

Effects of habitat alteration on the abundance and diversity of Pterygota at Cloudbridge Nature Reserve, Costa Rica.

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Abstract

This study sampled Pterygota (winged insects) attracted to a ripe fruit bait in three habitat types (primary cloud forest, forestry plantation and cattle pasture) in order to investigate the effects of habitat alteration. The study tested the hypotheses that diversity of insect groups would decline with increasing habitat alteration (H1) and that insect abundance would vary between habitat types (H2). 7 samples were taken from 3 sites in each habitat type, using traps baited with ripe banana and a sugar / water solution. Diptera were the most frequently collected insect group and were far more abundant in the primary forest than the other habitat types. A relationship between numbers of Diptera collected and rainfall was also noted. Hymenoptera were most frequently collected from the pasture, and least so from the forest. The greatest number of Hymenopteran species was also recorded from the pasture and was lowest in the forest. Coleoptera were most frequently collected in the pasture and least in the forest. H1 was not supported and H2 was supported in varying degrees depending on the habitat type and insect group considered. Contributing factors are suggested for the observed patterns of variation and the results are discussed in the light of the available comparative literature and with respect to potential ecological impacts.

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Introduction

Tropical forests worldwide are under threat from deforestation which is estimated to be occurring at around 1% per annum overall (Watt *et al.* 2002) and has already resulted in a dramatic decrease in total forest cover (Didham *et al.* 1996). Given that many of the world's species are to be found in these areas (Didham *et al.* 1996) and that loss of habitat is one of the primary reasons for species loss and overall reduction in biodiversity (Frankie *et al.* 1997) their protection is integral to biodiversity conservation. Yet while stretches of primary forest are clearly crucial, a growing number of reforestation projects aiming to off-set the effects of wide scale habitat clearance are also being designed and implemented as people become aware of the many ecosystem services forests provide. Examples in Central America include the Valhalla Project and the Chico Mendes Reforestation Group in Guatemala and the Cloudbridge Nature Reserve, Costa Rica, the latter of which was the focus of this study. Costa Rica is a country famed for its biological diversity, which is said to comprise an estimated 5-7% of the world's species (Zamora *et al.* 2000). This diversity is primarily attributed to the wide variety of habitat types present within the country and its geographical location in the tropics as a land bridge joining the North and South American continents. The Cloudbridge Project was established on land acquired in 2002 in an area naturally consisting of tropical lower montane rain forest, one of the 12 Holdridge Life Zones to be found within Costa Rica (Janzen 1983). The project has multiple goals, but primarily serves to protect an area of land bordering Chirripo National Park, on the Pacific slopes of the Cordillera Talamanca. Within the confines of the reserve, in addition to primary and secondary forest, are areas previously cleared for grazing which the project aims to reforest through the planting of native species and application of forestry methods thus speeding up natural succession and hastening the recovery of the natural habitat.

One of the challenges facing conservation biology is to develop an understanding of the ability of countryside habitats to support and retain biological diversity, and the ability of different taxa to survive in these habitats (Goehring *et al.* 2002). Ideally, knowledge should be available as to what species are likely to be supported in different habitat types, and at what abundances (Goehring *et al.* 2002). Habitat alteration in the form of deforestation may affect insect populations through modification of the abiotic and biotic environment. Native forest species are likely to undergo local extinction and be replaced by open area species (Halffter 2002). Not all species are affected equally, disturbance may cause some groups to increase in abundance where as others decrease (Schowalter and Ganio 1999). For example, a common trend documented for Carabid beetles is that large, poorly dispersing species decrease with increased disturbance while small generalist species with good dispersal ability increase (Rainio and Niemelä 2003). Generally speaking, however, it is to be expected that habitat alteration such as deforestation will reduce overall species diversity. High profile examples include Lawton *et al.* (1998 in Schulze *et al.* 2004), Watt *et al.* (2002) and Schulze *et al.* (2004). Indeed in a review by Dunn (2004), conversion of forest to agriculture substantially reduced species richness in 38 out of the 39 data sets examined. These effects may be further compounded as changes in ecosystem structure can disrupt biological processes that maintain biodiversity and ecosystem functioning such as pollination, seed dispersal and

nutrient recycling (Didham *et al.* 1996), processes which are for the large part mediated by insects (Janzen 1987).

There is still, however, a pressing need to measure the impacts of deforestation and forest disturbance on insect diversity and also to quantify the impacts on insect diversity of establishing plantations and other land uses after deforestation (Watt *et al.* 2002). With respect to this, I designed a simple study to compare the abundance and diversity of Pterygota (winged insects) attracted to ripe fruit in 3 habitat types found at Cloudbridge; primary forest, plantation and land cleared for pasture. The area of primary forest, had, by definition, never been cleared. The plantation (formerly grazed land) had been planted with a variety of species of native saplings some four years previously. The immediate area surrounding the base of the saplings is subject to cleaning to reduce competition, however the rest of the plantation is effectively left free for successional growth. The pasture was land recently acquired by the reserve that had been grazed until 4 months prior to the study.

The aims of the study were as follows.

1) To investigate the effects of habitat alteration on the abundance and diversity of Pterygota.

2) To provide an indication as to the plantations state of recovery through comparison with pasture and primary forest.

3) To provide a baseline for future studies at Cloudbridge, and add to the general knowledge of the reserve.

4). It has been argued that progress in estimating insect diversity and in understanding insect community dynamics will be enhanced by building local inventories of species diversity (Godfrey *et al.* 1999). The study therefore aimed to collate an inventory of insect life at Cloudbridge using samples from the traps as well as other collection methods. It was anticipated that most insects would only be identifiable to family level so this part of the study focused particularly on *Cerotoniinae* beetles (Family: Scarabidae) as they are attracted to ripe fruit and are one of the insect groups in Costa Rica for which a keyed guide enabling species level identification (Solis 2004) is readily available.

The study tested the following hypotheses:

H1 Diversity of insect groups would reduce with increasing levels of habitat alteration.

H2 Abundance of insect groups would vary between habitat types.

Method

Data was collected from the 11th to the 28th of November 2005, at the end of the rainy season. Examples of the three habitat types were selected for sampling; these were the linear strip of primary forest accessible via the river trail, the river trail plantation and the Gavillon pasture. I designated three sites in each habitat and sampled each site 7 times, thus taking 21 samples per habitat type. At each site I estimated five measures for the 100 metres squared surrounding the location that can be used to give an indication of

the vegetative characteristics of the site. These were the % ground cover of mature trees, the % ground cover of shrubs, bushes and immature trees, the % ground cover of ferns, grasses and weeds, the % ground cover of bare earth and the % canopy cover. The 100m squared were centered on the sample location with the sides of the square aligned parallel to the sampling transect. A tree was considered mature when it was more than approximately 5 metres in height. The % canopy cover was based on a scale where 100% is primary forest and 0% is open land, and was estimated only for the canopy directly above the 100m squared. The occurrence of rain during insect collection was also recorded, as was the daily average temperature and rainfall for the study area as a whole. The geographic co-ordinates and altitude for each site were recorded via GPS.

Each habitat type was roughly linear in shape, so it was deemed appropriate that the samples were taken from line transects running the length of the habitat types. Each location was separated by >50 metres and no location was <10m from the edge of the habitat. The exact locations of the sites were selected randomly, with the exception that fruiting trees were avoided.

So as to attain data for each site from under as wide a variety of abiotic conditions as possible I rotated the sample locations on a daily basis. Each sample constituted a trap deployed from 8:00am until 12:00pm. As different species maybe active at different times of day (Ugalde 2002) efforts were made to set traps as closely as possible to simultaneously and the order in which sites were sampled was varied during the course of the study. Traps were always collected in the order that they were set so as to ensure that the active time in the field was as constant as possible.

Traps were very loosely based on Imes (1992) but with considerable alteration to the design. Traps consisted of a 1.75 litre water bottle suspended from a tree by string with a rectangular section (6.4cm x 2.4cm) cut out from the upper half. To keep the design robust (and thus protect from interference by vertebrates) it was necessary to keep the rectangular section relatively small and reinforce its edges with duck-tape. Interference by vertebrates also restricted the length of time for which traps could be deployed.

Traps were baited with half a ripe banana sliced horizontally and 3 cm depth of sugar water solution placed in the bottom of the trap. The solution was prepared by dissolving sugar in warm water at a ratio of 6 heaped tablespoons of sugar : 1200ml water and then subsequently leaving the mixture to cool over night. On setting the traps, once the banana had been added to the solution the trap was shaken for 20 seconds to mix the components.

When collected, traps were closed by covering the entrances with Clingfilm. Only insects inside the trap were recorded.

Identification of Specimens

Species identification was problematic for a number of reasons. The biodiversity of the area, coupled with the lack of relevant field guides and observer inexperience meant that it was not possible to identify specimens to species level (an exception was to be made for *Cerotoniinae* were they encountered). These problems were compounded by the theft of the microscope during collection, enforcing the use of a 4x hand lens. Also, many of the insects collected were Dipterans, which are frequently small and notoriously difficult to identify (Borror and White 1970, Kearns 2001). Thus the following

approaches were taken. All specimens were identified to order, or were designated "Other" when order could not be ascertained with certainty. Hymenopterans were then identified to family level where possible using Ugalde (2004), and were also preserved and labeled as Species A, B, C etc. Non-insects found in the traps, and insects not belonging to the focal taxa (i.e. wingless insects) were also placed in the "Other" group. This group was then excluded from analysis.

Statistical Analysis

Following the decision to continue with data collection at the reserve using the same methodology after the departure of the author, it was decided that statistical analysis should be postponed until a greater amount of data had been collected.

Results

Site Attributes

Table 1 displays the geographical attributes of the sampling sites as recorded on the 18th December 2005. Co-ordinates and GPS Waypoints were recorded using a handheld GPS Unit, altitude was recorded by a handheld altimeter. Waypoint refers to the number assigned to each site by the GPS Unit. The table also displays the abbreviations used to describe each site from here on.

Table 1

| <u>Habitat Type</u> | <u>Site Number</u> | <u>Abbreviation</u> | <u>GPS Waypoint</u> | <u>Altitude (feet)</u> | <u>Degrees North</u> | <u>Degrees West</u> |
|---------------------|--------------------|---------------------|---------------------|------------------------|----------------------|---------------------|
| Primary Forest | 1 | PF1 | 352 | 5230 | 09 28.500' | 083 34.189' |
| Primary Forest | 2 | PF2 | 351 | 5249 | 09 28.530' | 083 34.156' |
| Primary Forest | 3 | PF3 | 350 | 5279 | 09 28.510' | 083 34.107' |
| Plantation | 1 | PL1 | 354 | 5230 | 09 28.433' | 083 34.245' |
| Plantation | 2 | PL2 | 353 | 5266 | 09 28.425' | 083 34.208' |
| Plantation | 3 | PL3 | 348 | 5407 | 09 28.455' | 083 34.137' |
| Pasture | 1 | GA1 | 357 | 5466 | 09 28.314' | 083 34.332' |
| Pasture | 2 | GA2 | 355 | 5548 | 09 28.290' | 083 34.340' |
| Pasture | 3 | GA3 | 356 | 5568 | 09 28.278' | 083 34.357' |

Table 2 displays the estimations made for the vegetative characteristics of the sampling sites. The "% Other" column refers to features such as rocks and tree stumps. Percentage ground cover of trees, shrubs and bare earth was higher in the primary forest

than in the other habitat types, whereas percentage ground cover of ferns, weeds and grasses was higher in the Plantation and Pasture than in the Primary forest. Correspondingly, the canopy cover was greater in the primary forest than in the Plantations and Pasture. There was little difference between the Plantation and the Pasture in terms of percentage ground cover by trees, by ferns, weeds and grasses, or by bare earth, or in the percentage canopy cover. However, the Plantation sites did have a higher percentage ground cover of shrubs than the pasture.

Table 2

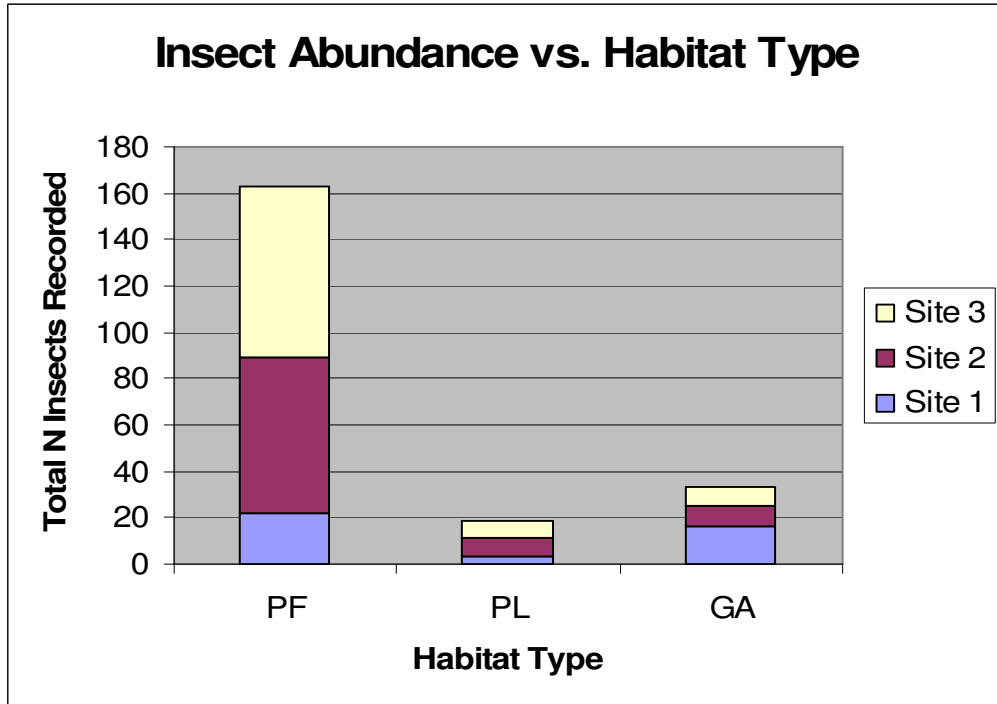
| <u>Site</u> | <u>% Trees</u> | <u>% Shrubs</u> | <u>% Ferns, etc</u> | <u>% Bare Earth</u> | <u>% Other</u> | <u>% Canopy cover</u> |
|-------------|----------------|-----------------|-------------------------|-------------------------|----------------|---------------------------|
| PF1 | 2 | 34.5 | 14 | 47 | 2.5 | 40 |
| PF2 | 10 | 25 | 15 | 50 | 0 | 75 |
| PF3 | 15 | 20 | 10 | 55 | 0 | 70 |
| PL1 | 0 | 1 | 99 | 0 | 0 | 0 |
| PL2 | 2 | 10 | 88 | 0 | 0 | 20 |
| PL3 | 0 | 10 | 90 | 0 | 0 | 3 |
| GA1 | 1 | 0 | 99 | 0 | 0 | 12.5 |
| GA2 | 1 | 0 | 96 | 0 | 3 | 10 |
| GA3 | 2 | 0 | 96 | 0 | 2 | 0 |

Insect Abundance

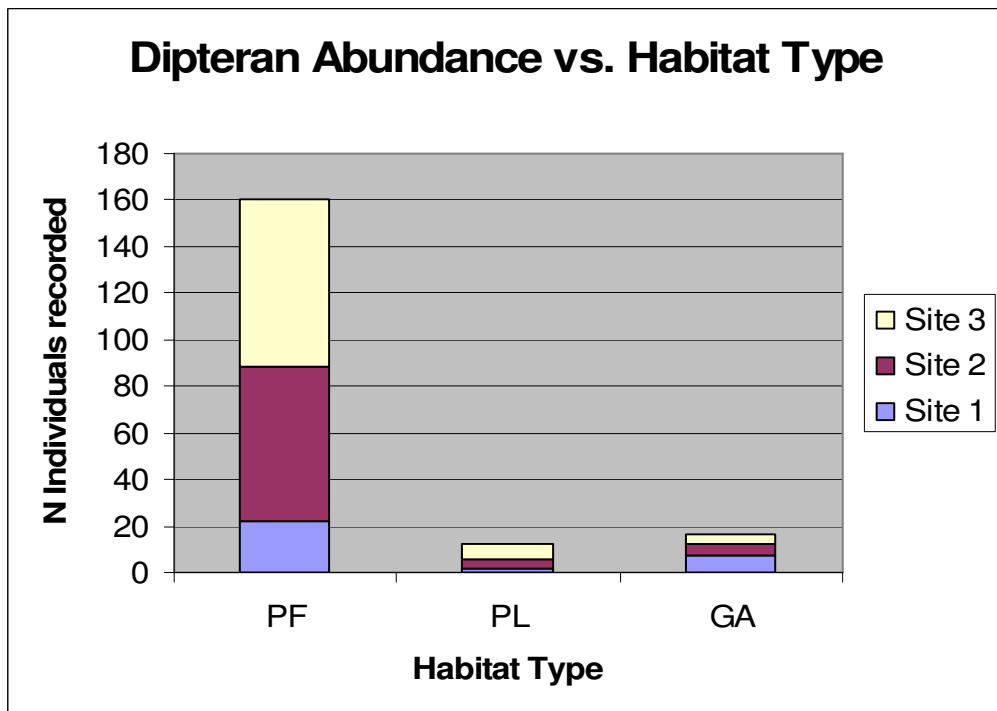
The following describes the most noteworthy findings of the study regarding insect abundances; the results in full may be seen in Appendix 1. Graph 1 displays the total insect abundance recorded per habitat type during the study period. The greatest number of insects (163) was collected in the primary forest comprising 3 orders; Coleoptera, Hymenoptera and Diptera. Far fewer were collected in the pasture (33) and least of all in the plantation (19). Coleoptera, Hymenoptera and Diptera also accounted for the individuals collected in the plantation and pasture, with the exception of 2 Lepidopterans recorded from the pasture; however this data will not be described further due to the small sample size.

By the far the most frequently recorded order was Diptera (188 individuals), followed by Hymenoptera (13) and Coleoptera (12). The variation in insect abundance between habitat types shown in the Graph 1 can therefore be attributed in a large part to Diptera (Graph 2), whose abundance was greatest in the primary forest (160), lowest in the plantation (12) and intermediate in the pasture (16).

Graph 1



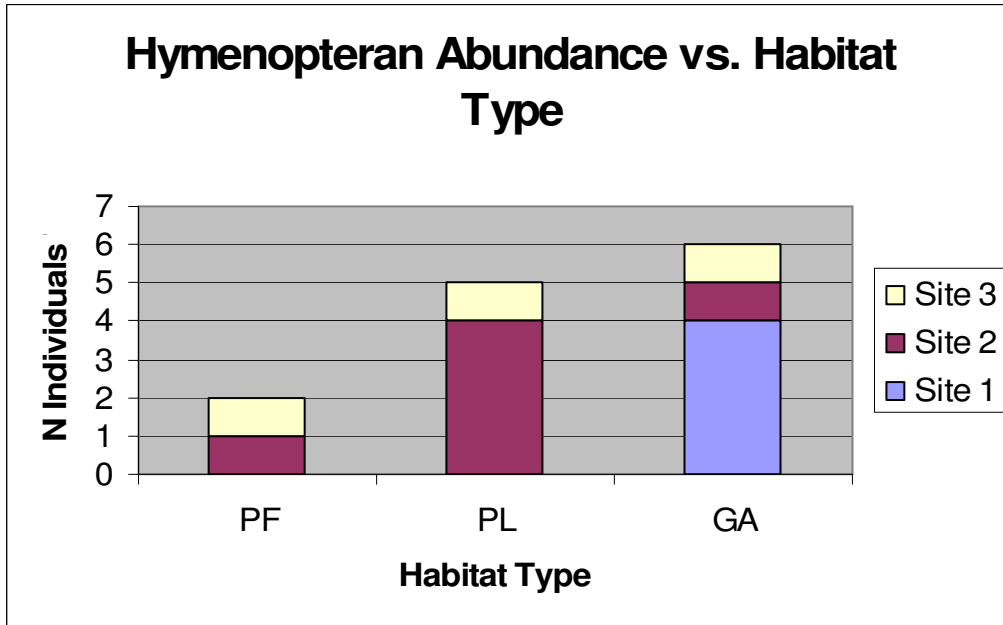
Graph 2



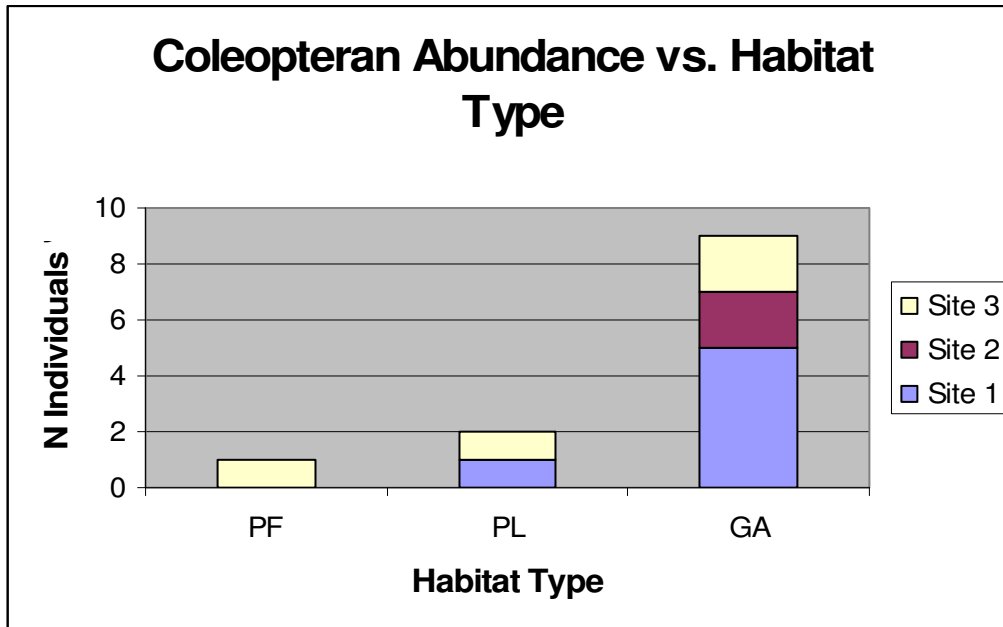
Hymenopteran abundance as displayed in graph 3 was lowest in the primary forest (2 individuals of 2 species), intermediate in the plantation (5 individuals of 3 species) and greatest in the pasture (6 individuals from 5 species).

Abundance of Coleopterans was recorded as greatest in the pasture (8) and much lower in the plantation (2) and primary forest (1) (see Graph 4).

Graph 3

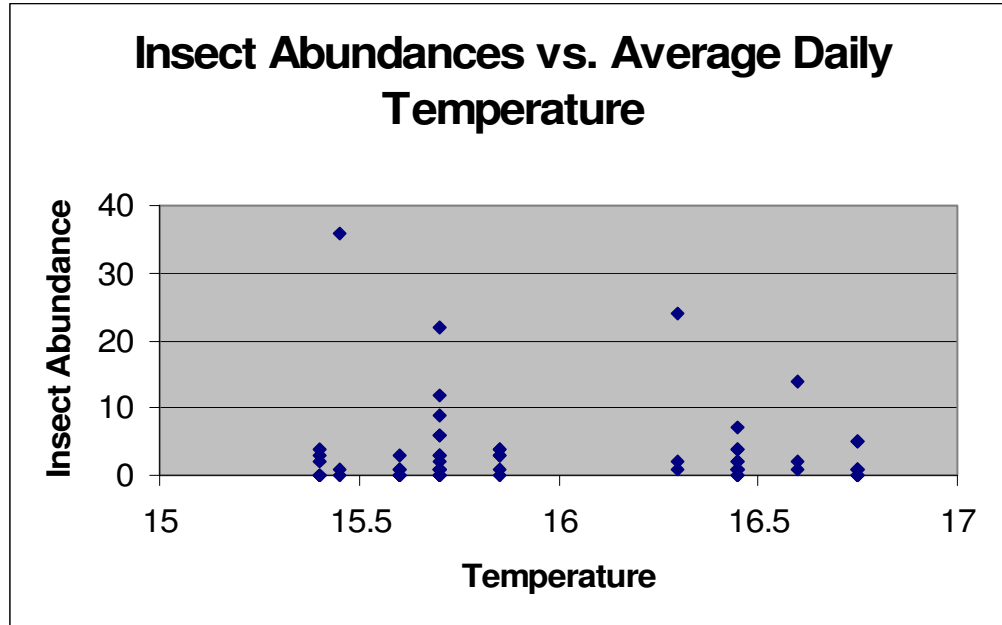


Graph 4

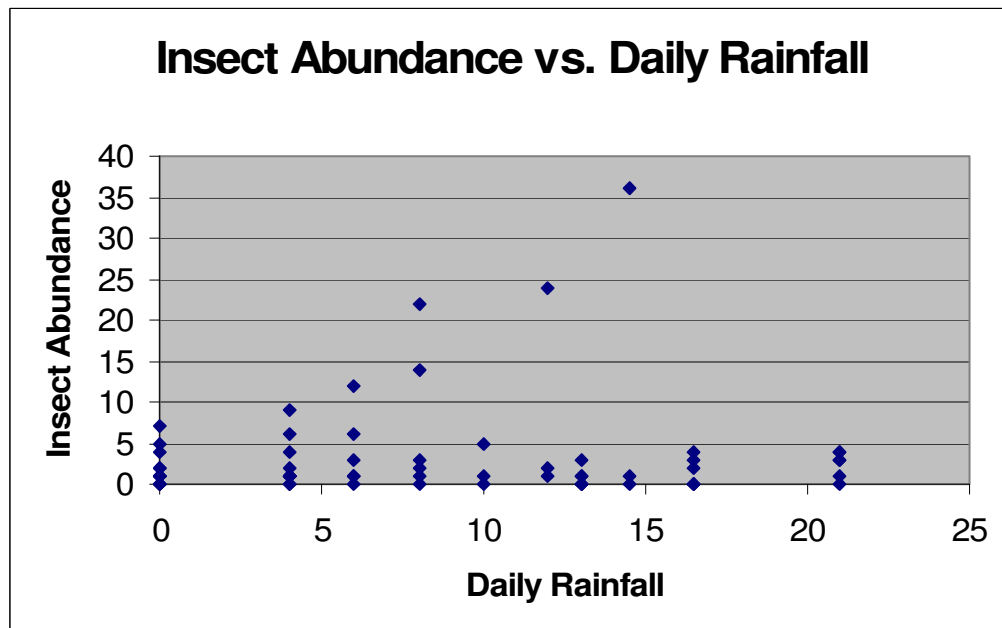


Total insect abundances (or the abundances of any particular order – not shown below) were not obviously correlated with either temperature (Graph 5) or daily rainfall (Graph 6).

Graph 5



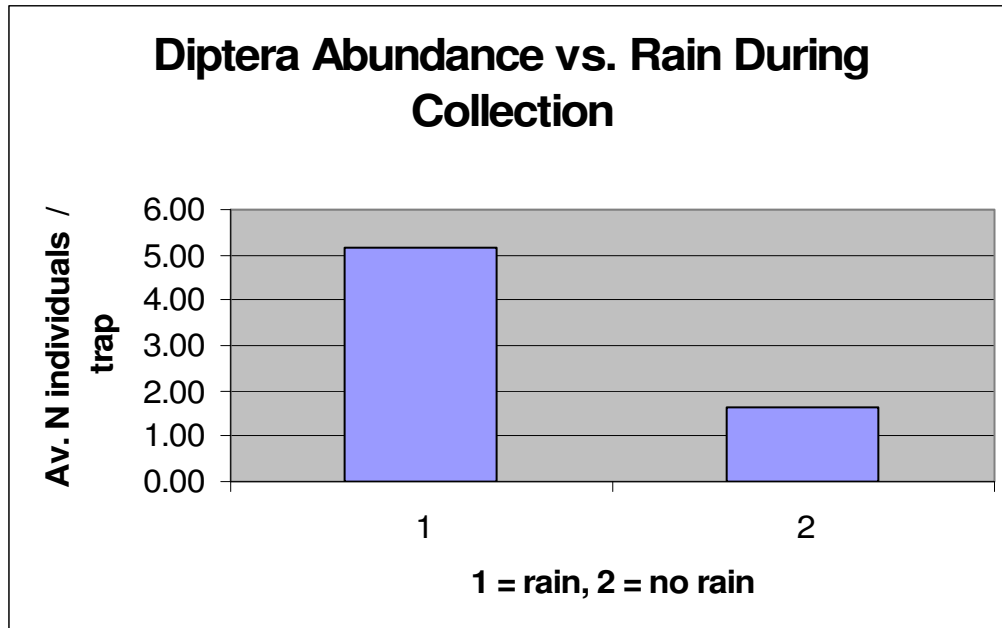
Graph 6



More insects (on average 5.54 individuals / trap) were collected when rainfall occurred during the collection period than when it did not (on average 2.10 individuals / trap). The average number of Hymenoptera collected per trap during rain was slightly lower (0.17) than without rain (0.23), whereas the average number of Coleopterans

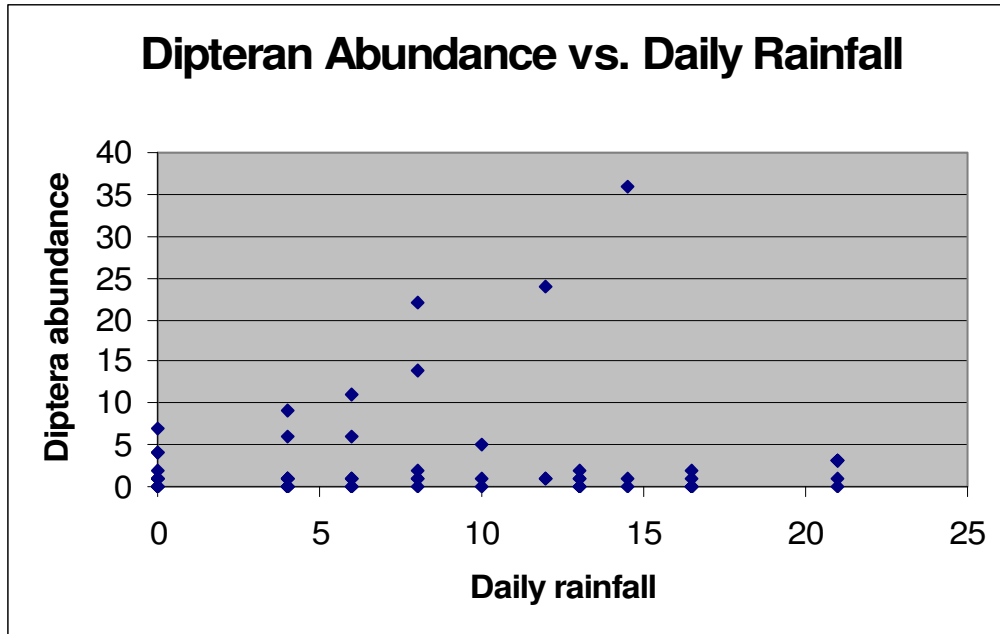
collected per trap was slightly higher during rain (0.21) than without rain (0.18). The rather striking difference in insects number collected during rainfall was therefore primarily due to Diptera, which averaged 5.17 individuals per trap during rain and 1.64 individuals without rain (see graph 7).

Graph 7

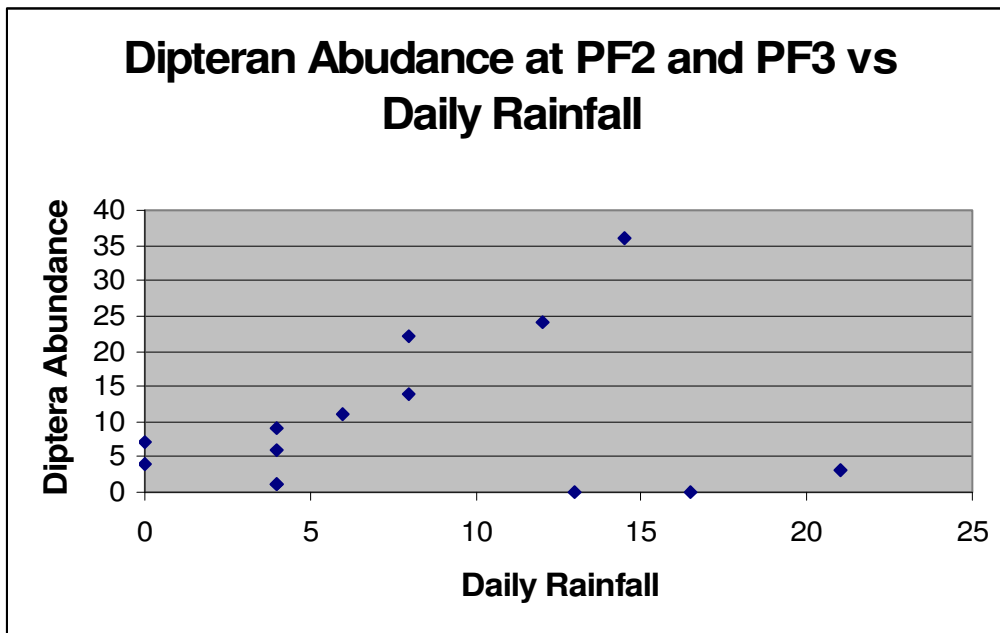


No clear correlation was apparent when Diptera abundance from all the traps was plotted against daily rainfall (graph 8). As previously mentioned, the primary forest accounted for the vast majority of Diptera collected, and so in order to further examine the relationship between rainfall and Diptera the plantation and pasture were removed from the analysis. Within the primary forest, sites PF2 and PF3 accounted for most individuals (66 and 72 respectively) whereas PF1 accounted for only 22 individuals. If PF1 was atypical in some way (comparison of the vegetative characteristics of each site reveal PF1 had fewer trees and less canopy cover) and as such we remove it from a scatter plot of daily rainfall vs. Diptera abundance, a possible relationship begins to emerge (Graph 9), whereby Dipteran abundance appears positively correlated with rainfall.

Graph 8



Graph 9



Discussion

Before discussing the results I will first outline the limitations of the study. The power of the results was weakened by the small sample size, the small number of sample locations within each habitat and also the lack of replicate habitat types. Abiotic factors, for example proximity to the river, varied between locations and habitat types and may have affected meant that the insects collected were not representative of the habitat types. Likewise small fragments such as those studied are subject to a number of processes (i.e. edge:area effects) that can affect species assemblages (Saunders 1991), and the study sites were part of a matrix of differing habitat types (indeed the primary forest and the plantation which were adjacent) meaning immigration from neighboring areas maybe have been a factor, especially considering the size and mobility of, for example, the larger Hymenopterans. Factors such as trap design and time in the field could have biased the results towards certain insect groups (for example through differences in olfactory capabilities) again meaning that the results can not be considered representative. Finally, bananas unavoidably differed in ripeness and size leading to some variation in the bait quality and quantity. It should also be taken into consideration that the biomass of the primary forest is spread out over a considerably greater vertical area than that of the other two habitats, indeed much life is contained within the canopy which was probably less affected by the traps. Thus comparison between plantation and pasture may be more productive than comparison with forest.

Effects of habitat alteration on Pterygota abundance

The estimates of the vegetative characteristics of each site demonstrated approximately what one would expect; that the primary forest differed greatly from the other two habitat types in terms of vegetative structure, with the plantation and pasture being similar in most respects excepting a higher proportion of shrubs found in the plantation. Indeed, the total numbers of insects collected were similar in quantity in pasture and plantation but far greater in forest, perhaps reflecting the greater biomass of the forest compared to the other habitats.

Diptera

On the basis of the results, Diptera appeared to be very severely affected by habitat alteration, with their abundance being far greater in the forest than the two disturbed habitat types. Bañkowska (1980 in Kearns 2001) showed that differences in Dipteran species composition between natural and disturbed areas can be dramatic, serving as excellent indicators of environmental degradation and similarly Kakutani *et al.* (1990 in Kearns 2001) found numbers of Diptera species to be poorest under maximum human disturbance. Although my study was unable to assess the effects of habitat alteration on species composition due to practicalities, it seems likely that such a large observed decrease in Dipteran abundance will affect species composition, and thus the results may support the above. Of course without knowledge of the biology and ecology of the species involved the exact consequences of this decline can not be predicted. However we can generalise that Diptera contribute to ecosystem functioning in a number of ways; they provide an important food source for other animals, as well as acting as

predators and parasitoids and consuming vegetation themselves, they can act as decomposers and pollinators, and they spread diseases (Vokeroth 2002). These roles coupled with the fact that Diptera are one the larger orders of insects, abundant as individuals aswell as species (Borror and White 1970) clearly indicate that Diptera are important in maintaining the earth's ecosystems.

Hymenoptera and Coleoptera

Hymenopterans were observed to be most abundant in the pasture and least so in the forest with the plantation falling inbetween, and with number of species recorded echoing the findings for abundance. Coleoptera were most abundant in the pasture, and noticeably less so in the plantation and forest. Unfortunately relatively few Hymenopterans and Coleopterans were collected meaning that these results were far from pronounced, however the continuation of data collection will hopefully go some way as to demonstrating whether these relationships apparent relationships hold true. At any rate, total Hymenopteran abundance did not appear to be as strongly negatively affected by habitat alteration as did that of Diptera (although as mentioned previously we should bear in mind that immigration from neighboring forest areas could have been influential, and that the forest canopy was probably not well sampled). However, with the exception of Apidae Species A, no Hymenopteran species were recorded as common to more than one habitat type thus species assemblages may be affected. Individuals of the Apidae superfamily were collected from every habitat type. This could potentially be explained by the number of flowering plants present in the disturbed habitats. If larval food is a key resource, insects such as Diptera may show significantly different patterns of fluctuations than bees, whose larvae are dependent on pollen for food (Kearns 2001). Personal observations suggest that the pasture contains a high diversity and abundance of flowering plants, whereas in the plantation the diversity appears lower but flowers such as that of Flor de Nino are abundant. If abundance of some Apidae species is not negatively affected by habitat alteration, this would appear a potentially positive note when contemplating the maintenance of ecosystem functioning and biodiversity through pollination. However even if population sizes of pollinators are maintained following environmental perturbation, disturbance may disrupt pollination processes through changes in pollinator foraging behaviour (Ghazoul and McLeish 2001). The number of Hymenopteran species was recorded as highest in the pasture and although this result lacks power, it should be noted that species richness doesn't always decrease with increasing habitat modification, indeed trap nesting bees and wasps may even become more diverse with increasing land use intensity (Klein *et al.* 2002 in Schulz *et al.* 2004).

A notably higher abundance of Coleoptera was recorded in the pasture than the other habitats. Flowering plants again may play a role and Coleoptera's apparent higher abundance in the pasture might also be explained by the large numbers of flowering plants found there. However, unlike Hymenoptera, Coleopteran abundance was notably different in the plantation when compared to the pasture. Possibly the diversity of flowering plants provides more suitable habitat for Coleoptera than is found in the plantation, where diversity appears lower as successional shrubs have began to dominate and shade out smaller plants. Alternatively, the shrubs might provide suitable habitat and cover for small birds which predate on Coleoptera. The loss of the microscope meant that the beetles collected, which were very small, could not be identified with certainty to

family level, but I suspect that all but one of them belonged to either Nitidulidae or Staphylinidae. Both families are ubiquitous but some Nitidulidae species are associated with flowers (Solis 2002). Again further data collection will hopefully elucidate the relationship, and the identification of Coleopterans to family level should now be possible. It is interesting to note that Harris and Burns (2000) in a study on beetle assemblages in forest and pasture in New Zealand, observed Nitidulidae only in pasture and not in forest. Nitidulidae are considered a minor pest species (Rodon *et al.* 2004), and so if the abundance of these beetles could be positively linked to distance from forest this might provide a possible incentive for farmers to preserve sections of forest close to agricultural land.

Recovery of the plantation

The second aim of the study was to provide an indication as to the state of the plantations recovery through comparison with the other habitat types. Comparison of the habitats in terms of Dipteran and Hymenopteran abundance revealed only slight variation between the plantation and pasture, with the plantation recording lower abundances. That little difference was found between the two habitats is to be expected considering the plantations age (approximately 4 years) and that minimum time for floristic recovery in the case of upper montane Costa Rican oak forest has been estimated at 65.9 years (Kapelle *et al.* 1994). The most noticeable difference between plantation and pasture was the reduction of Coleoptera abundance in the plantation, indeed abundance there was closer to that observed in the forest, providing evidence that succesional change is beginning to affect some insect populations.

Insect abundance and climatic variation

The relationship between rainfall and Dipteran abundance is an intriguing one, however unfortunately I do not have the resources available with which to compare the findings to other work. Insect abundances are known to exhibit seasonal variation in the Costa Rica (Janzen 1983), however in my study among the three most prevalent orders collected only Diptera were noted to show any association with rainfall. Preliminary results from the continuation of the study during the dry season suggest that far fewer Dipterans are being collected in the forest, supporting the idea that Diptera exhibit seasonal variation in abundance or activity. I suggest that this association might in part be due to a physiological constraint; Diptera are generally softer bodied than Hymenoptera and lack the hardened elytra of Coleoptera, as such I wonder if they may be less resistant to dessication and therefore tend to be more active during wetter conditions (of course other factors (i.e. larval food availability) are probably important). That Hymenoptera and Coleoptera did not display an association with rainfall could be due to the low numbers collected and / or because of the short time span of the study; possibly variations in abundance may become apparent through comparison with dry season data versus wet season data. Unlike some insect groups, the dry season is actually when Costa Rican bee activity in Guanacaste is highest, due to plants flowering (Janzen 1983) and so it will be interesting to see if the continuation of data collection during the dry season at Cloudbridge produces similar findings.

Insect Species Inventory

A further aim of the study was to begin an inventory of insect life at Cloudbridge. *Cerotoniinae* were used as a focus for this as they can be identified to species level and are attracted to fruit, however no individuals were recorded. Although more typical of tropical lowlands, *Cerotoniinae* have been encountered at altitudes higher than that of Cloudbridge, and as such their presence should not be discounted (Solis 2004). During the study an inventory of insect life was built up for the area using the data from the traps as well as other collection methods and this has been attached as appendix 2. Insects in the inventory were in general identifiable only to family level with the exception of the wasp *Pelecinus polyturator*.

Hypotheses and Summary

At order level the results did not support Hypothesis 1 (that number of insect groups recorded would decrease with increasing habitat alteration). If we include the presence of Lepidoptera in the data set, the study in fact found the greatest number of orders in the the pasture, contrary to the hypothesis. Likewise, when considering Hymenoptera, the only group which could be divided into species, the greatest number of species recorded was in the pasture. Hypothesis 2 (that abundance of insect groups would vary between habitat types) was supported in varying degrees, depending on the insect group and habitat type considered.

The results of the study present many further questions for future research at Cloudbridge. Seasonal patterns of variation in insect populations and the responses of insects at family level to habitat alteration both warrant further investigation. Regarding the latter, sampling by pitfall trapping might provide more useful data with which to compare forest and other habitat types. Although the study was severely limited, the results do draw one's thoughts to the idea that meadow-type habitats can support a different array of species to those found in forest. In order to conserve maximum biodiversity, the maintenance of areas such as these could be beneficial.

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References

Borror D.J. and White R.E. 1970. A Field Guide to Insects. Houghton Mifflin Company. New York.

Didham R.K., Ghazoul J., Stork N.E. and Davis A.J. 1996. Insects in fragmented forests: a functional approach. Trends in Ecology and Evolution 11 page 255

Dunn R.R. 2004. Recovery of faunal communities during tropical forest regeneration. Conservation Biology 18 page 302.

- Frankie G.W., Vinson S.B., Rizzardi M.A., Griswold T.L., O'Keefe S. and Snelling R.R. 1997. Diversity and abundance of bees visiting a mass flowering tree species in disturbed seasonal dry forest, Costa Rica. *Journal of the Kansas Entomological Society* 70 page 281.
- Ghazoul J. and McLeish M. 2001. Reproductive ecology of tropical forest trees in logged and fragmented habitats in Thailand and Costa Rica. *Plant Ecology* 153 page 335.
- Godfrey H.C.J., Lewis O.T. and Memmott J. 1999. Studying insect diversity in the tropics. *Philosophical Transactions: Biological Sciences* 354, Number 1391.
- Goehring D.M., Daily C.D. and Sekercioglu C.H. 2002. Distribution of ground-dwelling arthropods in tropical countryside habitats. *Journal of Insect Conservation* 6: page 83.
- Halffter G. and Arellano L. 2002. Response of Dung Beetle diversity to human-induced changes in a tropical landscape 1. *Biotropica* 34 page 144.
- Harris R.J. and Burns B.R. 2000. Beetle assemblages of kahikatea forest fragments in a pasture dominated landscape. *New Zealand Journal of Ecology* 24 page 57.
- Imes R. 1992. *The Practical Entomologist*. Simon and Schuster / Fireside, New York.
- Janzen, D.H. 1987. Insect diversity of a Costa Rican dry forest: Why keep it, and how? *Biological Journal of the Linnean Society*. 30 page 343.
- Janzen D.H. (Ed.) 1983. *Costa Rican National History*. The University of Chicago Press, Chicago.
- Kappelle M., Kennis P.A.F. and Vries R.A.J. 1994. Changes in diversity along a successional gradient in a Costa Rican upper montane *Quercus* forest. *Biodiversity and Conservation* 4 page 10.
- Kearns C.A. 2001. North American Dipteran Pollinators: Assessing the value and conservation status. *Conservation Ecology* 5 [online] URL: <http://www.consecol.org/vol5/iss1/art5>.
- Rainio J. and Niemela J. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation* 12 page 487.
- Rondon, S.I., Price J.F. and Cantliffe D.J. 2004. Horticultural Sciences Department, University of Florida. Available on-line at <http://edis.ifas.ufl.edu>
- Saunders D.A., Hobbs R.J. and Margules C.R. 1991. Biological consequences of habitat fragmentation: a review. *Conservation Biology* 5: page 18.

Schowalter T.D. and Ganio L.M. 1999. Invertebrate communities in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. *Ecological Entomology* 24 page 191.

Schulze C.H., Waltert M., Kessler P.J.A., Pitopang R., Shahabuddin, Veddeler D., Muhlenberg M., Gradstein S.R., Leuschner C., Steffan-Derwenter I. and Tschardtke T. 2004. Biodiversity indicator groups of tropical land-use systems: comparing plants, birds and insects. *Ecological Applications* 14: page 1321.

Solis A. 2002. *Escarabajos de Costa Rica*. Editorial INBio, Heredia, Costa Rica.

Solis A. 2004. *Escarabajos fruteros de Costa Rica*. Editorial INBio, Heredia, Costa Rica.

Ugalde, J.A. 2002. *Avispas, abejas y hormigas, Costa Rica*. Editorial INBio, Heredia, Costa Rica.

Watt A.D., Stork N.E. and Bolton B. 2002. The diversity and abundance of ants in relation to forest disturbance and plantation establishment in southern Cameroon. *Journal of Applied Ecology* 39 page 18.

Vokeroth J.R. 2002. Introducing the ubiquitous Diptera. *Biodiversity* 3 page 3.

Zamora Villalobos N., Jimenez Madrigal Q. and Poveda Alvarez, L.J. 2004. Editorial INBio, Heredia, Costa Rica.