

Aerial Insect Communities Above Tropical Forest Rivers: Are There Directional Patterns to Movement?

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Project Declaration

The final design of this project was an amalgamation of ideas from Dr. Rob Ewers, Sarah Luke MSc and myself. I collected all the data used here at the SAFE Project in Sabah, Malaysia in the summer of 2015. Sampling points used were on river transects designed by Matthew Struebig's lab group. All points were within or in the vicinity of the SAFE project. I identified and processed all samples in the field. I also carried out the statistical analyses, before they were checked by Adam Sharp MSc. Dr. Rob Ewers gave me feedback on my thesis before submission.

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Summary

1. An increasing human population is currently the greatest threat to global biodiversity, as large proportions of natural ecosystems are destroyed, fragmented and degraded to fuel a growing demand for resources. Tropical forests are home to 50% of the Earth's species and a large proportion of those are insects.
2. Insects play a vital role in many ecosystem functions such as pollination, herbivory and dung removal, whilst also being useful bio-indicators for ecosystem health. In ecological models it is often assumed that insect movement is a random process, despite a rapidly growing pool of literature to suggest otherwise.
3. Here we studied the communities of insects that fly above rivers in tropical forest of varying degradation in Sabah, Malaysia. Directional flight intercept traps sampled either insects flying *along* or *across* rivers. Insects were identified to order level.
4. A higher diversity of insects was found to fly across rivers compared to along rivers, with differing community compositions also present moving along these two vectors. We suggest that this is due to the river acting as a barrier to insect dispersal, rather than a highway, thus more terrestrial orders are predominantly found flying across rivers to minimize time spent over the water.

Keywords: Borneo, community composition, directional trapping, insect dispersal, insect flight, riparian reserves, rivers, tropical forest degradation

Introduction

Modification of natural ecosystems is the most pressing threat to global biodiversity (Reid et al., 2005). This threat is increasing as the human population grows exponentially and with it an unsustainable demand for resources (Cropper & Griffiths, 1994; Sala et al., 2000). Tropical forests, in particular, face more destruction, fragmentation and degradation than most other habitats (Sala et al., 2000). Tropical forests are thought to host over 50% of the world's terrestrial animal species, even though despite their total area coverings less than 7% of land globally (Wilson, 1988). High species richness in this biome is largely due to the sheer volume of insect species thought to inhabit tropical forests, with some estimates suggesting the total figure to be as much as 5 million (Godfray et al., 1999). It is probable that we will lose many species to extinction before they are described by science (Lawton & May, 1995). Thus, the impending threat of anthropogenic modification in this biome is likely to have severe impacts on insect diversity in the tropics.

Insects are a vital taxon in terrestrial and freshwater aquatic systems worldwide. Rainforests demonstrate this with particular clarity, as many ecosystem functions are hinged on insect groups. Pollination (Bawa, 1990), insect predation (Ewers et al., 2015), seed predation (Janzen et al., 1971; Ewers et al., 2015), dung removal (Slade et al., 2007) and herbivory (Coley & Barone, 1996), to name but a few functions, are all, contributed to by insects. Many of these have been shown to decrease with habitat fragmentation and degradation due to a change in the insect communities present (Slade et al., 2011; Ewers et al. 2015). Insects also act as a bio-indicators of ecosystems due to their relatively high abundance and diversity (Bisevac & Majer, 1999), cost effectiveness to study (Bisevac & Majer, 1999), high mobility allowing them to track changes in climate (Samways et al., 2010) and their short generation times and small size making them sensitive to local conditions

(Samways et al., 2010). As insects are important in ecosystem functions that are affected by degradation and fragmentation, as well as being a useful indicator taxon for a variety of reasons, they are thus a vital group to study in order to understand the effect of anthropogenic change on tropical forests.

Aerial insect communities above tropical rivers are an infrequently sampled group, despite their importance to many other taxa of conservation interest. The few papers that do sample them (e.g. Dudgeon, 1988), tend to focus primarily on aquatic insects rather than the entire taxon. These whole communities of terrestrial and aquatic insects are likely to be the primary source of food for many bat species, especially in tropical forest rivers where bat feeding activity is higher than in the surrounding forest (Hagen & Sabo, 2011). Furthermore, 'insect rain', i.e. the input of terrestrial insects falling into streams, has been shown to be an important aspect of aquatic food webs, particularly for fish (Nakano & Murakami, 2001; Chan et al., 2008). By sampling all aerial insects above rivers, studies may obtain data important to monitoring river and forest quality, rather than assuming that the two systems are independent.

Insects are the only invertebrate taxa to have evolved the power of flight; an evolutionary innovation that has markedly changed their movement capabilities (Woiwod et al., 2001). 'Movement' is defined here as including both migratory movement, where an individual travels greater distances to reach novel areas (Kennedy, 1975), and shorter vegetative movements between resources (Kennedy, 1985). Understanding insect migration, particularly aerial migration, is an important aspect of tropical forest ecology, as it can enable the comprehension of aspects of ecology such as meta-populations, source-sink dynamics and seasonal changes in community structure. Models of insect dispersal in regard to meta-population dynamics often assume a completely random movement of individuals (Molainen & Hanski, 1998). However, an ever-increasing body of literature shows that this is an assumption without factual backing (Stinner et al., 1983; Winterbourn et al., 2001; Arellano et al., 2008, Bogan & Boersma 2012). Vegetative

movements are also an important aspect of insect ecology to study. Flying towards, or in the search of, new ecological resources can have large impacts on broader patterns of movement. Corridors and barriers to vegetative movement will be present within landscapes. This is particularly true of tropical forests undergoing fragmentation; as more and more barriers are preventing insect dispersal (Lovejoy et al., 1986), it will be increasingly useful to understand where corridors of movement lie when trying to conserve remaining communities.

Rivers in many biomes have been used to study the dispersal of insects (Wright-Stow et al., 2006; Bogan & Boarsma 2012; Didham et al., 2012). We suggest that this is in part due to being a linear feature through an otherwise homogenous landscape. A linear structure makes them ideal for studying the dispersal of insects, as distinguishing the characteristics of where they are flying from or to becomes simpler: they either disperse up or down the river, or cross the river into the surrounding matrix. Defining what insects are dispersing away from or towards is much harder in a complex 3-dimensional habitat such as tropical forests, where environmental predictors are hard to quantify, map and model. Furthermore, rivers are likely to influence terrestrial and aquatic insect movement in a variety of ways. We might expect aquatic insects to disperse predominantly along the river, moving into the more hostile forest as a means to disperse to new watercourses (Didham et al. 2012). Terrestrial insects will likely suffer from higher predation from bats and other riparian species (Chan et al., 2008; Hagen & Sabo, 2011), but may also be able to disperse greater distances above an open, linear feature. Above the river, individuals would not be hampered by a complex, dense forest environment, where movement through vegetation may result in a lower dispersal distance as the crow flies. With only a few examples in the literature (e.g. Battacharya et al., 2002), linear features such as rivers have seldom been studied in regards to whether they act as a barrier to insect dispersal.

Many studies that attempt to analyse insect movement use mark-release-recapture methods (e.g. Arellano et al., 2008). An issue with this method is a lack of information on the trajectory of an individual; the data only reveals where the individual began its movement and where it was recaptured (Conradt et al., 2000). Low recapture rates also mean that large samples of a single species need to be collected over extended periods of time to gain useful data: a problem in tropical ecosystems where single species abundances are often low (Basset, 1999). There are relatively few studies that instead use directional insect trapping (e.g. Dudgeon, 1988; Wright-Stow et al., 2006; Cunningham et al., 2013); a method that allows trajectories of movement to be tracked. Capture of an insect by a directional trap is a proxy for movement through a landscape however, as insects do not move in perfectly straight lines. To use directional trapping, one has to assume that the insects entering the trap from a certain direction are, on average, flying along the trajectory of the entrance to the trap.

In this study we use directional flight intercept traps to sample insects flying *along* or *across* rivers in tropical forest at the SAFE Project in Sabah, Malaysia. We aim to understand whether insect community composition, mass, abundance, richness and alpha-diversity can be significantly influenced by the orientation of directional traps, even when insects are only identified to order. Flight intercept traps were suspended above rivers in a variety of surrounding forest types (continuous, disturbed, riparian reserve and oil palm), allowing a comparison of insect communities in differing levels of habitat disturbance and modification.

Materials and Methods

Study Site

All 10 rivers studied were located in Sabah, Malaysia within the Stability of Altered Forest Ecosystems (SAFE) Project (Ewers et al., 2011) or adjacent oil palm plantations (fig. 1). Two rivers were located in areas of continuous forest, logged and old growth respectively. Five SAFE Project rivers were chosen, which, in the future, will have experimental riparian reserves of differing widths that have not yet been fully established (Ewers et al., 2011). As these reserves are in the process of being set up, we have classified them as ‘disturbed’ forest in our analysis. The logged continuous forest and the forest around the SAFE Project rivers had previously undergone two rounds

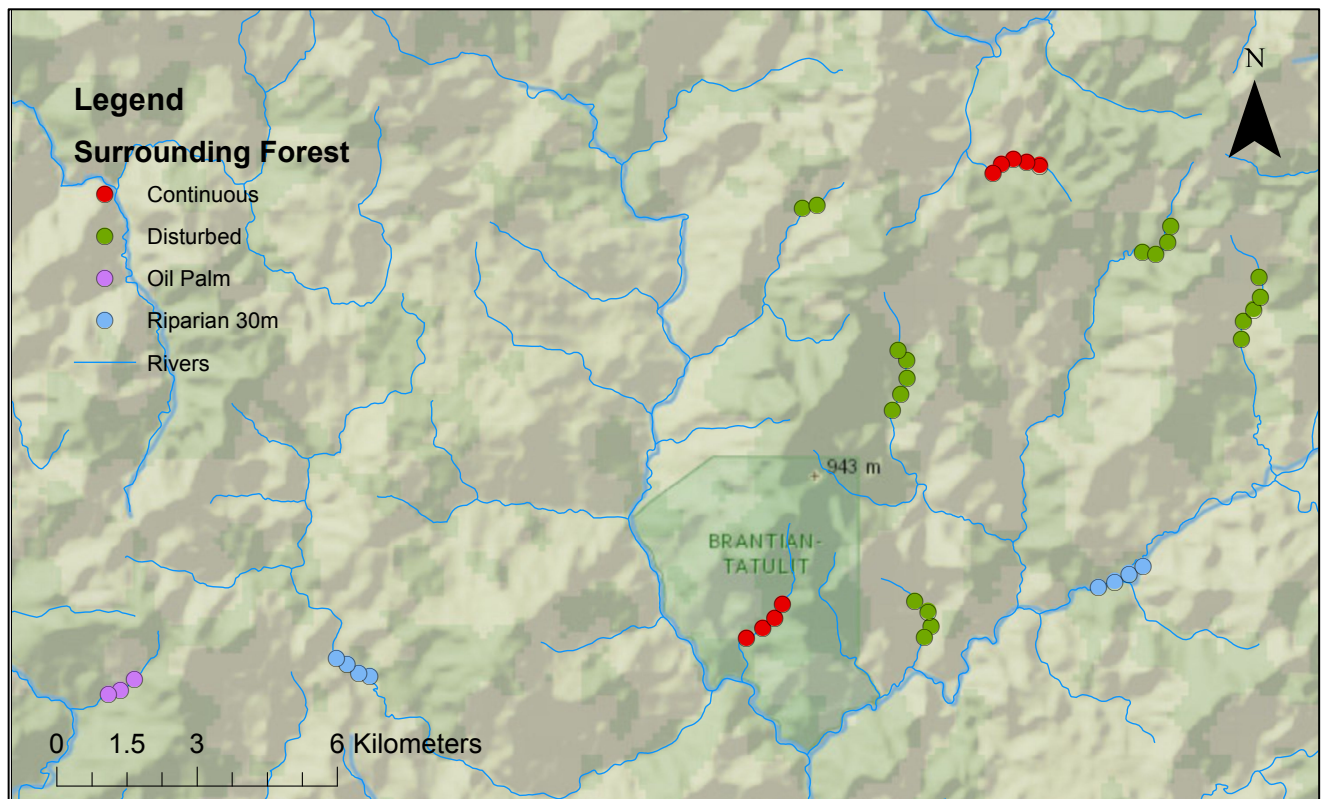


Fig. 1. Locations of sites of data collection in Sabah, Malaysia. Each point denotes one site where two traps of differing orientation collected insects. Colour is used to signify the surrounding forest type. The green highlighted area (Brantian-Tatulit) denotes the Virgin Jungle Reserve; an area of unlogged forest protected by Malaysian law.

of logging in the 1970s and then in the early 2000s (Struebig et al., 2013). Two rivers with 30m riparian reserves required by Malaysian law in oil palm plantations and an oil palm river with no riparian reserves were also measured. On each river 4-5 sites were studied on 10-point previously outlined river transects (Struebig et al., in press). All sites chosen were 2 points apart on a given transect (e.g. points 1,3,5,7,9), where each of the original individual points were spaced 180-200m apart. Given the distance between points, spatial autocorrelation was not considered in the analysis. All data was collected during a 2-month period between the 18th May and the 13th July 2015.

Insect Trapping

Standardised combination pitfall and malaise traps, currently being used for long-term Hymenopteran and Coleopteran surveys at the SAFE Project, were adapted for use above rivers (fig. 2). These traps operate using two planes of intersecting transparent plastic, giving a flight intercept area of $\sim 0.5\text{m}^2$ when approached from any side. Sheets lead to a collecting funnel and bottle at the top and bottom containing 95% ethanol to preserve specimens. Traps were modified to only collect insects that entered from opposing sides, i.e. 90° of open face on each side, by blocking entrances to the collection funnels with linoleum. Malaise netting extends from the top funnel and is usually pegged to the ground to increase trap efficacy. The netting in this study was altered so that it was only suspended above the open parts of the trap using metal poles. A single rope suspended a trap 0.5-1.1m above the surface of the river before being left to collect for 3 days. Two traps were placed at each sampling point, one oriented with the collecting sides facing the banks of the river and one oriented to collect insects flying down and up the river. These two traps were spaced $\sim 10\text{m}$ apart to minimize traps influencing each other's capture rates (5m to either side of the site coordinates) (fig. 3). Width of the river under each trap and at the midpoint between traps was taken and averaged for the site. Rainfall was measured over the 3-day collection period in a 50ml falcon tube attached to the side of a trap. Rainfall was converted from ml to mm before statistical analysis.

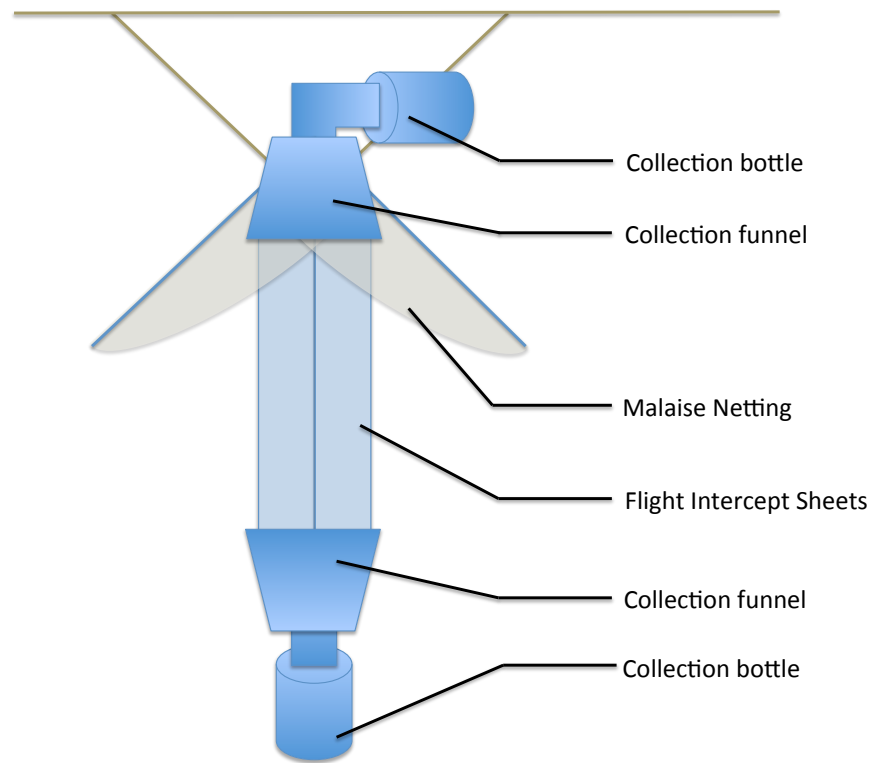


Fig. 2. Insect trap design for specimen collection. The flight interception sheets are two interlocking planes of transparent plastic forming a cross-shape when viewed from above. Flight interception area is 0.5m^2 when approached from any side.

Vegetation Data

Percentage canopy cover was estimated above each trap and at the midpoint between them on the river using a spherical densiometer. Tree basal area was measured using a relascope and the angle point method (Bitterlich, 1984), 5m perpendicularly into the forest from both banks at three points; next to each of the two traps and at the midpoint between them (fig. 3). Percentage canopy cover was also measured at these points.

Insect Identification

Samples from collection bottles were pooled into a single sample per trap. Insects were stored below 0°C in 95% ethanol before identification. All non-insects, wingless orders and individuals lacking wings (e.g. worker ants) were removed as they were assumed to have not flown into the trap or were not part of our study group. Individuals were identified to order level using a hand-lens. If insects were unidentifiable to order, due to a lack of experience or damaged remains, they were listed as so and were only used in total abundance and mass analyses. Total wet mass of specimens per trap was measured using electric scales, with a precision of 0.01g, after excess ethanol was removed with a muslin cloth. A second total wet mass was taken with all individuals weighing over 0.25g removed, to attain a mass measure with less

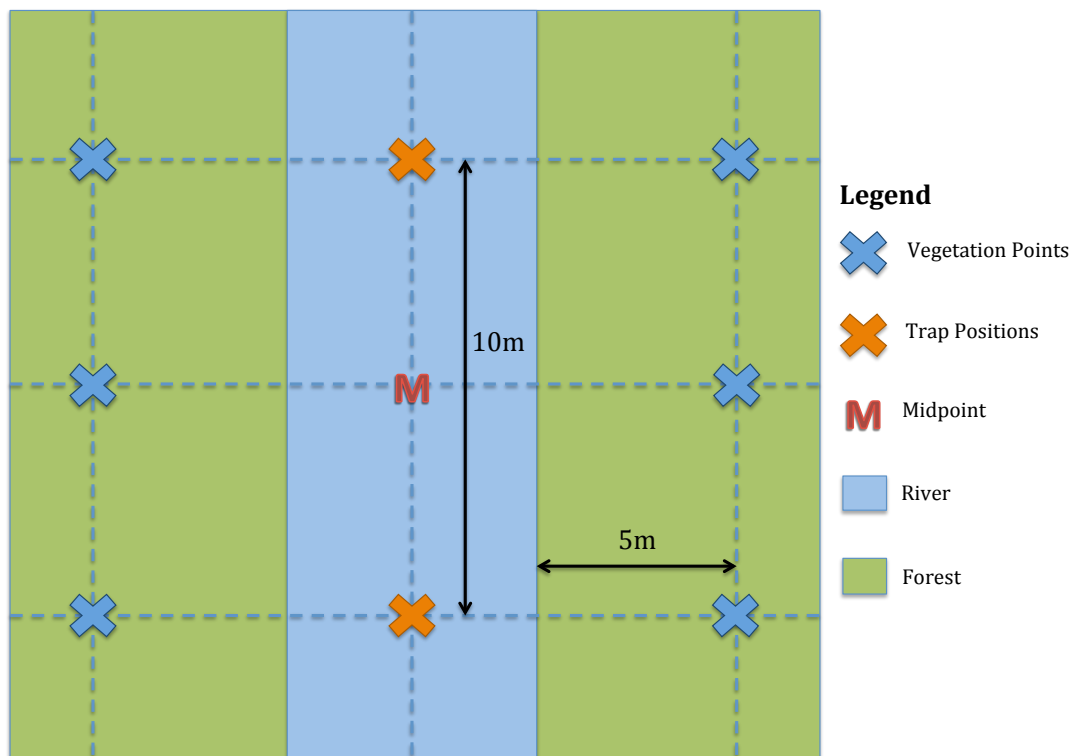


Fig. 3. A diagram depicting the methodology of data collection at each site. Each trap (orange crosses) was either oriented to catch insects flying along or across the rivers. Canopy cover was taken at all vegetation points, trap positions and at the midpoint. River width was measured at the traps and at the midpoint. Tree basal area was measured at all vegetation points.

variation from single large insects that may hide an effect on smaller insect masses.

Statistical Methods

All statistical analyses were conducted within R3.2.0 (R Core Team, 2015). With the exception of total abundance, non-normal variables were \log_{10} transformed to give normal distributions (river width, rainfall, tree basal area). Rainfall was \log_{10} transformed after adding 1 to each data point due to 0s present in the dataset. Linear mixed effect models (LMEs), from the lme4 R package (Bates et al., 2014), were used to analyse mass, mass excluding larger insects, and order diversity. A generalized linear mixed effects model (GLMM) with a poisson error structure was utilised to analyse abundance and order richness, as they were count data. River and sample site were used as random effects to account for similarity between insects on the same rivers and at the same sites. Orientation of the trap, forest type, percentage canopy cover on banks, percentage canopy cover on the river, rainfall, tree basal area, river width and a quadratic polynomial of date collected were used in initial models to predict the dependent variables. Due to low sample sizes, interactions were not included in any models. Likelihood ratio tests were used to remove terms and simplify the model in the LMEs and the GLMMs as required. P-values given were produced by removing the term of interest from the model and comparing the new model to the old using a Chi-squared test within the anova() function. All mixed effects models used unstructured covariance structures. Whenever surrounding forest type was a significant predictor, the lsmeans (Lenth & Hervé, 2015) and multcompView (Graves et al., 2015) packages were used to perform a Tukey HSD test to show which groups were significantly different.

A non-metric multidimensional scaling correspondence analysis (NMDS) using the vegan R package (Oksanen et al., 2015) was used to assess differences in community composition. The stress value of the model was checked to make sure it was within reasonable limits. 95% confidence ellipses were generated using code written by Fox and Weisberg (2011). The

adonis() function was used to run a PERMANOVA (a multivariate ordination analysis) that analysed which of the predictive variables used above affected community composition when river pseudo-replication was accounted for. All graphs were produced in ggplot2 package (Wickam, 2009). Lines and curves of best fit of graphs were generated using a separate linear model. Means are given ± 1 standard error. N denotes the total sample size and n denotes sub-sample sizes.

Results

82 traps from 41 sites were collected and analysed. We processed 3468 insects from 15 different orders; weighing a total of 23.75g. Samples were dominated by Coleoptera, which made up 77% of individuals.

Total Abundance

Total abundance of insects was only predicted by surrounding forest type ($\chi^2 = 15.03$, $p < 0.01$, $N = 82$, $df = 3$). Rivers in forest that were undergoing disturbance had a greater mean abundance (63.2 ± 8.5 , $n = 40$, $p < 0.05$) than our continuous controls (24.6 ± 4.6 , $n = 18$, $p < 0.05$) (fig. 4a) (table 1). Rivers in riparian reserves were not different from our control, but did have lower abundance than disturbed forest (22.7 ± 2.3 , $n = 18$, $p < 0.05$). Oil palm rivers without a riparian reserve were not significantly different to any other forest types (32.3 ± 7.3 , $n = 6$, $p < 0.05$).

Total Mass

\log_{10} transformed total mass was only predicted by a 2-factor polynomial of the date of collection ($\chi^2 = 4.17$, $p < 0.05$, $N = 70$, $df = 1$) (fig. 5a) (table 2). The generated curve of best fit shows a parabolic shape with a maximum on the 19/05.

Mass of Smaller Insects

\log_{10} -transformed mass was predicted by additional fixed effects when larger insects were removed from the analysis. Mass of small insects was significantly predicted by \log_{10} -transformed tree basal area ($\chi^2 = 7.16$, $p < 0.01$, $N=70$, $df = 1$), \log_{10} -transformed river width ($\chi^2 = 8.01$, $p < 0.01$, $N = 70$, $df = 1$), surrounding forest type ($\chi^2 = 17.48$, $p < 0.001$, $N = 70$, $df = 3$) and a 2-factor polynomial of date collected ($\chi^2 = 7.45$, $p < 0.01$, $N = 70$, $df = 1$) (table 3). Mass of smaller insects decreased with increasing tree basal area (fig. 6a) and river width (fig.6b). The 2-factor polynomial of date showed a similar pattern to the previous model of total mass, with a maximum on the 19/05 as

well (fig. 5b). Established riparian reserves had lower small insect mass than oil palm plantations with no reserve (fig. 4b) (table 4) ($99 \pm 20\text{mg}$, $n=38$, and $97 \pm 19\text{mg}$, $n = 6$ respectively, $p < 0.05$).

Order Richness & Diversity

Order Richness was not significantly predicted by any variables. Diversity was predicted by the orientation of the trap ($\chi^2 = 11.95$, $p<0.001$, $df=1$, $N=82$) (fig.7) (table 5). Insects flying along the river had a significantly lower Shannon-Wiener Index Diversity (0.861 ± 0.027 , $n = 41$) compared to those flying across the river (1.015 ± 0.037 , $n = 41$) (table 6). Diversity was also predicted by percentage canopy cover of surrounding forest ($\chi^2 = 6.49$, $p<0.05$, $df=1$, $N=82$) (table 5) (fig. 8).

Community Composition

Community composition of insects flying above rivers was affected by trap orientation ($F = 43.88$, $\text{Pr}(>F) < 0.001$, $df=81$, $N=82$) (fig. 9a) and by surrounding forest type ($F = 10.98$, $\text{Pr}(>F) < 0.001$, $df = 81$, $N = 82$) (fig. 9b) (table 7). The stress factor was within reasonable bounds for an NDMS analysis (0.097). Trap orientation explained 27.0% of variance and surrounding forest type explained 20.1% of variance in community composition.

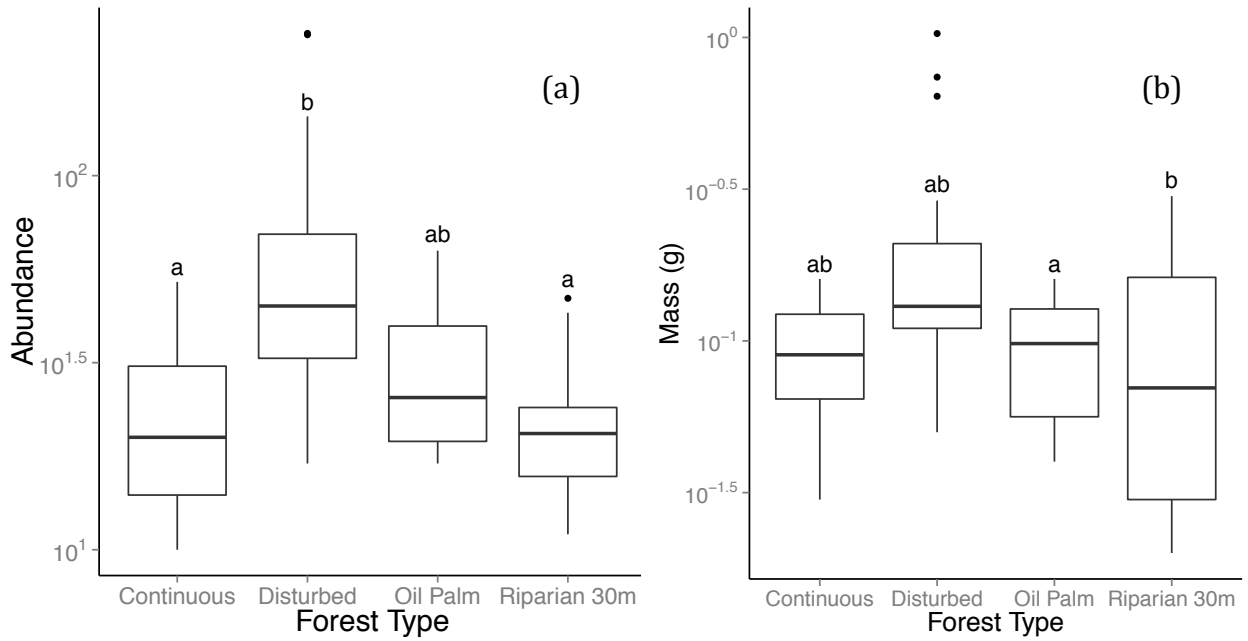


Fig. 4. The effect of surrounding forest type on the total abundance of insects (a) ($\chi^2 = 15.03$, $p < 0.01$, $N = 82$, $df = 3$) and log₁₀ mass of small insects (b) ($\chi^2 = 17.48$, $p < 0.001$, $N = 70$, $df = 3$) above rivers in Sabah, Malaysia. Abundance and mass are shown on a log₁₀ scale. Forest types that are not significantly different ($p < 0.05$) in least means squared test share the same letter above the plot. For (a) $n = 18, 40, 6, 18$ (forest type from left to right) and (b) $n = 8, 38, 6, 18$ (forest type from left to right).

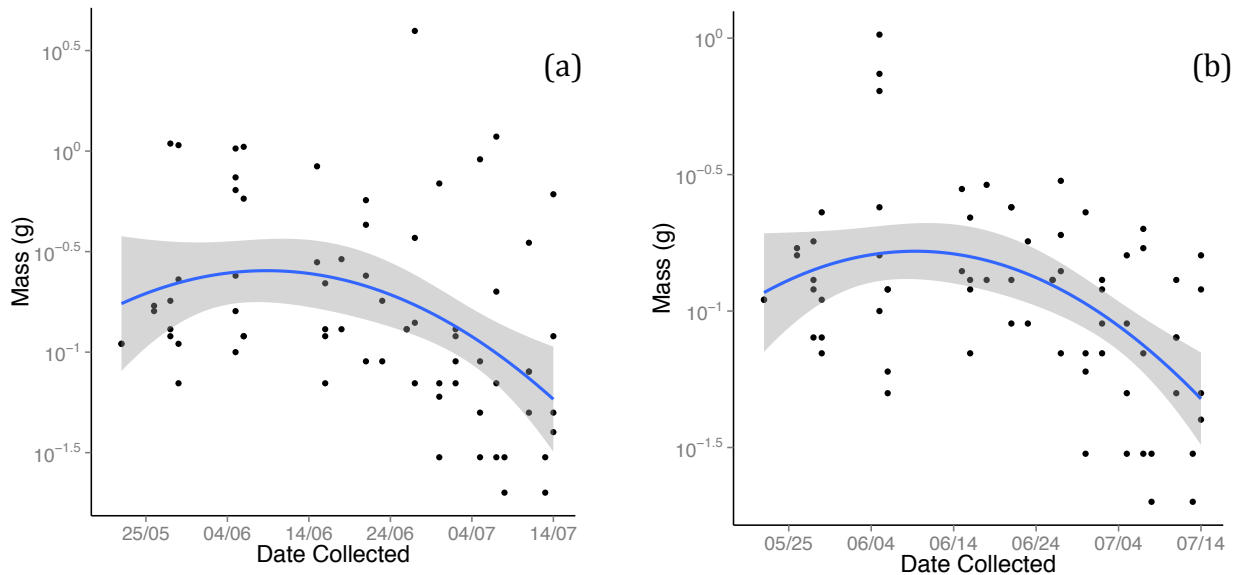


Fig. 5. The effect of date on the log₁₀ total mass of insects (a) ($\chi^2 = 4.17$, $p < 0.05$, $df = 1$, $N = 70$) and the log₁₀ total mass of small insects (b) ($\chi^2 = 7.45$, $p < 0.01$, $N = 70$, $df = 1$) above rivers in Sabah, Malaysia. 12 traps were excluded from the analysis due to a lack of data. Mass is shown on a log₁₀ scale. A 2-factor polynomial was used in a second *linear* model to generate the curve of best fit with grey areas around it showing 95% confidence intervals. Model $df = 6$ and 11 respectively. Both curves have a maximum on the 19/05.

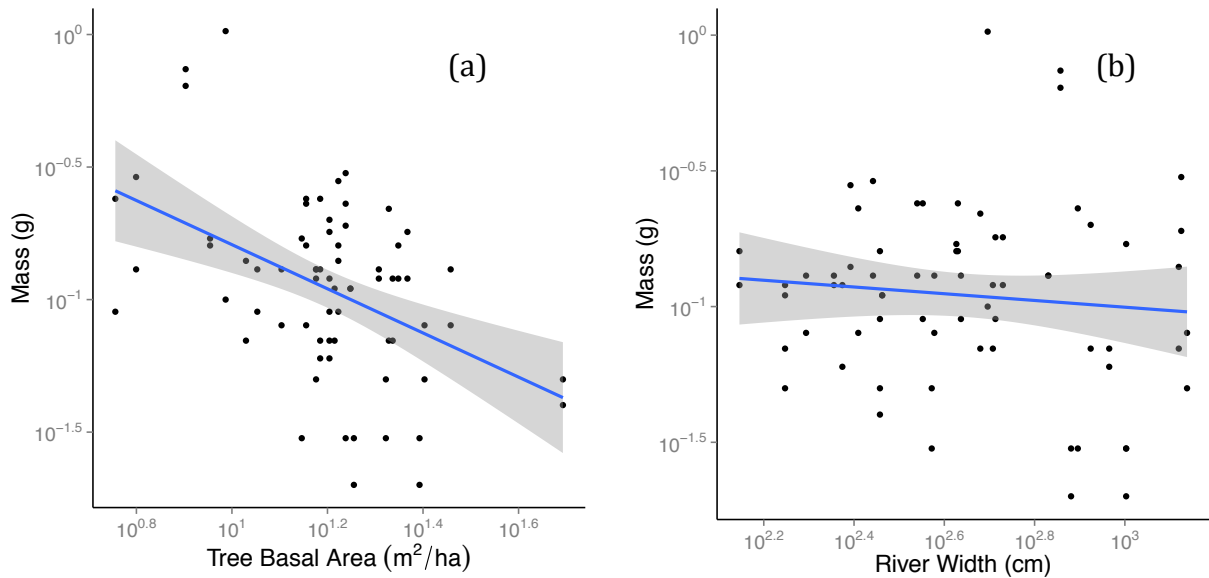


Fig. 6. The effect of tree basal area (m^2/ha) (a) ($\chi^2 = 7.16$, $p < 0.01$, $N=70$, $df = 1$) and river width (cm) (b) ($\chi^2 = 8.01$, $p < 0.01$, $N = 70$, $df = 1$) on the \log_{10} total mass of small insects above rivers in Sabah, Malaysia. 12 traps were excluded from the analysis due to a lack of data. Mass, tree basal area and river width are all shown on a \log_{10} scale. A second *linear* model was used to generate the line of best fit with grey areas around it showing 95% confidence intervals.

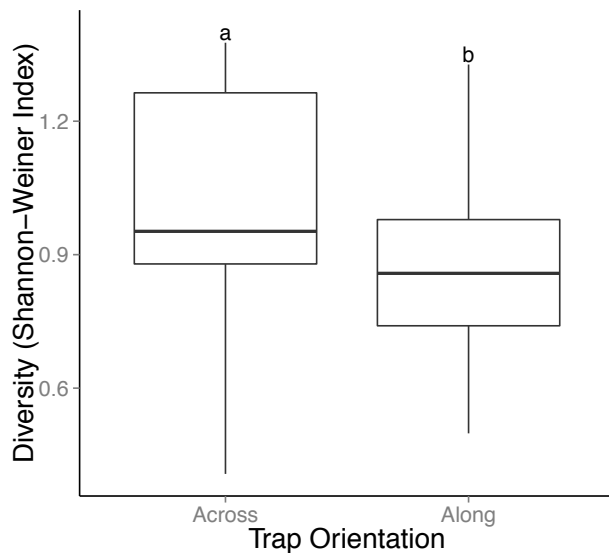


Fig. 7. The effect of trap orientation on the diversity ((Shannon-Wiener Index) of insects sampled ($\chi^2 = 11.95$, $p < 0.001$, $df = 1$, $N = 82$) above rivers in Sabah, Malaysia. Trap orientations that are not significantly different ($p < 0.05$) in least means squared test share the same letter above the plot.

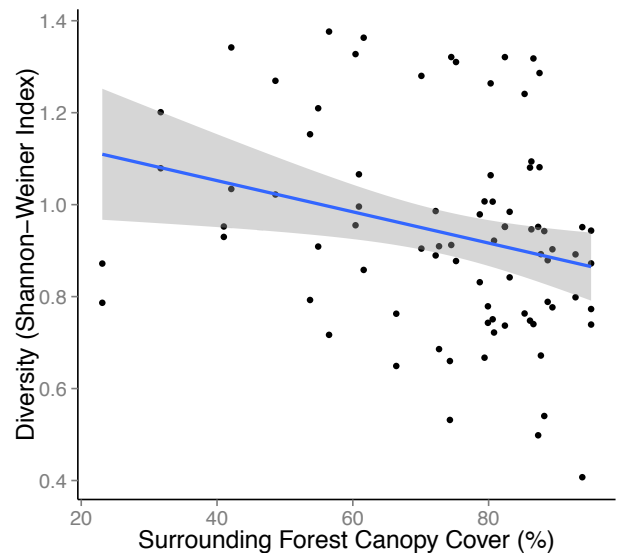


Fig. 8. The effect of surrounding forest canopy cover (%) ($\chi^2 = 6.49$, $p < 0.01$, $N = 82$, $df = 1$) on the diversity (Shannon-Weiner Index) of insects sampled above rivers in Sabah, Malaysia. A second *linear* model was used to generate the line of best fit with grey areas around it showing 95% confidence intervals.

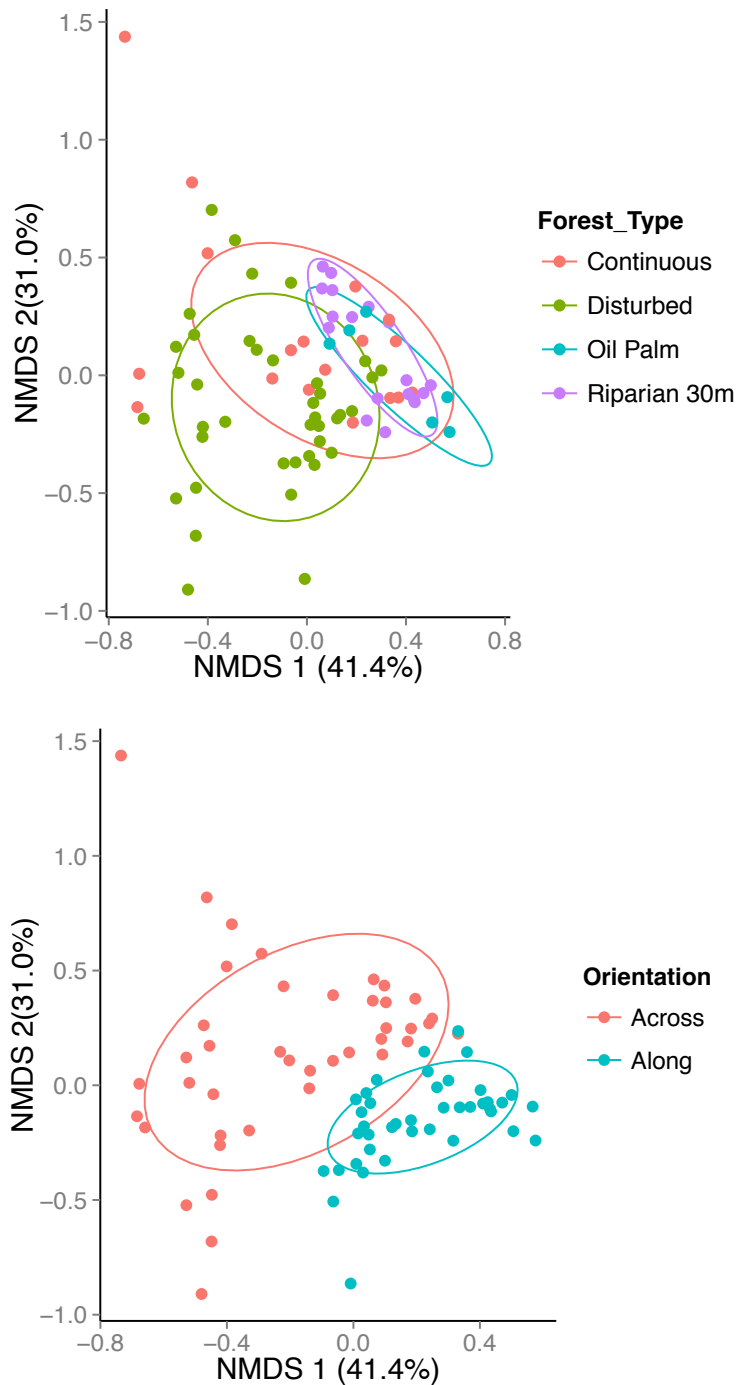


Fig 9. NMDS plots showing insect community composition flying above rivers grouped by (a) surrounding forest type ($F = 10.98$, $\text{Pr}(> F) < 0.001$, $df = 81$, $N = 82$, $R^2 = 0.20$) and (b) trap orientation ($F = 43.88$, $\text{Pr}(> F) < 0.001$, $df = 81$, $N = 82$, $R^2 = 0.27$). Community composition is shown using the two eigenvectors that represented the most variability in the abundance data (NMDS 1 accounts for 41.4% and NMDS 2 accounts for 31.0%). 95% confidence interval ellipses are given.

Table 1. Least squared means and standard errors generated from a generalised linear mixed effects model of abundance of insects above rivers against surrounding forest type in Sabah, Malaysia. Shared letters in 'group' denote no significant difference between those groups. Tukey HSD adjusted for multiple comparisons.

Forest Type	Mean	Standard Error	Group
Continuous	3.088	0.174	a
Disturbed	3.918	0.114	b
Riparian 30m	3.083	0.174	a
Oil Palm	3.404	0.298	ab

Table 2. Fixed effects model outputs for the linear mixed effects model of a 2-factor polynomial of date on a \log_{10} -transformed measure of insect mass above rivers in Sabah, Malaysia ($p < 0.05$, $df = 1$, $n = 70$). 12 traps were excluded from the analysis due to a lack of data. Model $df = 6$.

Fixed Effect	Estimate	Std. Error	t value
Intercept	-1.825	0.137	-13.323
Polynomial(Date)1	-2.989	1.354	-2.208
Polynomial(Date)2	-2.563	1.275	-2.011

Table 3. Fixed effects model outputs for the linear mixed effects model of a 2-factor polynomial of date, \log_{10} tree basal area, \log_{10} river width and forest type on \log_{10} -transformed insect mass above rivers in Sabah, Malaysia. 12 traps were excluded from the analysis due to a lack of data. Forest types are compared to the continuous control. Model $df = 11$, $N = 70$.

Fixed Effect	Estimate	Std. Error	t value
Intercept	-4.062	1.473	-2.758
Polynomial(Date)1	-3.501	1.678	-2.086
Polynomial(Date)2	-2.737	1.093	-2.505
\log_{10} (Tree Basal Area)	-0.564	0.229	-2.459
\log_{10} (River Width)	0.584	0.216	2.699
Forest Type - Disturbed	-0.153	0.382	-0.401
Forest Type - Riparian 30m	-0.619	0.348	-1.778
Forest Type - Oil Palm	1.510	0.465	3.247

Table 4. Least squared means and standard errors generated from a linear mixed effects model of \log_{10} transformed mass of small insects above rivers against surrounding forest type in Sabah, Malaysia. Shared letters in 'group' denote no significant difference between those groups. Tukey HSD adjusted for multiple comparisons.

Forest Type	Mean	Standard Error	Group
Continuous	-1.700	0.370	ab
Disturbed	-1.853	0.193	ab
Riparian 30m	-2.319	0.357	a
Oil Palm	-0.190	0.678	b

Table 5. Fixed effects model outputs for the linear mixed effects model of a trap orientation, and surrounding canopy cover on diversity (Shannon-Weiner Index) above rivers in Sabah, Malaysia. Trap orientation is compared to the across the river orientation. Model $df=6$, $N=82$.

Fixed Effect	Estimate	Std. Error	t value
Intercept	1.265	0.100	12.611
Trap Orientation - Along	-0.154	0.043	-3.624
Surrounding Canopy Cover	-0.003	0.001	-2.620

Table 6. Least squared means and standard errors generated from a linear mixed effects model of diversity (Shannon-Weiner Index) of small insects above rivers against trap orientation in Sabah, Malaysia. Shared letters in 'group' denote no significant difference between those groups. Tukey HSD adjusted for multiple comparisons.

Trap Orientation	Mean	Standard Error	Group
Continuous	0.861	0.035	a
Disturbed	1.015	0.035	b

Table 7. Model outputs of a PERMANOVA of environmental measures against an NDMS analysis of community composition. R^2 values denote the proportion of variance explained by the model term. $\text{Pr}(> F)$ values in bold are significant.

Predictor Variable	<i>df</i>	F	R^2	$\text{Pr}(> F)$
Trap Orientation	1	43.88	0.270	0.001
Surrounding Forest Type	3	19.87	0.201	0.001
Surrounding Canopy Cover	1	1.64	0.010	0.212
$\log_{10}(\text{Tree Basal Area})$	1	2.29	0.014	0.478
$\log_{10}(\text{Rainfall} + 1)$	1	1.25	0.008	0.302
$\log_{10}(\text{River Width})$	1	3.05	0.188	0.062
River Canopy Cover	1	2.21	0.014	0.051
Date	1	4.74	0.029	0.071
Residuals	71		0.436	
Total	81		1.000	

Discussion

Directional Movement of Insects

Alpha diversity of flying insects was higher when traps selected insects approaching from riverbanks as opposed to up or down river. Orientation of the trap is here used as a proxy for insect movements across or along rivers. A higher diversity of insect orders traveling across rivers indicates that there may be insect orders that are found less frequently flying along the rivers. This could be due to a variety of reasons: firstly, the movement patterns that are shown here could be due to shorter vegetative movements, distinct from longer migratory movements (Kennedy, 1985). Vegetative movements suggest that an individual is simply tracking ecological resources, namely food resources, through a landscape. We might expect a greater availability of niche space in the forest as a result of the more complex and larger nature of the ecosystem, when compared to a river ecosystem. If this is the case, we can also expect there to be a greater number of feeding guilds, and thus insect orders, supported in the forest. If these guilds are moving directly towards new resources, e.g. deadwood, fresh leaves, flowering or fruiting plants, they will be traveling across the river from one resource to the next, rather than down river. These orders would be greater in diversity than those moving along rivers vegetatively.

Alternatively, flying across, rather than along, a river may also be a danger-avoiding behavior for many insects, particularly if insects are poor flyers or poorly adapted to travel above aquatic systems. On rivers flying insects face the risks of falling into the water or being predated by fish or by other insects such as odonatans (Nakano & Murakami, 2001). Furthermore, bat activity is known to be higher on tropical forest rivers (Hagen & Sabo, 2011), which may indicate a higher predation risk for insects. Thus, movement directly across a river may simply reduce the chance of death, whilst allowing insects to vegetatively reach new ecological resources or to permit longer distance

migration. River avoidance may also simply equate to gap avoidance, rather than a specific river response, as a means to remain within a habitat of choice. In this way, rivers may be seen to generally act as a barrier to movement and an obstacle that a terrestrial insect must overcome, rather than a distinct linear highway for longer distance dispersal. Gap avoidance behavior with regards to a linear feature has been studied in a species of one European honeybee (Battacharya et al., 2002), where it was shown that individuals avoided crossing railways and roads. Similar barrier effects have been shown in tropical forest birds and roads, where the movement of feeding guilds was affected differently by the linear gap in the landscape (Laurence et al., 2004). However, this is not to say that rivers could not be acting as *both* a highway for and a barrier to dispersal for different species or even groups, but simply that, as a whole taxon, our results would suggest the former seems to be the case. It would be useful to run further analyses

A change in community composition between the two trap orientations was found in addition to a difference in diversity. The NDMS plot shows virtually non-overlapping grouping of the two trap orientations, thus supporting the idea of differing orders flying across rather than down river. These clear results advocate future research into this poorly understood area. Such studies could entail re-analysing the insects collected in order to divide them into aquatic and terrestrial groupings, in an attempt to determine whether these movement patterns are based on ecological factors or not. Given the time, it would also be useful to take this data set further and analyse exactly which orders are responsible for this shift in community composition described here. Furthermore, it could be interesting to choose orders that can be easily mark-release-recaptured (such as dung-beetles or butterflies) and model how rivers affect dispersal through a forest system (i.e. whether rivers act as barriers or highways for dispersal in different groups). Traps used were cheap, simple and easy to build, which is of particular importance within a remote area of a tropical country. The fact that they were so effective in picking up patterns of insect movement, with a relatively low sample size,

suggests that this design could be implemented in further entomological research in similar research stations.

Surrounding Forest Effects on Aerial Insect Communities

Surrounding forest type affected several of our dependent variables. Firstly, rivers situated in disturbed forest were shown to have a higher total abundance of insects than both the rivers in established riparian reserves as well as our continuous forest control rivers. Usually, diversity is higher in intermediately disturbed ecosystems with a lower total abundance (Abugov, 1982; McCabe & Gotelli, 2000). It could be that although there is a lower abundance of individuals in these habitats, there is a higher abundance of aerially moving individuals due to displacement via disturbance. By this token, the assumption that our flight intercept traps act as a direct proxy for local abundance could be untrue. It would be informative to investigate whether these patterns hold true for different trapping methods such as pitfall traps or active trapping in the surrounding forest.

Surrounding forest type also determined insect mass once larger insects had been removed. Oil palm plantation rivers without a reserve had higher insect mass than in oil palm rivers with riparian reserves. This result could reflect a higher insect mass per individual, as abundance did not differ between the two forest types. However, one should view this result with caution, as only one oil palm river was sampled and therefore may not be representative of oil palm rivers in general.

Forest type also demonstrated a strong influence on the community composition of insects caught in traps. It is currently not possible to carry out multiple comparisons of factors with more than two levels with the vegan package (Oksanen et al., 2015), so differing forest types have been determined by looking at the confidence intervals of the NMDS plot. In the disturbed habitat, the difference between oil palm and riparian reserve rivers is clear, and could be due to certain orders having been temporarily displaced more readily, causing a differential capture rate, even though total

abundances of each order have not changed. Alternatively, disturbed forest could alter the niche availability of an area, causing temporary fluxes in abundance, e.g. in groups that rear their offspring in deadwood. Furthermore, due to an increase in the mass of flying insects we may expect insect predators to be present in greater numbers. Due to logging, other groups may experience a decrease in abundance, such as canopy dwelling species and herbivorous insects. We might expect these shifts to rebalance from disturbance into a similar community in riparian reserves, as forests recover from logging. Although riparian strips have been shown to have a lower diversity of insect species (Gray et al. 2015), it seems that at an order level, assemblage remains fairly similar to continuous forest. Oil palm plantation rivers with and without riparian reserves are not significantly different, perhaps suggesting that these reserves have little effect on flying insect assembly above rivers. However, as previously stated, low sample sizes may actually prevent us from ascertaining any difference between the two surrounding vegetation types.

It is also important to note that data from trapping is not necessarily indicative of the actual insects present in a given area due to trap bias (Muirhead-Thompson, 1991). That is to say, some insect orders will be captured more readily than others, e.g. the ratio of coleopterans to odonatans caught was very different from those observed when we were at the sites. Thus, our data would have to be used in conjunction with other trapping methods to give a more rounded view on total insect community diversity, composition and abundance.

Environmental Predictors of Community Traits

Unexpectedly, rainfall had no effect on any measures of insect communities. It has been shown in other biomes that rainfall can trigger mass emergence and thus higher abundances of insects (Bogan et al. & Boersma, 2012). Due to the high frequency of heavy precipitation in tropical forests however, it may be the case that rainfall affects abundance less than in more arid regions. Other environmental factors, such as temperature or pressure, may play a more

active role in determining mass emergence in groups such as ants and termites. It could also simply be that our measure of rainfall was poor, with overhanging canopy and evaporation from the falcon tube affecting the accuracy of readings.

Order diversity was also negatively affected by increasing canopy cover in surrounding forest. If anything, we expected to find the inverse relationship, with a strong canopy cover being symptomatic of a healthy forest and thus a more diverse insect community. We suggest that this result is an artifact of the inaccuracy of using a spherical densiometer to measure percentage canopy cover. As the meter only measures a proportion of the sky covered from a waist-level viewpoint, any vegetation higher than this will contribute to the measure of canopy cover, including low and mid-story vegetation. In particular, areas of forest that have been highly disturbed, such as old logging trails, are covered in very dense thickets of Zingiberaceae, giving high canopy scores whilst lacking any true mid or upper-story canopy. Thus, canopy cover here may be a poor proxy for forest health. Many tropical studies use simple methods such as these for vegetation analysis (e.g. Gray et al. 2015), however new technologies such as light detection and ranging (LiDAR) may in the future give much more accurate measures of tropical forest structure (Hancock et al. 2011).

A quadratic function of date was significantly predictive of mass, with and without larger insects included. Due to the cyclical nature of date, we often expect polynomic functions to be more predictive of ecological variables than a linear function. It would be interesting to see if this correlated with a peak in polarized moon-light, as Nowinsky et al., showed to be the case in their 1979 paper. Measures of smaller insect mass were also predicted by tree basal area and river width. A decreasing tree basal area predicts a lower mass of insects. This may also simply be a measure of recent disturbance affecting what is usually a measure of forest health. If the area of forest measured was logged in recent years, there may be a high density of young trees giving a high tree basal area using the relascope. Thus these areas may simply have a

higher mass due to a greater level of disturbance. Smaller insect mass also decreased with increasing river width. This may be due to our previous hypothesis of rivers acting as a barrier to insect movement. As certain insect groups avoid flying above rivers, the extent of this avoidance may increase with river width. Thus in the centre of wider rivers, a lower total mass of insects will be caught, particularly with smaller insects which are likely to be weaker fliers. However, this relationship had a very small effect and could simply be a result of multiple testing. This statistical problem was only accounted for in between group testing in comparisons of forest types.

Studying Insects at the Order Level

There are very few papers that attempt to quantify insect movements in this biome and those that do generally focus on a small target group or species rather than on the insect community as a whole (e.g. Arellano et al., 2008). As a consequence, conservation tends to focus heavily on data from a few species or one family's assemblage (Stewart & New, 2007), rather than using data from the whole Insecta class. As there is such an abundance of insect species and a lack of funded, willing and trained entomologists, there is no way to investigate the ecology of them all. We must study general patterns at the community level of insects to understand, not only the impact of degradation, destruction and fragmentation (Kitching, 1993; Basset et al., 1998), but also the movement of insects within tropical forests. The time required to accurately identify all samples to species-level is impractical for broad ecological studies and thus coarser units must be used when categorizing communities. Perhaps a more efficient use of resources would be efforts guided by general trends within communities as we have shown here, rather than a handful of easy-to-study, and often charismatic, species.

Conclusion

In this study we found that diversity in insect communities flying *across* rivers was higher than in those flying *along* rivers. Community composition differed between these two orientations, suggesting that different orders prefer to fly straight across rivers rather than using them to fly down them. Our results adds to the expanding pool of data that suggests that contrary to

many meta-population models, insect dispersal is not entirely random. Further research into how rivers shape insect movements is justified from the data produced here. We also demonstrated, with clarity, that it is possible and useful to conduct studies of the whole class of *Insecta*. Clear differences in our variables of interest were shown, whilst only identifying individuals to order level. If a short study such as this can produce interesting results, with little taxonomic expertise, when compared to many similar studies, this may motivate similar research in the future.

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