niche to be filled and the artificially extirpated species to be compensated for. Although our results seems to suggest the negative effects of land use on scavenger communities are limited in terms of efficiency it is important to note that mesopredator releases and their trophic interactions often lead to declining secondary prey populations, unstable communities and drive local extinction rates (Prugh *et al.* 2009; Eagan *et al.* 2011; Richie and Johnson, 2009).

Evidence provided also demonstrates that the populations of *V. s. macromaculatus* after mesopredator release demonstrate significant changes to their morphological and phenotypical parameters. Generally individuals from disturbed areas show trends to longer lengths, larger masses

and higher body condition residuals (see Fig. 6), with the opposite also being displayed in more pristine sites there is a trend towards shorter lengths, lower masses and lower body condition residuals. This is expected as water monitor populations in areas of high anthropogenic pressures experience decidedly reduced inter-specific competition as well as accessing a new resource in the form of human trophic subsidies (human refuse, domesticated animals, edible products of agriculture) (Uyeda, 2009; Eagan *et al.* 2011). Initially this suggests that these individuals are in better health than less disturbed populations however is offset when considering the observed skewed sex ratios and increased level of scarring as indicators of population health (See Fig. 7). These adverse effects although more difficult to empirically quantify are just as valid in assessing the health of a community (Jessop *et al.* 2012). Individuals from areas of higher disturbance (lower above ground biomass) are in better morphological health, however highly biased sex ratios increase sexual competition for mates and can potentially decrease overall reproductive success. Parasite load directly reduces overall fitness however this was not a significant factor and increased scarring is indicative of elevated social conflict and territoriality resulting from hyper-abundance. However it is integral to note that to truly examine and compare any of these factors a higher sample size would be required, due to time constraints in these results there is potential for bias as capture rates were notably higher (for *V.s. macromaculatus*) in sampling sites of low AGB (OP, 120m) which means generally data sets pertaining to morphometric characteristics of individuals from sampling sites with a high AGB are significantly smaller than those with a low AGB which will skew results especially if anomalies were present.

In areas of active habitat change (i.e. logging) species richness, abundance and effectiveness of scavenger communities is greatly decreased demonstrated by the mean no. of days before removal of carrion increased significantly (by 24.6% and 26.9%) after logging took place at the two sampling sites. Examination of results from 5m provides explanation for this observed pattern, after habitat change scavenger community composition experiences significant perturbations with apex scavengers (i.e. *Helarctos malayanus* and *Lutrogale perspicillata*) becoming absent, suggestive of emigration away from disturbance. This practically instantaneous removal of dominant scavenger species causing an increase in mesopredator occupancy (*V. tangalunga*) but decrease in holistic scavenging efficiency is reminiscent of the previously discussed paper Olson *et al.* (2012) which reported similar results. It is also in agreement with other literature that supports the notion that habitat change will lead to a decline in ecosystem services due to loss of species from higher trophic levels (Dobson *et al.* 2006). However this paradigm was not observed at the 0m sampling site, there was no observed emigration of apex scavengers (not possible to observe as no dominant scavengers had been recorded) and there was also a marked decrease in both species of mesopredator present (*V. tangalunga* and *V.s. macromaculatus*). Although the outcome of decreased scavenger community efficiency was the same

at both sampling sites and changes in occupancy and composition provide appropriate explanation for the prolonged presence of carrion in each case, the explanation of the observed variation in composition changes at the sampling sites may have due to differences in quality of forest yet this remains equivocal. This extended presence of carrion has direct implications on ecosystem functioning by delaying natural nutrient cycles which can interfere with trophic interactions and natural food webs (McCann *et al.* 1998; Berger *et al.* 2008) but also increasing chance of disease prevalence and spread by increasing the amount of time bacteria is present in the environment and therefore increasing the longevity it has to replicate and infect local wildlife (DeVault *et al.* 2003). This is a hugely understudied area, however the limited research that does exist is in consensus; the extirpation of scavengers from a community will indirectly alter disease dynamics, however there is disagreement in how so. Certain literature agrees with the premise of this investigation that delayed carrion removal will increase spread of disease simply through prolonged presence of disease on the carcass (Ogada *et al.* 2012) while other research suggests by removing an apex scavenger there will be a parallel increase in canine and rodent abundance increasing chances of human contact with these animal groups and the disease risks that follow (Markandya *et al.* 2008). However due to the results from established areas of land-use (OP), it is expected that this reduced efficiency in removal would only be ephemeral, and given the appropriate temporal gap disturbance tolerant scavengers would colonize the area and compensate to stabilise rate of carrion removal.

The use of live trapping in this study was necessary for collecting data on population dynamics, phenotypic parameters and community health however has obvious draw backs in comparison to increasingly popular camera trapping method. Live trapping is less logistically possible due to required man power and maintenance than camera trapping (Lal, 2008) , furthermore of increased importance is the effect of trap avoidance of wild animals and the effects of such on resulting data collection which is especially significant when targeting such typically shy elusive species as this investigation does (Rendall *et al.* 2014). However that is not to say that camera trapping is an infallible method, recent research demonstrates there are many considerations must be addressed such as camera placement and orientation, triggering, detection system and behavioural responses of the animals to the cameras (Meek *et al.* 2015). Recent research has suggested that pairing camera traps with live traps may be the most advantageous solution (Ariefiandy *et al.* 2014) and this investigation would support this conclusion for any future research, however due to funding limitations such a method was not possible in this instance.

Another limitation of this study is the effects of heterogeneity, due to the huge spatial scale of the SAFE project and funding limitations it made it impossible to sample all locations simultaneously. This could possibly affect results due to different levels of activity annually caused by seasonal variation in

rainfall potentially causing variation in capture rates (Auliya, 2003; Royle, 2006). This was partially addressed by commencing research on both occasions during the wet season however the first trapping effort ran into the dry season and the effects of this were intangible. A further limitation was the inability to gather sufficient data on dietary variation across land-use gradients, although attempted in this investigation through collection of regurgitated contents an insufficient sample size was reached. Future research should include line transects through the sample sites to facilitate the collection fecal samples for analysis. Such data would enable the effect of land-use on scavengers functional ecology to be more fully understood and it would also provide evidence for the drivers of such observed responses to land use such as trends to much larger masses and lengths in areas of high anthropogenic disturbance.

In conclusion long term land-use reduces overall species richness and alters scavenger community composition by driving the localised extinction of apex mammalian scavengers causing a mesopredator release. This release is known to have detrimental ecological effects on the localised environment and co-inhabitants, however in the long term it has little negative effect on scavenger communities efficiency and the larger ecological implications a decreased efficiency would produce. However areas of active habitat change display a marked decrease in occupancy and efficiency of scavenger species although the extent of this on other ecological processes and disease dynamics is yet to be fully understood, highlighting the importance of this for future research. In regards to community health although initially populations of mesopredators in agricultural areas may appear to be in good health when assessed by their morphometrics. It is important to investigate less obvious adverse community responses including but not limited to biasing of sex ratios, parasite transmission, increased sexual and territorial competition and disease susceptibility. Future research should aim to investigate such phenotypic responses and their wider ecological implications more fully not only by broadening the focal species to mammalian scavenger species but through more in-depth physiological testing such as blood sampling for parasites and diseases as well as behavioural research assessing and quantifying the increase in negative social interactions between individuals intra- and inter-specifically and radio-tracking to investigate the effect on home-range and activity levels.

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