

The effect of land-use modification in Sabah,
Malaysia on the morphology of two beetle families:
Carabidae and Chrysomelidae

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Declaration

The forest data used in this project was collected by SAFE project's core research team as part as an ongoing survey of the forest. Adam Sharp sorted beetles to family level. Members of the Natural History Museum helped with difficult identifications. The final project design was put together by Adam Sharp and myself. I conducted all measurements.

I entered and processed the raw data and performed all statistical analyses in R with guidance from Adam Sharp and Cris Banks-Leite.

Alice Haughan, 21st March 2016

Supervisor: Adam Sharp

The effect of land-use modification in Sabah, Malaysia on the morphology of two Coleoptera families: Carabidae and Chrysomelidae.

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Abstract: Conversion of primary forest to oil palm is a major cause of biodiversity loss in SE Asia. There is growing concern over the effect this loss of species has on ecosystem functioning. Recent studies have found that logged forests may provide a haven for species after primary forest is converted to plantation but the extent of this is not fully known. With many species showing major declines in plantations and the oil palm industry expanding every year it is crucial to understand the impact conversion of primary forest will have on the ecosystem processes. Previous studies have mainly focused on the impact on biodiversity and less speciose but charismatic taxa. In contrast, this study focuses on the effect on feeding morphology and body size of the highly speciose, Carabidae and Chrysomelidae. 752 beetles collected in Sabah, Malaysia were measured. Results suggest that mouthparts associated with sensory functions are most affected by land-use modification with these mouthparts declining in size with conversion to oil palm. Conversion to oil palm also had a greater effect on Chrysomelidae than Carabidae, indicating families do not respond uniformly to land-use modification. This study found no effect of forest conversion on the body size of either family.

Keywords: Coleoptera, feeding, land-use modification, morphology, oil palm, SAFE project

1. Introduction

South East Asia is well-renowned as a key biodiversity hotspot (Edwards *et al.* 2013). However, in recent years increased logging and conversion of primary forest to oil palm plantation has become a major threat to biodiversity in the area (Gardner *et al.* 2009, Krashevskaya & Klaner 2015, Struebig *et al.* 2013). The loss of forest in SE Asia has resulted in rapid declines in biodiversity (Edwards *et al.* 2010, Struebig *et al.* 2013, Turner & Foster 2008) and the area is now the focus of numerous studies assessing the impact of land-use modification on community assemblages (Struebig *et al.* 2013). The main cause of forest area declines is conversion of the primary forest to oil palm plantations (Edwards *et al.* 2014, Gardner *et al.* 2009, Gray *et al.* 2014). Production of oil palm in the tropics is rapidly increasing due to its widespread use for cosmetics (Koh & Wilcove 2007), as a food source and the growing interest in its potential as a biofuel (Corley 2009, Sheil *et al.* 2009).

Malaysia and Indonesia together produce 84% of the world's palm oil (Edwards *et al.* 2010, Levin 2012), and in 45 years Malaysia has increased the land area of the crop by 4 million ha (Turner & Foster 2008). The increased threat of logging and reliance on oil palm in SE Asia has led it to become a focus area for assessing the impacts of land-use change on community assemblages. In the Malaysian states of Sabah and Sarawak, just 22% of forest remains unlogged, with much of the remaining forest being subjected to multiple rounds of logging (Bryan *et al.* 2013). Thus, understanding of the value of a logged forest in maintaining biodiversity is critical (Barlow *et al.* 2007, Struebig *et al.* 2013).

In the past there has been conflicting evidence concerning the value of a logged forest. Some studies have shown there to be little biodiversity retained after logging (Davis 2000, Gardner *et al.* 2008, Rodrigues *et al.* 2016, Slade *et al.* 2011), leading to a reduction in effort to conserve them from being converted to oil palm plantation (Edwards *et al.* 2010a). However, many recent studies have found logged forests to be valuable havens for biodiversity in the face of conversion to plantation (Barlow *et al.* 2007, Chung *et al.* 2009, Konopik *et al.* 2015, Nichols *et al.* 2007,

Struebig *et al.* 2013). Berry *et al.* (2010), showed that biodiversity in logged forests was significantly greater than oil palm and more similar to primary forest, this has been supported by other studies (Dunn 2004, Lee-Cruz *et al.* 2013), some even finding higher levels of biodiversity in logged forest (Luke *et al.* 2014). It is beginning to become apparent that there is value to a logged forest, in that they may hold similar levels of biodiversity to primary forest (Barlow *et al.* 2007). For this reason it is imperative to include logged areas in studies assessing the impact of conversion to oil palm (Gardner *et al.* 2008).

The drastic effect of homogenisation of the landscape due to crop plantations, such as oil palm, is widely accepted. It is characterised by a loss of canopy cover and diversity of plant assemblages (Cusack *et al.* 2015, Struebig *et al.* 2013). It has been shown that conversion of forest to oil palm plantations leads to a reduction in the abundance and diversity of species (Gray *et al.* 2014, Shahabuddin 2005, Tews *et al.* 2004, Yaap *et al.* 2010). Turner & Foster (2008), a study conducted into the effect of oil palm conversion on abundance and biomass of arthropods in Sabah, Malaysia, showed a 78.3% decline in the abundance of non-social arthropods and a 99% decline in abundance of termites. A study by Edwards *et al.* (2010) found that abundances of imperilled bird species were 200 times lower in oil palm than primary forest. Plantations seem to reduce the numbers of specialist species (Clavel *et al.* 2011, Senior *et al.* 2012). This reduction is thought that a loss of specific food sources combined with specialist species inability to tolerate rapid change and a harsher microclimate is the reason for their decline in plantations (Bommarco *et al.* 2010, Nitterus *et al.* 2007). There is also an effect on body size, with species becoming smaller in plantations. It is hypothesised that the lower quality food source in oil palm plantations results in a reduction in body size (Emlen 1997). Another possibility is that investing less resources on body size is preferential in a changing environment (Edwards *et al.* 2014).

Given the increased rate of logging, conservationists need to understand the impact land-use modification has on species assemblages in order to establish how to sustainably log with minable impact to species diversity (Barlow *et al.* 2007, Chapin *et al.* 2000, Slade *et al.* 2011, Turner &

Foster 2008). Identifying which species are going to prevail in an oil palm landscape is crucial to inform management of these areas in the future, and particularly to allow and assessment of what ecosystem services are going to be affected in the long-term (Barragan *et al.* 2011, Bommarco *et al.* 2010, Chapin *et al.* 2000, Ewers *et al.* 2015, Slade *et al.* 2011, Turner & Foster 2008).

The fundamental question many studies have tried to answer is whether the reduction in plant diversity, caused by the homogenisation of plantations, reduces species diversity. There is a particular dearth of studies focusing on changes in feeding morphology considering the strong connections to diet. Many studies have suggested that a reduction in species diversity also leads to a reduction in functional diversity (Mayfield *et al.* 2010) however, this is still uncertain (Mayfield *et al.* 2010), investigating a direct link to ecosystem functioning through functional diversity is important. Ecosystem functioning is driven by a diversity of species filling many functional roles (Newbold *et al.* 2012). The functional role a species fits into depends on its morphological characteristics it possesses (Newbold *et al.* 2012). In order for conservationists to ascertain which ecosystem functions will be affected by land-use change, it must first be understood which morphological characteristics of these organisms are changing to assess which functional roles will be affected (Bihn *et al.* 2010). Past studies have shown a reduction in functional diversity with land-use modification (Edwards *et al.* 2013, Flynn *et al.* 2009). Edwards *et al.* (2013), showed that conversion to oil palm led to a reduction in diversity resulting in the few species remaining maintaining the functional roles that would normally be provided by many more species in primary forest. Retaining these remaining species then becomes crucial for maintaining ecosystem functions. Other studies have shown diet specialisation (Newbold *et al.* 2012) and morphology, such as wing shape, (Phommexay *et al.* 2011) to be correlated with risk of extinction due to land-use modification. These studies demonstrate the importance of taking morphological change and feeding morphology into account.

In the past, the majority of studies addressing the impacts of oil palm have focused on mammals, birds or charismatic invertebrates like butterflies (Barlow *et al.* 2007, Didham *et al.* 1998). A

study by Tews *et al.* (2004) found that a third of the papers in their search focused on avian species that account for half a percent of species diversity globally. There is a call to focus on less charismatic groups that are more speciose and have a larger contribution to ecosystem function (Barlow *et al.* 2007, Bommarco *et al.* 2010, Tews *et al.* 2004, Turner 1996). Ascertaining how these groups respond to oil palm plantations will broaden our knowledge of the effects land-use change has on ecosystem processes and functioning (Chapin *et al.* 2000, Gray *et al.* 2014). Most studies have focused on changes in biodiversity or abundance but they have yielded conflicting evidence (Barragan *et al.* 2011, Curran *et al.* 2004, Didham *et al.* 1998, Rodrigues *et al.* 2016). In this study we try a new approach, focusing on the changes in the feeding morphology of Coleoptera with conversion to oil palm. This study seeks to ascertain whether land-use modification selects for a certain mouthpart morphology in oil palm plantations. This is important as it may indicate whether conversion to oil palm plantations will drive a shift from niche separation to a more homologous community structure.

This study focuses on two beetle (order: Coleoptera) families, the Carabidae and Chrysomelidae, both of which are abundant and diverse components of the tropical forest (Ewers *et al.* 2015). Insects are good indicators of habitat disturbance responding quickly and effectually to environmental change (Pearce & Vernier 2006, Rainio & Niemelä 2003, Werner & Raffa 2000). Carabidae are mainly predatory beetles (Lövei & Sunderland 1996, Werner & Raffa 2000) and are widely recognised as good candidates for use as bio-indicators (Nitterus *et al.* 2007, Pearce & Vernier 2006). They demonstrate the effect of habitat change on other biotic components of the ecosystem (Pearce and Vernier 2006, Werner & Raffa 2000). In order to obtain a more complete understanding of the effects of logging and oil palm plantations on insects, we also included a plant-feeding family, the highly speciose and much studied family Chrysomelidae (Chapman 2007). These two families encompass many species crucial to ecosystem function (Ewers *et al.* 2015) and through this study we aim to provide better insight into the possible effects land-use modification has on the insect community.

There are no current papers known to the authors investigating the change in feeding morphology of insects with conversion to oil palm in tropical forests. A paper by Manjeri *et al.* (2013) performed a morphometric analysis of *Oryctes rhinoceros*, an oil palm pest, between oil palm plantations in different locations however, this was primarily focused on overall morphology and not feeding morphology and did not take into account other land-use types. This study aims to provide an understanding of the effects of land-use modification on these two families.

In this study, mouthpart and body size morphology data are combined with forest quality data to investigate whether the feeding morphology of Carabidae and Chrysomelidae is affected by logging or conversion of old growth forest to oil palm plantation. We further examined the effect this change in land-use had on body size as body size has previously been shown to be correlated with sensitivity to land-use modification (Nichols *et al.* 2013). We hypothesised that: (1) the homogenous landscape of the oil palm plantation would result in a change in mouthpart morphology and (2) The change of land-use type to oil palm plantation will favour smaller individuals.

2. Methods

2.1 Study Sites

The beetles used in this study were collected in Sabah, Malaysia Borneo as part of the Stability of Altered Forest Ecosystems (SAFE) project. SAFE Project encompasses a myriad of studies focused on the impacts that forest fragmentation and oil palm plantations have on the ecosystem as a whole. The block design of the experimental site was novel in its attempt to sample over different spatial scales (Ewers *et al.* 2011, Marsh & Ewers 2013, Turner *et al.* 2012). Sampling points were situated across three different land-use gradients. These ranged from old growth forest, logged forest and oil palm plantation. Old growth forest was situated in Maliau Basin Conservation Area. This comprised of three sites, two of which have never been logged and one which had been lightly logged in the past but was still representative of the surrounding primary forest (Ewers *et al.* 2011). The logged forest sites are part of a large experimental area at SAFE which has undergone two rounds of selective logging in the past. Finally, the oil palm plantation sites, managed by Benta Wawasan, part of the Sabah Foundation, are located 7km from the logged forests and comprise crop that varies from 9 to 15 years old (Ewers *et al.* 2011). In total 579 traps across the sites were sampled. A combination of pitfall, Malaise and intercept (Turner *et al.* 2012), the traps used were specially designed for SAFE project in order to compile a wide range of species. The distance between all traps was at least 56m.

2.2 Data Collection

2.2.1 Mouthpart Measurements

Measurements took place in the Natural History Museum, London using the free downloadable program ImageJ (Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, <http://imagej.nih.gov/ij/>, 1997-2016). The study comprised all beetles from the families *Carabidae* and *Chrysomelidae* caught in the traps between 2011 and 2012. A total of 742 beetles (414 Carabids, 328 Chysomelids) were measured. Beetle collections are part of an ongoing survey

conducted twice a year by the core team at SAFE, however, for logistical reasons in 2012 only one collection was made.

A microscope was set up with a camera attached to the eyepiece, the camera fed into the image processing software. A graticule was used to calibrate the image program at each magnification. The graticule was placed under the microscope and a 1mm line drawn along the projected image of the scale. Using the “set scale” tool, ImageJ calculated the number of pixels per millimetre for each magnification. This was recorded so that recalibration was not necessary before each measurement. Prior to each measurement the number of pixels per millimetre was re-entered into the “set scale” tab.

From reviewing the literature, a series of measurements were chosen that would best represent feeding morphology. Visual comparisons between the two families were conducted prior to choosing which mouthparts to measure in case certain structures were present in one family but not the other but may be worth measuring. In addition to this, both body length and antennae length were also measured. Body length was measured as it has previously been shown to be correlated with sensitivity to land-use modification (Nichols *et al.* 2013). Antennae length was used in this study as they are widely recognised as important olfactory sensors for locating food, mating partners and thought to be important for determining environmental conditions (Mutis & Palma 2014).

Total body length was calculated by measuring the pronotum down the central line to the top of the elytra, then combining this with the length of the left elytra (unless the left was not present, in this case the right was measured in its place). This is a common method for measuring the body size of beetles (Ribera *et al.* 2001). The head segment was not measured, as it is not directly related to feeding morphology. Mean antennae length was measured one segment at a time, in order to avoid error due to the curvature of the antennae. The labrum width was measured across the widest point. An average maxillary palp length was calculated by measuring the length from the tip to the stipes (Forsythe 1983).

The distance that the mandibles protruded from the labrum was also measured. The measurement was taken down centre of the labrum to the furthest extending mandible. The continuous measurements collected were standardised by body length in order to focus on the shape rather than size of the features. In the chrysomelids, the width of the mandibles was also measured, as this noticeably extended wider than the labrum in this family. This was the distance across the widest point from the edge of one mandible, across the labrum to the edge of the opposing mandible.



Figure 1. Microscope image of *Carabidae* mouthparts (a) labrum (b) mandibles (c) maxillary palps (d) protrusion

2.3 Forest Data

At each trap site environmental data was also collected. For this study we focused on the type of forest present at the trap site. For each trap it was recorded whether the location was in old growth forest (Turner *et al.* 2012), logged forest (an experimental area that had been logged twice), or oil palm plantation.

2.4 Analysis

2.4.1 PCA of feeding groups

A Principal Components Analysis (PCA) was conducted, using R (v.3.2.3), on the morphology data to determine whether the number of feeding groups changed with forest type (Ribera *et al.* 2001).

Species were clustered based on the first two principal components that contain 61% of the variation, to separate the families into feeding groups. 95% confidence ellipses were drawn around each cluster and if no overlap was observed the feeding groups were likely to be significantly different. A PCA was conducted for each family.

2.4.2 Assessing change in mouthpart morphology and body size with forest type using ANOVA

Analysis of variance (ANOVA) was used to test whether there was an effect of forest type on mouthpart morphology and body size. A separate ANOVA was conducted for each mouthpart measurement for both Carabidae and Chrysomelidae. This was in order to focus on each mouthpart separately to see if there was any change that would not show up in a PCA. In addition to this, a post-hoc test (Tukey HSD) was used to establish whether there was any significant difference in each mouthpart or body size between each forest type.

3. Results

3.1 Effect of forest type on the feeding morphology

The PCA conducted focused on feeding morphology of Carabids between forest types. All the 95% confidence ellipses overlapped resulting in a strong likelihood that there is no significant difference in feeding morphology between forest types for either Carabids (Figure 2a) or Chrysomelids (Figure 2b).

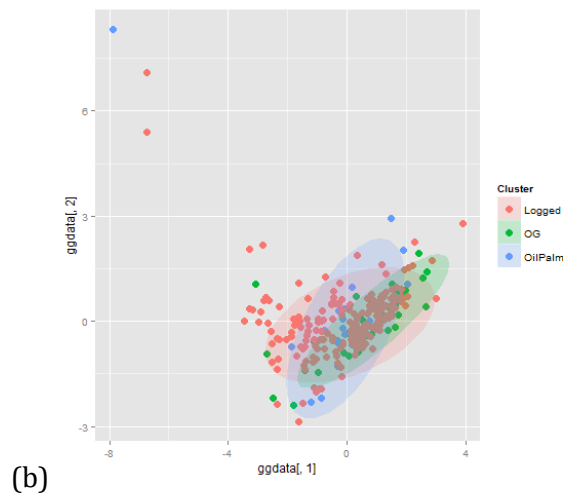
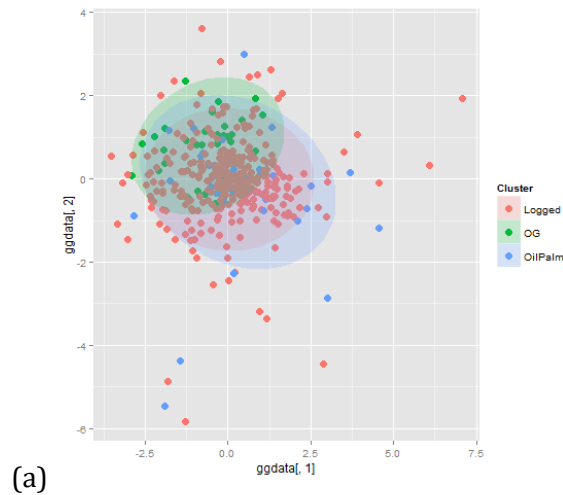


Figure 2. PCA output comparing Carabid (a) and Chrysomelid (b) mouthpart morphologies between forest types. The overlapping 95% confidence intervals show no significant difference in morphology between forest types.

3.1.2 Effect of forest type on individual mouthparts in Carabids

For Carabids, four mouthpart measurements were taken; labrum width, mean maxillary palp length, distance that the mandibles protruded from the labrum and the number of hairs visible on the upper lip. Mean antennae length was also included. An ANOVA was conducted on each measurement to ascertain whether forest type had an effect on it.

There was a significant effect of forest type on both mean antennae length (ANOVA: $F_{2,385}=13.48$, $p<0.001$) and labrum width (ANOVA: $F_{2,385}=16.98$, $p<0.001$). There was no significant effect of forest type on any of the remaining mouthpart measurements (see Appendix 1).

Further post-hoc tests (Tukey HSD) showed antennae length to be significantly shorter in old growth forest compared to oil palm (Tukey's HSD: $p<0.001$), and between old growth and logged (Tukey's HSD: $p<0.001$) but no significant difference between logged forest and oil palm (Tukey's HSD: $p=0.687$).

Labrum width was also significantly smaller in old growth compared to oil palm (Tukey's HSD: $p<0.001$) and between old growth and logged (Tukey's HSD: $p<0.001$) but no significant change between logged and oil palm (Tukey's HSD: $p=0.609$).

3.1.3 Effect of forest type on individual mouthparts in Chrysomelidae

For Chrysomelidae there were five mouthpart measurements. These were labrum width, mandible width, mean maxillary palp length, distance that the mandibles protruded from the labrum and the number of hairs visible on the upper lip. Mean antennae length was also measured. As with the Carabid analysis, an ANOVA was conducted on each measurement to see the effect of forest type.

There was a significant effect forest type on mean antennae length (ANOVA: $F_{2,263}=6.318$, $p<0.001$), mean maxillary palp length (ANOVA: $F_{2,263}=5.5$, $p<0.01$) and the number of hairs on the upper lip (ANOVA: $F_{2,263}=10.48$, $p<0.001$). There was no significant effect of forest type on either mandible width, labrum width or the distance the mandible protrudes from the labrum (see Appendix 2).

Further post-hoc tests (Tukey HSD) showed antennae length to be significantly shorter in old growth forest compared to logged forest (Tukey's HSD: $p<0.01$), but no significant difference between logged forest and oil palm (Tukey's HSD: $p=0.999$), or between old growth and oil palm (Tukey's HSD: $p=0.085$).

Mean maxillary palp length was significantly longer in old growth compared to logged (Tukey's HSD: $p < 0.01$), however, there was no significant difference between old growth and oil palm (Tukey's HSD: $p = 0.189$), or between logged and oil palm (Tukey's HSD: $p = 0.943$).

There was significantly less hairs present on the upper lip in old growth forest compared oil palm (Tukey's HSD: $p < 0.001$) and less hairs present in old growth compared to logged forest (Tukey's HSD: $p < 0.01$). There was also significantly less hairs present on individuals in logged forest compared to oil palm (Tukey's HSD: $p < 0.05$).

Despite the ANOVA showing no significant effect of forest type on labrum width, the further post-hoc test showed labrum width to be significantly larger in old growth compared to logged forest (Tukey's HSD: $p < 0.05$) and but insignificant between old growth and oil palm (Tukey's HSD: $p = 0.503$) and between logged and oil palm (Tukey's HSD: $p = 0.907$).

3.2 Effect of forest type on body size

In Chrysomelidae there was a significant effect of forest type on body length (ANOVA: $F_{2,263} = 3.469$, $p < 0.05$). Further Tukey HSD test showed the significant difference to be between old growth and logged forest, with body length significantly shorter in old growth (Tukey's HSD: $p < 0.05$). There was no significant difference between logged forest and oil palm (Tukey's HSD: $p = 0.999$) or old growth and oil palm (Tukey's HSD: $p = 0.240$).

In Carabidae, there was no significant effect of forest type on body length (ANOVA: $F_{2,385} = 2.625$, $p = 0.07$).

4. Discussion

Effect of forest type on feeding morphology

In this study, we investigated how land-use modification effects the feeding morphology and body size of beetles in the families *Carabidae* and *Chrysomelidae* in Sabah, Malaysia. From researching the literature, the effects of land-use modification on feeding morphology has been relatively understudied.

Past studies have predominantly focused on the effects of conversion of primary forest to oil palm plantation on species abundance (Nichols *et al.* 2007, Senior *et al.* 2012, Turner & Foster 2008) or functional diversity (Edwards *et al.* 2014, Slade *et al.* 2011). Although results vary between taxa (Chung & Eggleton 2001, Struebig *et al.* 2013, Tews *et al.* 2004), most have concluded that abundance and functional diversity decline dramatically when logged forest is converted to plantation, a less structurally complex habitat (Nitterus *et al.* 2007, Parui *et al.* 2015, Slade *et al.* 2007). A study conducted by Edwards *et al.* (2014) showed that functional richness and specialisation both declined in oil palm, also showing a loss of some functional traits. Declines in functional diversity with conversion to oil palm have been recorded in many other taxa studied (Edwards *et al.* 2013, Gardner *et al.* 2008, Tews *et al.* 2004). Thus, it was expected that this loss of functional diversity would result in generalist species with mouthpart morphologies capable of a range of feeding techniques remaining (Edwards *et al.* 2013, Flynn *et al.* 2009). From this it was hypothesised that mouthpart morphology would be significantly different in oil palm plantations compared to both logged and old growth forests in the *Carabidae* and *Chrysomelidae*. By contrast, this study did not find a significant change in mouthpart morphology in general between primary forests, logged forests and oil palm in either family (see Figure 2).

When mouthparts were looked at individually, there were some significant changes observed between the forest types. In both families, mean antennae length was significantly shorter in old growth forests compared to logged forest and in *Carabidae* antennae length was also significantly shorter in old growth compared to oil palm. There was a smaller labrum width between old

growth and logged forest and old growth and oil palm in the Carabids. In contrast, the Chrysomelids showed a tendency towards a larger labrum in old growth forest compared to oil palm plantation. The number of hairs present in the Chrysomelids was significantly less in old growth compared to oil palm and logged. The possible explanation for seeing an effect of forest type on these features but not on either mandible measurements, which are more related to processing food (Bernays 1998), is that these are key sensory structures. The antennae being one of the main sensory structures on many organisms harbouring a concentration of sensilla (Klowden 2007, Mutis & Palma 2014). The labrum is similarly important for sensory reception with a membranous surface covered in sensory receptors and hairs extending from the lip (Labandeira, 1997). The less complex oil palm habitat (Cusack *et al.* 2015) may offer less protection, a lower variety of food sources and potentially a lower abundance of mates (Edwards *et al.* 2013, Phommexay *et al.* 2011). Thus, enhanced sensory reception may be increasingly necessary to optimise chances of finding food and mates and avoiding predators (Klowden 2007, Larsson *et al.* 2001, Mutis & Palma 2014).

The significant effect of forest type on a number of mouthpart measurements was expected to be seen between old growth forest and oil palm plantation, given the literature showing the dramatic effects oil palm can have on species diversity (Chung & Eggleton 2001, Edwards *et al.* 2010, Fitzherbert *et al.* 2008). However, the effect that logging alone would have on mouthpart morphology was less obvious. The results of this study show there was also a number of variables differing greatly between old growth and logged forests but not logged forests and oil palm. This contradicts much of the literature showing logged forests to be much more alike to primary forest (Edwards *et al.* 2013, Nichols *et al.* 2007, Struebig *et al.* 2013). These results may suggest that logged forests select for similar mouthpart morphology as oil palm in these families.

There was a greater effect of forest type on more mouthparts in the Chrysomelid family. Few studies have compared how Carabidae (Rainio & Niemelä 2003) and Chrysomelidae react to habitat change so it is inconclusive why one would respond to a greater extent than the other.

One possible explanation for the effect on more mouthparts in the Chrysomelids is that Carabids are less susceptible to decline in species when habitat changes, some Carabids have even been shown to prefer managed land (Latty *et al.* 2006). This is supported by Turner & Foster (2008), in their study they showed an increase in abundance of Carabidae in oil palm compared to primary forest. The authors hypothesise that they are less susceptible to disturbance, and competitively excluded more specialist families (Clavel *et al.* 2011). Another possibility is that the Chrysomelids are predominantly herbivores (Bienkowski 2010, Chapman 2007) and so respond faster to change in vegetation structure (Haddad *et al.* 2009, Murdoch *et al.* 1972, Woodcock 2010) and the effect on other families with more diverse feeding habits takes longer to appear.

It could be that mouthpart morphology is perhaps not an important trait in deciding which organisms will survive land-use modification. It is also possible that there are more appropriate morphological features to measure that might have detected a response. Forsythe (1983) wrote a paper detailing different morphological features and feeding habits of the Carabids. He wrote of the importance of whether there was a presence of setal cages on the head, the size of the eyes and the number of setae on each lacinia. In another study by Cabrera & Durante (2003) they frequently measure the mola area to determine the feeding morphology of chrysomelids.

Effect of forest type on body size

This study also shows no effect of forest type on body size in Carabids. Shahabuddin *et al.* (2005) found a similar result in dung beetles (Coleoptera, Scarabaeidae), with no change in body size with land-use intensity. However, a significant effect was found between old growth and logged forest in Chrysomelidae with body size significantly smaller in old growth. This contradicts much of the literature which shows body size to get progressively smaller from primary forest to oil palm (Edwards *et al.* 2014, Gardner *et al.* 2008, Nichols *et al.* 2013). The theory behind this is that a smaller body size is beneficial as it takes less time to develop and is less likely to have habitat change affect it during growth. One possible explanation for the reduction of Chrysomelidae size in old growth is that due to the less densely forested logged areas and plantations it was simply

easier to catch larger beetles in logged forest and oil palm than in old growth forest (Cusack *et al.* 2015, Saint-Germain *et al.* 2005), although if this was the case it would be expected to see the same response in Carabids. Another possibility is that the smaller Chrysomelidae species are more susceptible to habitat change and so are not found in the plantation habitat.

Future study design considerations

There were some limitations to this study. These were primarily that the beetles measured were already mounted on card. This meant that we were limited to measurements taken from the top of the beetle. It also meant that they were not easily manoeuvred so some had to be eliminated from the study if mounted in an unusual position or their head was curled under the body. This could have resulted in some species not being represented in this study if they were eliminated because of their head positioning.

In future studies it would be beneficial to look at effects on morphology in conjunction with biodiversity on the same families to directly compare the relationship, as it might turn out that biodiversity of these families also does not change. It would be interesting to assess change over a longer time period to see if there was more of an effect on Carabids given a longer time to adapt, this would make the data more reliable. Further studies on the change in feeding morphology with other forest variables such as canopy cover and amount of above ground biomass would be valuable to support this study and to better conclude the effect of forest modification on these families.

Effect on ecosystem functioning

A major concern for a change in morphology with land-use modification is the potential impact on ecosystem functioning (Barragan *et al.* 2011, Chapin *et al.* 2000, Ewers *et al.* 2015, Turner & Foster 2008). This study has focused on mouthpart morphology due to the direct connection with feeding. The changes shown in mouthparts with land-use modification in this study may be used to indicate which species will survive in a plantation habitat. It is possible to infer which ecosystem functions will be affected by the change in size of certain characteristics. Species differ

greatly in their sensitivity to land-use modification (Struebig *et al.* 2013). Thus, in order to do this it is necessary to extend this study to encompass more families and a greater number of morphological characteristics.

Wider Implications

This study has furthered our knowledge of the effects of land-use modification on two highly speciose families. It has provided more support for arguments that species react differently to conversion of primary forest to plantations (Chung & Eggleton 2001, Dunn 2004, Turner & Foster 2008). This is important for future management of plantations to know which species prevail in oil palm as these will be driving force behind many of the ecosystem processes (Dunn 2004, Ewers *et al.* 2015).

It has been suggested, in other taxa, that logged forests may provide a haven for biodiversity and functional diversity. This study shows that for mouthpart morphology this is not the case. It is apparent from this study that other indicators for the effect of land-use modification, such as morphology, should be considered. Results from both families showed logged forest to retain measurements much more like oil palm than old growth forest, with most of the significant differences in mouthpart sizes to be between old growth and logged forest.

In addition, study demonstrates that conversion to oil palm is having an effect on organism morphology and although the extent of the effect is not yet understood, it is clear that changes in communities across the tropics are occurring (Chapin 2000, Curran *et al.* 2004). We need to understand the extent to which these changes impact our most speciose families that contribute most to ecosystem processes in order to effectively manage these landscape changes in the future (Ewers *et al.* 2015, Gray *et al.* 2014, Konopik *et al.* 2014).

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Literature Cited

Barlow, J., Gardner T.A., Araujo, I.S. *et al.* (2007) "Quantifying the Biodiversity Value of Tropical Primary, Secondary, and Plantation Forests." *Proceedings of the National Academy of Sciences*, 104, (47), 18555–60. doi:10.1073/pnas.0703333104.

Barragán, F., Moreno, C.E., Escobar, F. *et al.* (2011) "Negative Impacts of Human Land Use on Dung Beetle Functional Diversity." *PLOS ONE*, 6 (3). doi:10.1371/journal.pone.0017976.

Bernays, E.A. (1998) "Evolution of Feeding Behavior in Insect Herbivores." *BioScience*, 48 (1), 35–44. doi:10.2307/1313226.

Berry, N.J. & Phillips, O.L. (2010) "The High Value of Logged Tropical Forests: Lessons from Northern Borneo." *Biodiversity and Conservation*, 19(4), 985–97. doi:10.1007/s10531-010-9779-z.

Bieńkowski, A. O. (2010) "Feeding Behavior of Leaf Beetles (Coleoptera, Chrysomelidae)." *Entomological Review*, 90 (1), 1–10. doi:10.1134/S001387381001001X.

Bihn, J.H., Gebauer, G. & Brandl, R. (2010) "Loss of functional diversity of ant assemblages in secondary tropical forests." *Ecology*, 91(3).

Bommarco, R., Biesmeijer, J.C., Meyer, B. *et al.* (2010) "Dispersal Capacity and Diet Breadth Modify the Response of Wild Bees to Habitat Loss." *Proceedings of the Royal Society of London B: Biological Sciences*, 277 (1690), 2075–82. doi:10.1098/rspb.2009.2221.

Bryan, J.E., Shearman, P.L., Asner, G.P. *et al.* (2013) "Extreme Differences in Forest Degradation in Borneo: Comparing Practices in Sarawak, Sabah, and Brunei." *PLOS ONE*, 8, (7), 69679. doi:10.1371/journal.pone.0069679.

Cabrera, N.C., & Durante, S.P. (2003) "Comparative Morphology of Mouthparts in Species of the Genus *Acalymma* Barber (Coleoptera, Chrysomelidae, Galerucinae)." *The Coleopterists Bulletin*, 57 (1), 5–16. doi:10.1649/0010-065X(2003)057[0005:CMOMIS]2.0.CO;2.

Chapin III, F.S., Zavaleta, E.S. & Eviner, V.T. (2000) "Consequences of Changing Biodiversity." *Nature*, 405 (6783), 234–42. doi:10.1038/35012241.

Chapman, R.F. (2007) Foraging and Food Choice of Phytophagous Insect in *Chemical Ecology*. University of Arizona, Phoenix.

Chung, A.Y.C. & Eggleton, P. (2001) "The Diversity of Beetle Assemblages in Different Habitat Types in Sabah, Malaysia." *Bulletin of Entomological Research*, 90 (6), 475–96.

- Clavel, J., Julliard, R. & Devictor, V. (2011) "Worldwide Decline of Specialist Species: Toward a Global Functional Homogenization?" *Frontiers in Ecology and the Environment*, 9 (4), 222–28. doi:10.1890/080216.
- Corley, R.H.V. (2009) "How Much Palm Oil Do We Need?" *Environmental Science & Policy*, 12 (2), 134–39. doi:10.1016/j.envsci.2008.10.011.
- Curran, L. M., Trigg, S.N., McDonald, A.K. *et al.* (2004) "Lowland Forest Loss in Protected Areas of Indonesian Borneo." *Science*, 303 (5660), 1000–1003. doi:10.1126/science.1091714.
- Cusack, J.J., Wearn, O.R., Bernard, H. & Ewers, R.M. (2015) "Influence of Microhabitat Structure and Disturbance on Detection of Native and Non-Native Murids in Logged and Unlogged Forests of Northern Borneo." *Journal of Tropical Ecology*, 31 (1), 25–35. doi:10.1017/S0266467414000558.
- Davis, A.J. (2000) "Does Reduced-Impact Logging Help Preserve Biodiversity in Tropical Rainforests? A Case Study from Borneo Using Dung Beetles (Coleoptera: Scarabaeoidea) as Indicators." *Environmental Entomology*, 29 (3), 467–75. doi:10.1603/0046-225X-29.3.467.
- Didham, R.K., Hammond, P.M., Lawton, J.H. *et al.* (1998) "Beetle Species Responses to Tropical Forest Fragmentation." *Ecological Monographs*, 68 (3), 295–323. doi:10.1890/0012-9615(1998)068[0295:BSRTTF]2.0.CO;2.
- Dunn, R.R. (2004) "Managing the Tropical Landscape: A Comparison of the Effects of Logging and Forest Conversion to Agriculture on Ants, Birds, and Lepidoptera." *Forest Ecology and Management*, 191 (1), 215–24. doi:10.1016/j.foreco.2003.12.008.
- Edwards, D.P., Hodgson, J.A., Hamer, K.C. *et al.* (2010) "Wildlife-Friendly Oil Palm Plantations Fail to Protect Biodiversity Effectively." *Conservation Letters*, 3(4), 236–42. doi:10.1111/j.1755-263X.2010.00107.x.
- Edwards, D.P., Larsen, T.H., Teegan, D.S. *et al.* (2010a) "Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests." *Proceedings of the Royal Society B: Biological Sciences*, DOI: 10.1098/rspb.2010.1062. Accessed online: <http://rspb.royalsocietypublishing.org/content/early/2010/08/03/rspb.2010.1062>
- Edwards, F.A., Edwards, D.P., Hamer, K.C. & Davies, R.G. (2013) "Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland." *Ibis*, 155 (2), 313–326.
- Edwards, F.A., Edwards, D.P., Larsen, T.H. *et al.* (2014) "Does Logging and Forest Conversion to Oil Palm Agriculture Alter Functional Diversity in a Biodiversity Hotspot?" *Animal Conservation*, 17(2), 163–73. doi:10.1111/acv.12074.
- Emlen, D. J. (1997) "Diet Alters Male Horn Allometry in the Beetle *Onthophagus Acuminatus* (Coleoptera: Scarabaeidae)." *Proceedings of the Royal Society B: Biological Sciences*, 264, (1381), 567–74. doi:10.1098/rspb.1997.0081.
- Ewers, R.M., Didham, R.K., Fahrig, L. *et al.* (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 (1582), 3292–3302. doi:10.1098/rstb.2011.0049.

Ewers, R.M., Michael, J. W., Boyle, R.A. *et al.* (2015) "Logging Cuts the Functional Importance of Invertebrates in Tropical Rainforest." *Nature Communications*, 6(6836) doi:10.1038/ncomms7836.

Fitzherbert, E.B., Struebig, M.J., Morel, A. *et al.* (2008) "How Will Oil Palm Expansion Affect Biodiversity?" *Trends in Ecology & Evolution*, 23(10), 538–45. doi:10.1016/j.tree.2008.06.012.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T. *et al.* (2009) "Loss of functional diversity under land-use intensification across multiple taxa." *Ecology Letters*, 12, 22–23.

Forsythe, T. G. (1983) "Mouthparts and Feeding of Certain Ground Beetles (Coleoptera: Carabidae)." *Zoological Journal of the Linnean Society*, 79(4), 319–76. doi:10.1111/j.1096-3642.1983.tb01170.x.

Gardner, T.A., Hernández, M.I.M., Barlow, J. & Peres, C.A. (2008) "Understanding the Biodiversity Consequences of Habitat Change: The Value of Secondary and Plantation Forests for Neotropical Dung Beetles." *Journal of Applied Ecology*, 45(3), 883–93. doi:10.1111/j.1365-2664.2008.01454.x.

Gardner, T.A., Barlow, J., Chazdon, R. *et al.* (2009). "Prospects for Tropical Forest Biodiversity in a Human-Modified World." *Ecology Letters*, 12(6), 561–82. doi:10.1111/j.1461-0248.2009.01294.x.

Gray, C.L., Slade, E.M., Mann, D.J. & Lewis, O.T. (2014) "Do Riparian Reserves Support Dung Beetle Biodiversity and Ecosystem Services in Oil Palm-Dominated Tropical Landscapes?" *Ecology and Evolution*, 4(7), 1049–60. doi:10.1002/ece3.1003.

Haddad, N.M., Crutsinger, G.M., Gross, K. *et al.* (2009) "Plant Species Loss Decreases Arthropod Diversity and Shifts Trophic Structure." *Ecology Letters*, 12(10), 1029–39. doi:10.1111/j.1461-0248.2009.01356.x.

Keller, I. & Largiadèr, C.R. (2003) "Recent Habitat Fragmentation Caused by Major Roads Leads to Reduction of Gene Flow and Loss of Genetic Variability in Ground Beetles." *Proceedings of the Royal Society of London B: Biological Sciences*, 270(1513), 417–23. doi:10.1098/rspb.2002.2247.

Klowden, M.J. (2007) *Physiological systems in insects*, 2nd edn. Academic Press, Amsterdam.

Koh, L.P. & Wilcove, D.S. (2007) "Cashing in Palm Oil for Conservation." *Nature*, 448(7157), 993–94. doi:10.1038/448993a.

Konopik, O., Gray, C.L., Ulmar Grafe, T. *et al.* (2014). "From Rainforest to Oil Palm Plantations: Shifts in Predator Population and Prey Communities, but Resistant Interactions." *Global Ecology and Conservation*, 2, 385–94. doi:10.1016/j.gecco.2014.10.011.

Konopik, O., Steffan-Dewenter, I. & Ulmar Grafe, T. (2015) "Effects of Logging and Oil Palm Expansion on Stream Frog Communities on Borneo, Southeast Asia." *Biotropica*, 47(5) 636–43. doi:10.1111/btp.12248.

Krashevskaya, V. & Klärner, B. (2015) "Impact of Tropical Lowland Rainforest Conversion into Rubber and Oil Palm Plantations on Soil Microbial Communities." *Biology and Fertility of Soils*, 51, 697–705. doi:10.1007/s00374-015-1021-4.

Labandeira, C.C. (1997) "Insect Mouthparts: Ascertaining the Paleobiology of Insect Feeding Strategies." *Annual Review of Ecology and Systematics*, 28, 153–93.

- Larsson, M. C., Leal, W.S. & Hansson, B.S. (2001) "Olfactory Receptor Neurons Detecting Plant Odours and Male Volatiles in *Anomala Cuprea* Beetles (Coleoptera: Scarabaeidae)." *Journal of Insect Physiology*, 47(9) 1065–76.
- Latty, E.F., Werner, S.M., Mladenoff, D.J. *et al.* (2006) "Response of Ground Beetle (Carabidae) Assemblages to Logging History in Northern Hardwood–hemlock Forests." *Forest Ecology and Management*, 222(1–3), 335–47. doi:10.1016/j.foreco.2005.10.028.
- Lee-Cruz, L., Edwards, D.P., Tripathi, B.M & Adams, J.M. (2013) "Impact of Logging and Forest Conversion to Oil Palm Plantations on Soil Bacterial Communities in Borneo." *Applied and Environmental Microbiology*, 79(23), 7290–97. doi:10.1128/AEM.02541-13.
- Levin, J. (2012) "Profitability and Sustainability in Palm Oil Production." WWF-UK. Accessed March 18, 2016. http://www.wwf.org.uk/wwf_articles.cfm?unewsid=5879.
- Lövei, G.L. & Sunderland, K.D. (1996) "Ecology and Behavior of Ground Beetles (Coleoptera: Carabidae)." *Annual Review of Entomology*, 41, 231–56. doi:10.1146/annurev.en.41.010196.001311.
- Luke, S.H., Fayle, T.M., Eggleton, P. *et al.* (2014) "Functional Structure of Ant and Termite Assemblages in Old Growth Forest, Logged Forest and Oil Palm Plantation in Malaysian Borneo." *Biodiversity and Conservation*, 23(11), 2817–32. doi:10.1007/s10531-014-0750-2.
- Manjeri, G. & Muhamad, R. (2013) "Morphometric Analysis of *Oryctes Rhinoceros* (L.) (Coleoptera: Scarabaeidae) from Oil Palm Plantations." *The Coleopterists Bulletin*, 67(2). doi:10.1649/0010-065X-67.2.194.
- Marsh, C.J. & Ewers, R.M. (2013) "A Fractal-Based Sampling Design for Ecological Surveys Quantifying β -Diversity." *Methods in Ecology and Evolution*, 4(1), 63–72. doi:10.1111/j.2041-210x.2012.00256.x.
- Mayfield, M.M., Bonser, S.P., Morgan, J.W. *et al.* (2010) "What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change." *Global Ecology and Biogeography*. 19(4), 423-431.
- Murdoch, W.W., Evans, F.C. & Peterson, C.H. (1972) "Diversity and Pattern in Plants and Insects." *Ecology*, 53(5), 819–29. doi:10.2307/1934297.
- Mutis, A. & Palma, R. (2014) "Morphology and Distribution of Sensilla on the Antennae of *Hylamorpha Elegans* Burmeister (Coleoptera: Scarabaeidae)." *Neotropical Entomology*, 43 (3).
- Newbold, T., Scharlemann, J.P.W., Butchart, S.H.M. *et al.* (2012) "Ecological traits affect the response of tropical forest bird species to land-use intensity." *Proceedings of the Royal Society B: Biological Sciences*, 280: 20122131
- Nichols, E., Larsen, T., Spector, S. *et al.* (2007) "Global Dung Beetle Response to Tropical Forest Modification and Fragmentation: A Quantitative Literature Review and Meta-Analysis." *Biological Conservation*, 137(1), 1–19. doi:10.1016/j.biocon.2007.01.023.
- Nichols, E., Uriarte, M., Bunker, D.E. *et al.* (2013) "Trait-Dependent Response of Dung Beetle Populations to Tropical Forest Conversion at Local and Regional Scales." *Ecology*, 94(1), 180–89.
- Nittérus, K., Åström, M., & Gunnarsson, B. (2007) "Commercial Harvest of Logging Residue in Clear-Cuts Affects the Diversity and Community Composition of Ground Beetles (Coleoptera:

Carabidae)." *Scandinavian Journal of Forest Research*, 22(3), 231–40. doi:10.1080/02827580701352955.

Parui, A.K., Chatterjee, S. & Basu, P. (2015) "Habitat Characteristics Shaping Ant Species Assemblages in a Mixed Deciduous Forest in Eastern India." *Journal of Tropical Ecology*, 31(3), 267–80. doi:10.1017/S0266467415000036.

Pearce, J.L., & Venier, L.A. (2006) "The Use of Ground Beetles (Coleoptera: Carabidae) and Spiders (Araneae) as Bioindicators of Sustainable Forest Management: A Review." *Ecological Indicators*, 6(4), 780–93. doi:10.1016/j.ecolind.2005.03.005.

Phommexay, P., Satasook, C., Bates, P. *et al.* (2011) "The impact of rubber plantations on the diversity and activity of understorey insectivorous bats in southern Thailand." *Biodiversity and Conservation*, 20(7), 1441-1456.

Rainio, J., & Niemelä, J. (2003) "Ground Beetles (Coleoptera: Carabidae) as Bioindicators." *Biodiversity & Conservation*, 12(3), 487–506. doi:10.1023/A:1022412617568.

Ribera, I., Dolédec, S., Downie, I.S. & Foster, G.N. (2001) "Effect of Land Disturbance and Stress on Species Traits of Ground Beetle Assemblages." *Ecology*, 82(4) 1112–29. doi:10.1890/0012-9658(2001)082[1112:EOLDAS]2.0.CO;2.

Rodrigues, D.J., Florêncio, F.P., Oliveira, J. *et al.* (2016). "Habitat Associations of Woodcreeper (Aves: Dendrocolaptidae) Assemblage in Selectively Logged Areas of Southern Amazonia." *Journal of Tropical Ecology*, 32(1), 63–74. doi:10.1017/S0266467415000565.

Saint-Germain, M., Larrivée, M. & Drapeau, P. *et al.* (2005) "Short-Term Response of Ground Beetles (Coleoptera: Carabidae) to Fire and Logging in a Spruce-Dominated Boreal Landscape." *Forest Ecology and Management*, 212(1–3) 118–26. doi:10.1016/j.foreco.2005.03.001.

Senior, M.J.M., Hamer, K.C. & Bottrell, S. *et al.* (2012). "Trait-Dependent Declines of Species Following Conversion of Rain Forest to Oil Palm Plantations." *Biodiversity and Conservation*, 22(1), 253–68. doi:10.1007/s10531-012-0419-7.

Shahabuddin, Schulze, C.H. & Tschardtke, T. (2005) "Changes of Dung Beetle Communities from Rainforests towards Agroforestry Systems and Annual Cultures in Sulawesi (Indonesia)." *Biodiversity & Conservation*, 14(4), 863–77. doi:10.1007/s10531-004-0654-7.

Sheil, D., Casson, A., Meijaard, E. *et al.* (2009) "*The Impacts and Opportunities of Oil Palm in Southeast Asia: What Do We Know and What Do We Need to Know?*" CIFOR Occasional Paper no. 51. Center for International Forestry Research (CIFOR), Bogor, Indonesia. Available at: http://www.cifor.org/publications/pdf_files/occpapers/op-51.pdf.

Slade, E.M., Mann, D.J., Villanueva, J.F. & Lewis, O.T. (2007) "Experimental Evidence for the Effects of Dung Beetle Functional Group Richness and Composition on Ecosystem Function in a Tropical Forest." *Journal of Animal Ecology*, 76(6), 1094–1104. doi:10.1111/j.1365-2656.2007.01296.x.

Slade, E.M., Mann, D.J. & Lewis, O.T. (2011) "Biodiversity and Ecosystem Function of Tropical Forest Dung Beetles under Contrasting Logging Regimes." *Biological Conservation*, 144(1), 166–74. doi:10.1016/j.biocon.2010.08.011.

Struebig, M.J., Turner, A., Giles, E. *et al.* (2013) "Chapter Three - Quantifying the Biodiversity Value of Repeatedly Logged Rainforests: Gradient and Comparative Approaches from Borneo." Change in Multispecies Systems: Part 3 in *Advances in Ecological Research*, 48:183–224. Global Academic Press. Available: <http://www.sciencedirect.com/science/article/pii/B9780124171992000033>.

Tews, J., Brose, U., Grimm, V. *et al.* (2004). "Animal Species Diversity Driven by Habitat Heterogeneity/diversity: The Importance of Keystone Structures." *Journal of Biogeography*, 31(1), 79–92. doi:10.1046/j.0305-0270.2003.00994.x.

Turner, I. M. (1996) "Species Loss in Fragments of Tropical Rain Forest: A Review of the Evidence." *Journal of Applied Ecology*, 33(2), 200–209. doi:10.2307/2404743.

Turner, E.C. & Foster, W.A. (2008) "The Impact of Forest Conversion to Oil Palm on Arthropod Abundance and Biomass in Sabah, Malaysia." *Journal of Tropical Ecology*, 25 (1), 23–30. doi:10.1017/S0266467408005658.

Turner, E. C., Abidin, Y.Z., Barlow, H. *et al.* (2012). "The Stability of Altered Forest Ecosystems Project: Investigating the Design of Human-Modified Landscapes for Productivity and Conservation." *The Planter*, 88, 453–68.

Werner, S.M. & Raffa, K.F. (2000) "Effects of Forest Management Practices on the Diversity of Ground-Occurring Beetles in Mixed Northern Hardwood Forests of the Great Lakes Region." *Forest Ecology and Management*, 139(1–3), 135–55. doi:10.1016/S0378-1127(99)00341-2.

Woodcock, B. A. (2010) "Impact of Habitat Type and Landscape Structure on Biomass, Species Richness and Functional Diversity of Ground Beetles." *Agriculture Ecosystems & Environment*, 139(1–2), 181–86. doi:10.1016/j.agee.2010.07.018.

Yaap, B., Struebig, M.J., Paoli, G. & Koh, L.P. (2010) Mitigating the biodiversity impacts of oil palm development. *CAB Reviews*, 5(19), 1-11.

Appendices

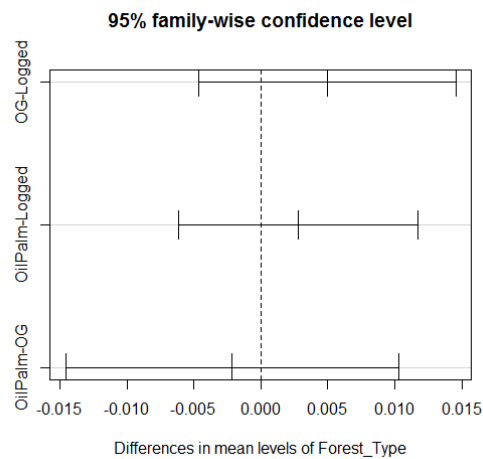
Appendix 1- Further Carabid results

Distance of mandible protrusion from the labrum

ANOVA results

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Forest_Type	2	0.00092	0.0004605	0.923	0.398
Residuals	385	0.19202	0.0004988		

Tukey HSD plot

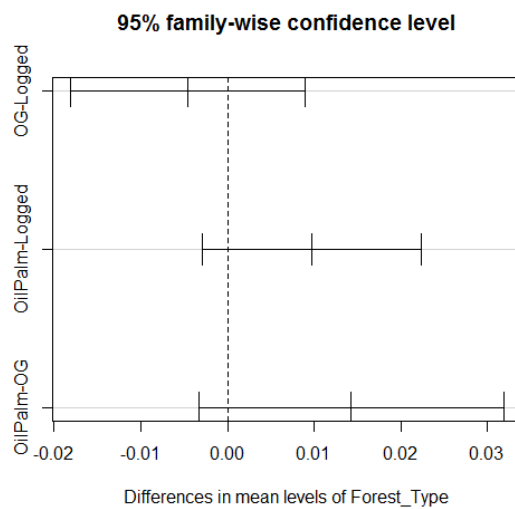


Mean maxillary palp length

ANOVA results

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Forest_Type	2	0.0042	0.0021196	2.131	0.12
Residuals	385	0.3829	0.0009947		

Tukey HSD plot

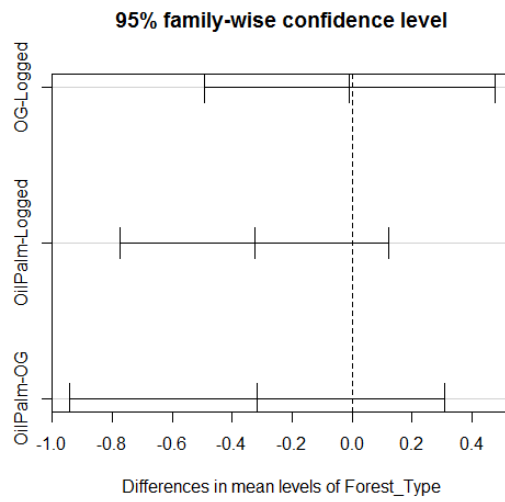


Number of hairs on the upper lip

ANOVA results

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Forest Type	2	3.7	1.856	1.465	0.232
Residuals	385	487.8	1.267		

Tukey HSD plot



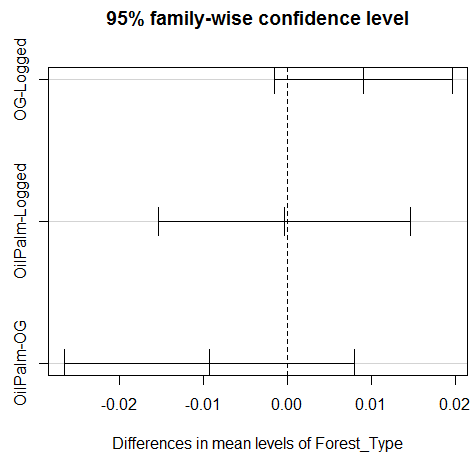
Appendix 2 – Further Chrysomelid results

Mandible width

ANOVA results

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Forest_Type	2	0.00287	0.0014357	2.037	0.132
Residuals	263	0.18538	0.0007049		

Plot of Tukey HSD

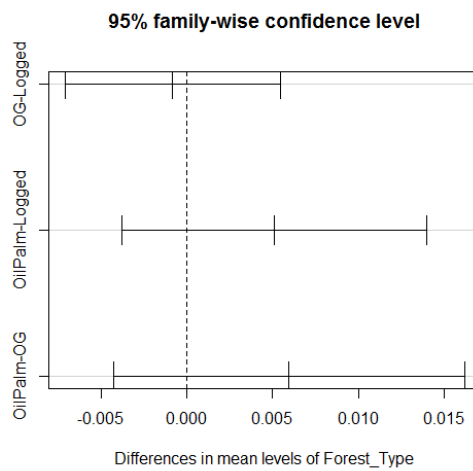


Distance of mandible protrusion from the labrum

ANOVA results

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Forest_Type	2	0.00051	0.0002548	1.03	0.358
Residuals	263	0.06505	0.0002473		

Tukey HSD plot



Labrum width

ANOVA results

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Forest_Type	2	0.00196	0.0009811	2.937	0.0548 .
Residuals	263	0.08785	0.0003340		

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Tukey HSD plot

