DAVIS EXPEDITION FUND

REPORT ON EXPEDITION / PROJECT

Expedition/Project Title:	Tropical Biology Association Field Course 2024
Travel Dates:	09/07/24 – 11/08/24
Location:	Kibale National Park, Uganda
Group Members:	Sabina Schneider
Aims:	Develop skills in tropical ecology and conservation.

Photography consent form attached: ☐ Yes
(*please refer to your award letter)* ☒ No

Outcome (a minimum of 500 words):-

TROPICAL BIOLOGY ASSOCIATION FIELD COURSE

MAKERERE UNIVERSITY BIOLOGICAL FIELD STATION

KIBALE NATIONAL PARK

2024

OVERVIEW

THE TROPICAL BIOLOGY ASSOCIATION:

TROPICAL BIOLOGY ASSOCIATION

The Tropical Biology Association (TBA), established in 1993, organises intensive field courses aimed at the next generation of conservation leaders. The TBA has launched the careers of over 2000 environmental scientists, drawn from over 50 nationalities, many of which have leading roles in national and international level conservation organisations.

The organisation's annual field courses are aimed at early career conservationists and recent graduates. Delivered by leading experts in a range of conservation niches, the month-long programmes provide hands-on learning opportunities and encourage participants to develop independent academic thought.

I participated in the 2024 TBA field course, delivered in and around the Makerere University Biological Field Station (MUBFS) in Kibale National Park (KNP) in south-western Uganda.

The Kibale Forest is an especially biologically rich area, supporting both west and east African species, as well as covering a range of altitudes and a mosaic of different habitats. The national park lies south east of Fort Portal and covers 766 km^2, with links to the Queen Elizabeth national park via a corridor at the southern tip. This corridor is an important link between savanna and forest habitats facilitating movement and dispersal of animals among protected areas.

The forest is home to 12 primate species including chimpanzee, over 300 bird species, a growing forest elephant population, and many other terrestrial animals including buffalo and antelope. The vegetation is very rich and there is a wide variety of aquatic ecosystems including two major rivers, Mpanga and Dura, as well as swamps and volcanic crater lakes. The park is among the best examples of medium altitude tropical moist forest ecosystems in Africa. There is a history of logging activity and degradation dating back to the 50's and 60's, with significant regeneration efforts following the withdrawal of plantations from the 90's onward.

MAKERERE UNIVERSITY BIOLOGICAL FIELD STATION

LEARNING OBJECTIVES:

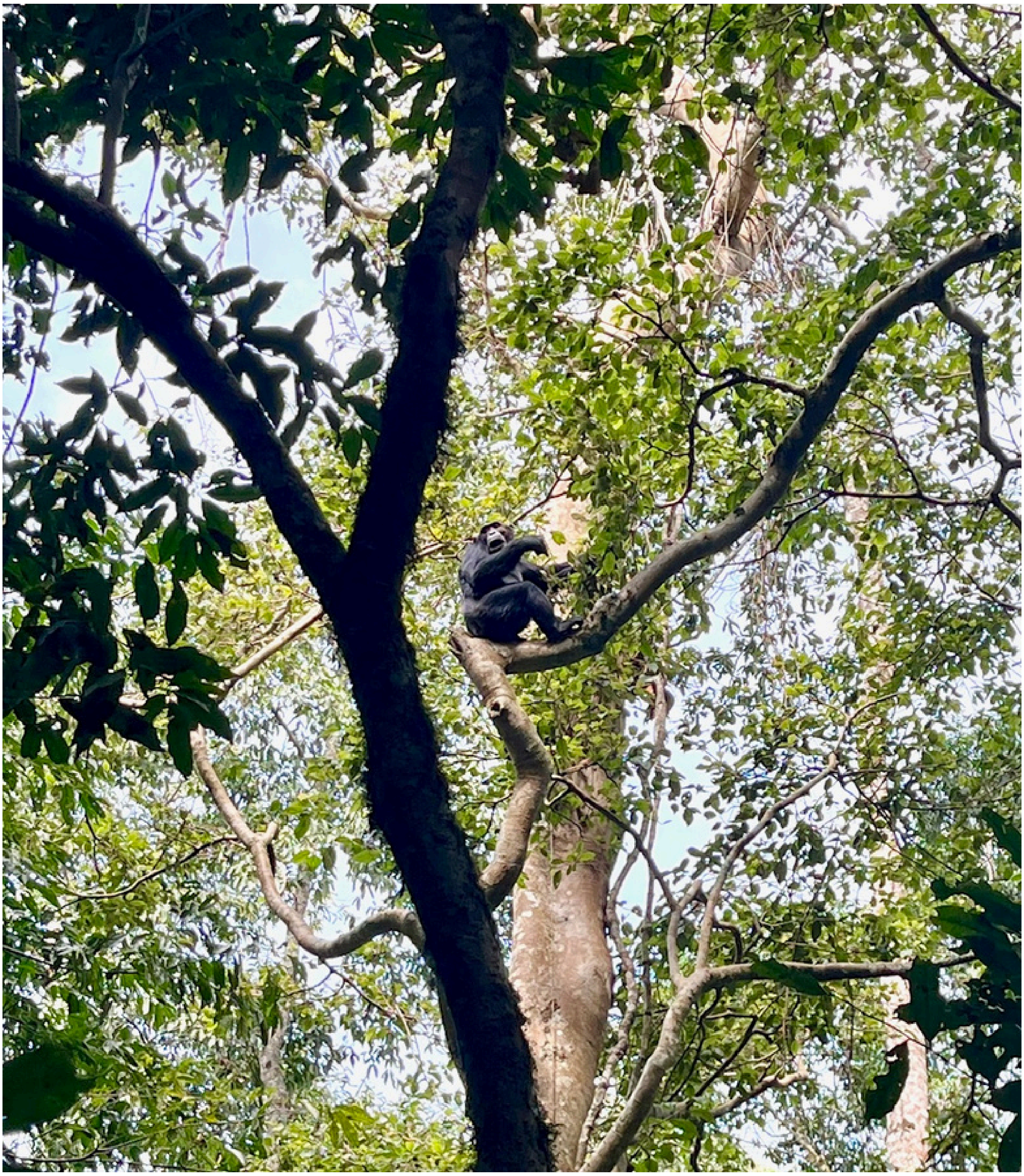
ACADEMIC

1. Expand my limited knowledge of tropical plants, fungi, and animals.
2. Gain experience in species/family level identification and recognition of functional groups within tropical ecosystems.
3. Learn about tropical ecosystem processes, particularly similarities and differences with northern biomes.
4. Learn from local researchers and specialists.
5. Develop ecological measurement techniques, experimental design, and critical thinking.
6. Actively pursue topics outside my immediate sphere of study/interest.

PERSONAL

1. Expand my professional network within the conservation ecology sector.
2. Use this unique opportunity to learn from and exchange knowledge with other participants, both culturally and professionally.
3. Develop collaborative skills such as academic co-writing and project management.
4. Improve my understanding of how climate change and conservation issues affect people differently around the world.
5. Explore the possibility of a career in tropical conservation.

COURSE CONTENT:



Pictured: A special encounter on my first excursion into the forest, a chimpanzee!

COURSE CONTENT

WEEK 1

Field workshops: tropical birds, insect-plant interactions, forest ecology

Seminar: formulating ecological research questions

Talks: Chimpanzee behaviour and conservation issues (Dr Emily Otali), acacia pollination (Professor Graham Stone)

WEEK 2

Field exercises: three mini experiments increasing in complexity while input from the teaching team decreased

Seminar: communities and conservation - stakeholder mapping

Talks: Uganda Wildlife Authority (Dorothy Kirumira), tropical bird conservation (Dr Eric Sande), Ugandan lepidoptera (Dr Perpetra Akite), 'conservation in my country' (participants)

WEEK 3

Projects: guidance, clinics, planning and development

Excursion: Bigodi wetlands - nature walk and community meal

Talks: Bird adaptations to rain-driven environments; microbiomes and evolution (Dr Irene Tieleman), communities and conservations: a public health perspective (), 'conservation in my country'

WEEK 4

Projects: final preparations, data collection, processing, data analysis, experiment write-ups, presenting results

Seminars: data analysis, scientific writing skills

Talks: 'conservation in my country'

FIELD WORKSHOPS

The field exercises organised in the early stages of the course were intended to familiarise the group with the common plants, birds, mammals, reptiles, and insects encountered within Kibale National Park. Additionally, the sessions covered a broad range of ecological concepts demonstrated via examples and demonstrations. I found this very useful, having a very solid knowledge of theoretical ecology, but limited experience with tropical systems, especially species recognition. The teaching team, and my peers, pushed me to improve my taxonomic fluency, particularly in birds and insects, which I have studied only to a very limited extent.

The major topics of these workshops were: bird identification by observation and call recognition, invertebrate sampling techniques, and forest ecology.

These exercises involved exploring the forest extensively to maximise our exposure to the incredible wealth of biodiversity on display. The team of field guides at MUBFS were invaluable assets to the plans of the teaching team, able to identify most species encountered; I found the recognition of bird calls among the most impressive.

Upon seeing the forest ecosystem for ourselves, we were prompted to begin considering interesting ecological questions which may be answerable within the scope of a short research project. I found this a useful skill to practice: forming questions directly from observations and applying inductive reasoning to generate predictions. This process is challenging but important to master in science and my experience on this course has undoubtedly improved my skills.

FIELD WORKSHOPS

Pictured: Myself, using a beating tray and pooter to sample invertebrates from understory vegetation

SEMINARS

Whilst many of us could have happily explored the forest from dawn until dusk, we benefitted from supplementary seminars that solidified our understanding of the processes and interactions observed in the field. These sessions also facilitated group discussions which were great for sharing and exchanging knowledge and ideas, since academic interests were very varied amongst the cohort. These were also useful opportunities to discuss the socioeconomic and political aspects of conservation, an increasingly important topic for scientists since change is only achieved by collective action.

TALKS

We were privileged on this course to have a teaching cohort with a wide range of expertise, covering entomology, primatology, ornithology, public health, and global conservation. It was inspiring to hear about the academic careers, both their successes and failures, of the team, which many of us found inspiring and aspirational. In particular, the academics from Makerere University and MUBFS imparted some fascinating knowledge about the rewards and challenges of conservation and ecology in Uganda. I left with much admiration for their determination to preserve the environment for future generations in the face of some significant barriers.

FIELD EXERCISES

We completed three field exercises in the next stage of the course, each demanding more independence from students than the last. The first was an experiment based around the leaf preferences of invertebrate herbivores, and the distribution of invertebrate functional types by plant species. We sampled leaves to estimate herbivore damage by area, and collected invertebrate herbivores found on the plants. In the second exercise, we estimated forest carbon stocks using DBH measurements and allometric biomass equations. Finally, I along with two other students, designed an observation-based experiment to identify patterns between floral characteristics and both growth habit and light availability. We collected detailed and interesting data but struggled to identify patterns given the limited availability of flowers in the dry season.

EXCURSIONS:

Bigodi Wetlands

We took a day trip away from MUBFS to the Bigodi wetlands nature reserve. The team of guides took us on a tour of the reserve pointing out important species en route. Highlight sightings included marsh mongoose, L-Hoest's monkeys, fire ants, and Great Blue Turaco.

L'Hoest's Monkey

Tropical wetland habitat

Groundnut crop

EXCURSIONS:

Lake Mburo National Park

After leaving Kibale forest, we travelled south-east over the equator to Mbarara and Lake Mburo. Here, we were treated to a safari game drive where we observed zebra, many antelope species, giraffe, and warthogs. Following this, we took a boat ride around the lake where saw the incredible resident hippo population of nearly 300 individuals, as well as Nile crocodiles and fish eagles.

RESEARCH PROJECT

Background

As a culmination of our learning on this course, we undertook a two-week research project, with creative freedom over the topic, protocol, and analysis - within the limits of time and resources. Together with my project partner Samara Brandsen, we designed a concise investigation of leaf-litter invertebrate communities. We were looking for patterns in invertebrate abundance and order-level richness, in response to leaf litter characteristics: depth, pH, humidity, and canopy cover.

Field Work

Samara and I defined four transects branching from a forest path, each with three sample points along a consistent slope: at the top, middle, and bottom. At these points, we sampled invertebrates using simple pitfall traps emptied twice daily, morning and evening. We also measured leaf litter characteristics at these points. These data collection days were intense and required constant vigilance in an area with aggressive forest elephants and large colonies of safari ants.

RESEARCH PROJECT

Pictured: Leaf litter invertebrates collected in pitfall traps, here transferred to a petri dish for order-level specimen identification.

RESEARCH PROJECT

Results and Findings

I have included the full write-up of this experiment in the appendix of this report for context but will summarise our findings briefly. We found that invertebrate biomass increased with canopy cover and soil moisture. We were surprised that leaf litter thickness had no effect on invertebrate richness or biomass, since we expected niche space to increase with litter thickness.

We found higher order richness in traps left overnight than during the day. However, the sampling periods were uneven due to restrictions on night access to the forest. The order Hymenoptera (ants, bees, wasps) was an outlier to this relationship, showing higher diurnal abundance. This fits with our understanding of ant behaviour, foraging in large groups as a 'superconsumer', and experiencing lower predator threat as a result.

For future work, we recommended using a taxonomy of functional type, rather than order richness to assess the composition of leaf-litter invertebrate communities. This approach may provide more useful information on the niche space provided by leaf litter. We had also hoped to implement experimental manipulations, such as litter wetting, but were unable due to time constraints.

REFLECTIONS

Obtaining a place on this course meant so much to me. I'd somewhat given up on trying to find authentic opportunities to learn about tropical ecology on a professional level; the ecotourism, volunteering holiday type packages had never grabbed my interest and were always out of budget. When an email from Graham Stone was circulated to my cohort at the University of Edinburgh about the TBA, it was the first time I'd heard the name and after reading the course flyer I instantly knew I wanted to apply.

I was delighted to find that, thanks to the Davis Expedition Fund, there was a chance I could actually afford to go should my application prove successful. I found out I'd been offered a place just days before submitting my undergraduate dissertation which – unsurprisingly – reenergised and remotivated me, so I have the TBA and the Davis Trust to thank in part for my performance there.

I know my 23 fellow course mates, and new TBA alumni, feel as privileged as I do to have had the opportunity to learn in such a unique and refreshing way. I think we can claim to have gained each other as friends along the way, which makes everything even more special and memorable; you can't underestimate the power of a shared experience like this to preserve friendships across time, and space.

REFLECTIONS

Pictured: The diversity of passports we were able to collect here shows just how multicultural this course was.

EXPENDITURES

I am incredibly grateful to the Davis Trust for funding this experience for me. I could not have afforded to participate otherwise. I would encourage anyone to apply for TBA courses in future years, they are truly life changing experiences, and I hope the Davis Expedition Fund will continue to support applicants from The University of Edinburgh.

Expenditure	**Cost (£)**
Course fee (reduced for partner institutions)	1000.00
Return Flight to Entebbe	966.99
Immunisations/anti-malaria prophylaxis	413.90
Insurance	71.08
Visa	40.69
Total	**2,492.66**

Pictured: My favourite photo of the trip! Fearless Red Colobus monkeys.

APPENDIX

Do environmental characteristics affect leaf litter invertebrates in Kibale National Park?

Brandsen, S. & Schneider, S.

ABSTRACT

Leaf litter plays a role in many ecosystem functions, including nutrient cycling, carbon transfer, and habitat creation. Whilst there is a substantial body of research on decomposition processes in tropical forests, little is known about tropical leaf litter dynamics and species assemblages. Invertebrates within the leaf litter regulate rates of decomposition and constitute an important basal trophic level within tropical forest ecosystems. The resulting inference is that the diversity of litter invertebrates may be important for biodiversity more generally, providing important prey niches. We have attempted to build a picture of variation in invertebrate diversity by investigating the effect of local soil and litter properties on invertebrate biomass and abundance in Kibale National Park. We found that invertebrate biomass increases with increasing soil moisture and canopy cover, with higher biomass and diversity within night samples than day. Understanding the common orders of tropical leaf litter invertebrates, and their relative abundances, forms a starting point from which to further classify leaf litter assemblages by functional type. Furthermore, we expect functional types may be more sensitive to local environmental conditions than taxonomic orders given their specific niches. We hope that future work will expand on invertebrate niche space in the leaf litter and reveal more about how lower trophic levels may influence biodiversity in tropical forest ecosystems.

Keywords: invertebrates, leaf litter, Kibale National Park, soil moisture, canopy cover

1. INTRODUCTION

Leaf litter is an important and often neglected component of forest ecosystems, particularly in tropical biomes. Rates of turnover and decomposition can be rapid under warm, wet tropical conditions and leaf litter is produced year-round, contrasting temperate zones. The leaf litter layer is a critical conduit of major fluxes within forest carbon and nutrient cycling. Processes include organic matter decomposition and associated respiration of decomposers, deposition of soil organic carbon (SOC), humus formation, and ephemeral carbon storage. Rates of litter decomposition are affected by many climatic factors, primarily temperature and precipitation, but additional factors influence local scale variation such as soil properties and chemical cycles (Wieder, Cleveland and Townsend, 2009).

Leaf litter provides a diverse habitat for small mammals, reptiles, amphibians, and particularly terrestrial invertebrates. Invertebrates within the leaf litter are important regulators of cycling processes in the litter (Guzmán and Alvarez-Sánchez, 2003); for instance, detritivores such as earthworms, millipedes and gastropods break down the leaf litter, accelerating decomposition and subsequent nutrient and carbon inputs to the soil. Additionally, some orders such as Orthopterans can play a role in seed dispersal in tropical systems (Santana et al., 2016). These invertebrates are a key component of forest food webs, contributing to biodiversity across trophic levels. More diverse leaf litter invertebrate communities may therefore promote higher diversity of insectivorous species, with radiating effects throughout the ecosystem.

Microclimate conditions and habitat structure may influence the diversity of litter invertebrates via variation in niche space and resource availability. Kibale Forest, within Kibale National Park (KNP) Uganda, is a semi-montane tropical rainforest with high biodiversity and a long history of ecological monitoring. However, there is a gap in our understanding of leaf litter dynamics in this area, particularly invertebrate distributions. Understanding how invertebrate assemblages change with conditions provides a starting point for identifying more complex ecosystem dynamics. Holistic approaches to ecosystem monitoring are especially important in areas like KNP where there is a strong incentive to conserve biodiversity and maintain ecosystem services including carbon sequestration.

The forest's topographical variation generates an opportunity to sample invertebrate abundance and diversity along existing environmental gradients. Our main objective is to sample litter invertebrates at three locations on transects along slopes within the forest, between a disused logging road and swamp valley. We aim to observe how environmental characteristics affect the diurnal and nocturnal leaf litter invertebrates along this altitudinal gradient in KNP. We expect to find higher invertebrate biomass at lower altitudes, where the swamp is adjacent, associated with higher soil moisture and leaf litter humidity. Furthermore, we expect that higher litter depth will be linked to increased invertebrate biomass and diversity via higher niche space. Additionally, we expect a similar response in areas with higher canopy cover due to more humid conditions and litter accumulation. Finally, we aimed to observe differences between diurnal and nocturnal invertebrate biomass and diversity, since captured biomass of leaf litter specialists may be higher at night (Lieberman and Dock, 1982).

2. METHODS

2.1 STUDY SITE The study was carried out during the dry season over 4 consecutive days between the 27th of July and the 1st of August 2024 in Kibale National Park, in western Uganda. The research site is in unlogged forest, south of Karambi road, within sector K30 close to the Makerere University Biological Field Station. This area has an elevation from 1476 to 1518 m with a swamp at lower altitude (Fig. 1).

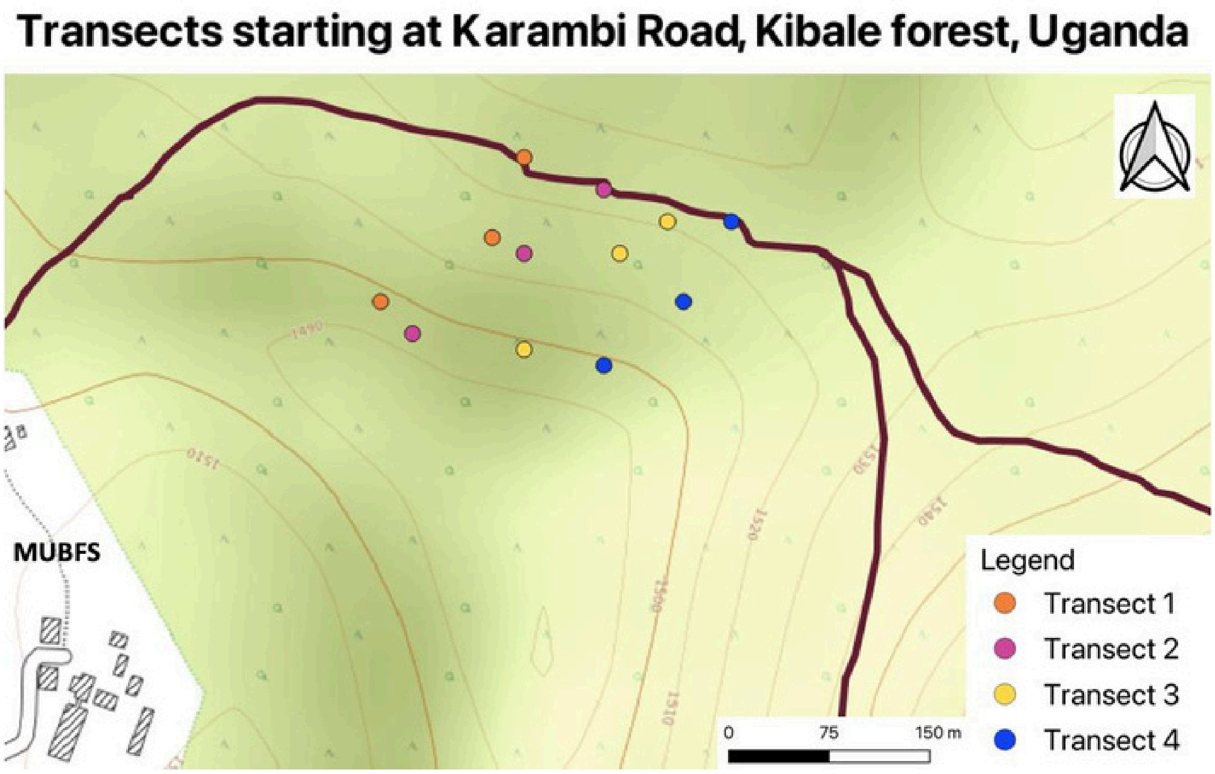


Figure 1: Study site

2.2 RESEARCH DESIGN

The research design comprised 4 transects, each containing 3 plots, one per altitude (low, middle, high) along the slope leading to the swamp. We sampled litter invertebrates using pitfall traps containing soapy water, with 2 traps placed in each plot. We collected the invertebrates twice daily, from 08:30 to 09:30 and from 16:00 to 17:00. We classified sampled invertebrates to taxonomic order and recorded total invertebrate biomass per trap for each plot. We also calculated order level richness for each plot.

As potential explanatory variables for patterns in invertebrate biomass and diversity, we measured soil moisture, soil pH, and leaf litter humidity daily, taking 3 measurements per plot between 09:30 and 10:30 using a three-way meter. Additionally, we used a ruler to measure the leaf litter depth. We could not re-measure these variables within repeatable areas as measurements disturbed the leaf litter layer. As a result, analyses used the average values over the 4 data collection days for all records from each plot. We measured canopy cover once per plot using a spherical densiometer, taking the average value from north, south, east and west measurements.

2.3 DATA ANALYSIS

We looked at the relationships between leaf litter depth and soil moisture across plot heights and tested differences between plots using Kruskall-wallis tests, since the data violated ANOVA normality assumptions.

We constructed two linear models to analyse the relationship the response variable invertebrate biomass and the explanatory variables: soil moisture, soil pH, leaf litter depth, leaf litter humidity, and canopy cover using RStudio (RCoreTeam, 4.2.2). We first explored the relationships between litter invertebrate biomass and environmental characteristics within the dataset. Following this, we began with a linear model incorporating all our explanatory environmental variables since a multicollinearity test revealed low correlation between variables. We removed variables which explained very little variation in biomass data: leaf litter humidity, leaf litter depth, and soil pH. Both canopy cover and soil moisture appeared to be good candidates for explanatory variables, but canopy cover explained more variation when they were both included in the model. Our final model of invertebrate biomass contained percent canopy cover and time of day as explanatory variables. The second model of invertebrate biomass included soil moisture, leaf litter depth and time of day as explanatory variables. Finally, an ANOVA tested how the abundance of invertebrates caught differed by order, and between day and night. We confirmed normality of model residuals for both models using Q-Q plots and the Shapiro-Wilk normality test.

3. RESULTS

3.1 ENVIRONMENTAL CHARACTERISTICS

Litter depth was higher in the low and high altitude than the mid altitude plots (Kruskal-Wallis: H 2=91.802, $p < 0.001$; Fig. 2). The mid altitude had higher soil moisture than low and high altitudes (Kruskal-Wallis: H 2=48.9, $p < 0.001$; Fig. 2). Humidity of the leaf litter and the soil pH did not change along the altitudinal gradient.

Figure 2: The moisture and leaf litter depth along the altitudinal gradient.

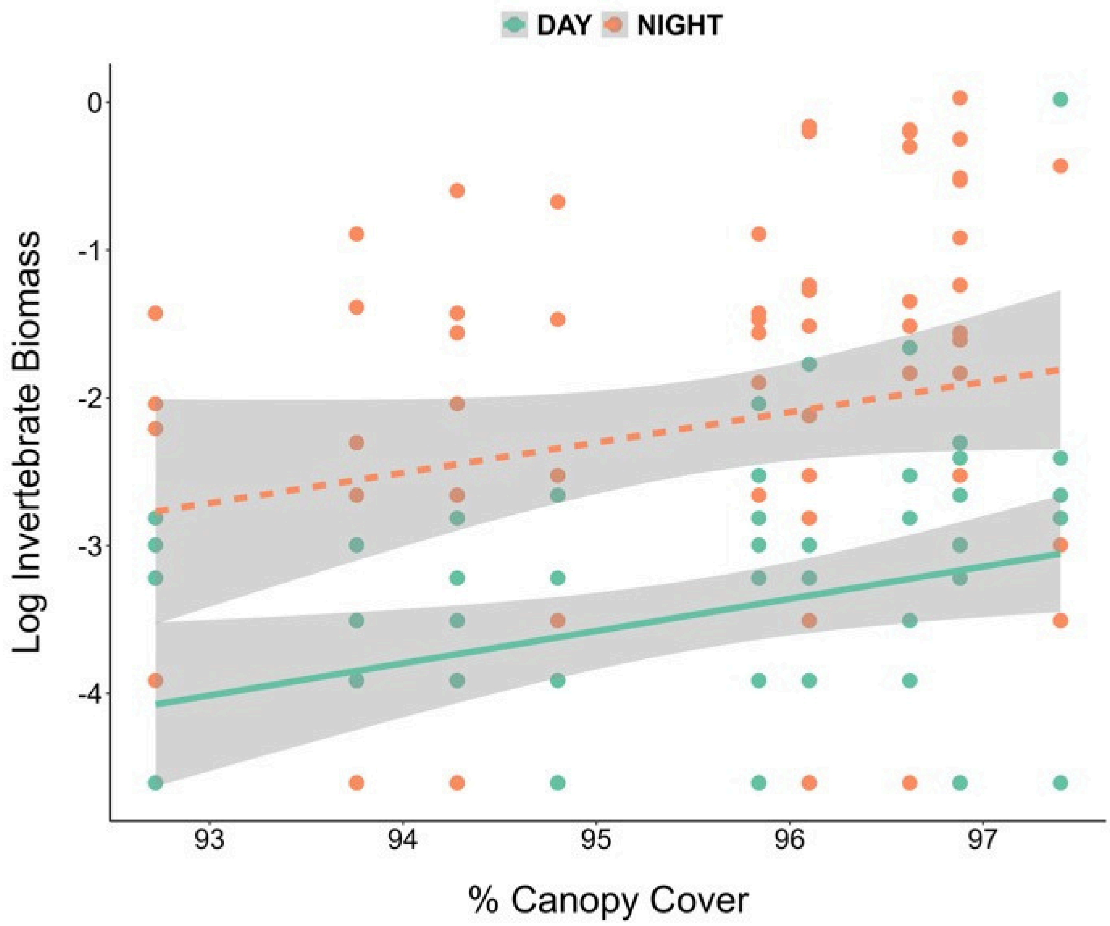


Figure 3:The effect of canopy cover (%) on the invertebrate biomass (log).

3.2 PATTERNS IN INVERTEBRATE BIOMASS

Overall, nocturnal invertebrate biomass was significantly higher than diurnal (linear model: F 2,140=24.92, p < 0.001; R^2 = 0.23; Table 1; Fig. 3), and both showed increased biomass with increasing percentage canopy cover (linear model: F 2,140=24.92, p=0.005; R^2 = 0.23; Table 1; Fig. 3). Soil moisture was also positively correlated with invertebrate biomass linear model: F 3,139=15.01, p=0.034; Table 2;
Fig. 3), however this variable was not significant in a linear model including canopy cover.

Table 1: Final linear model which includes canopy cover in percentage and time (night/day) as significant variables.

Explanatory variable	Estimate	Std. Error	t value	p-value
Intercept	-23.709	7.020	-3.378	< 0.001
Percent Canopy Cover	0.212	0.073	2.887	0.005
Time (NIGHT/DAY)	1.268	0.197	6.437	< 0.001

Table 2: Final model which includes soil moisture as a significant variable.

Explanatory variable	**Estimate**	**Std. Error**	**t value**	**p-value**
Intercept	-3.992	0.435	-9.185	< 0.001
Soil Moisture	0.128	0.060	2.143	0.034
Leaf Litter Depth	0.002	0.147	0.054	0.957
Time (NIGHT/DAY)	1.268	0.200	6.340	< 0.001

3.3. DAY AND NIGHT PATTERNS OF ORDINAL ABUNDANCE

We found a significant interaction between time and order, suggesting a conserved relationship between nocturnal and diurnal abundances across orders (ANOVA: $F_{6,40} = 2.67$, $p < .028$; Table 3; Fig. 4). There were more Hymenoptera during the day than night (Fig. 4) contrasting the other orders and the general relationship.

Table 3: Final ANOVA with a significance of the interaction between taxonomic order and time (night/day).

Explanatory variable	**df**	**Sum Sq.**	**Mean Sq.**	**F value**	**p-value**
Taxonomic Order	6 1	23080	3847	23.883	< 0.001
Time (NIGHT/DAY)	6	1049	1049 430	6.513	0.015
Taxonomic Order × Time	40	2581	161	2.671	0.028
Residuals		6442			

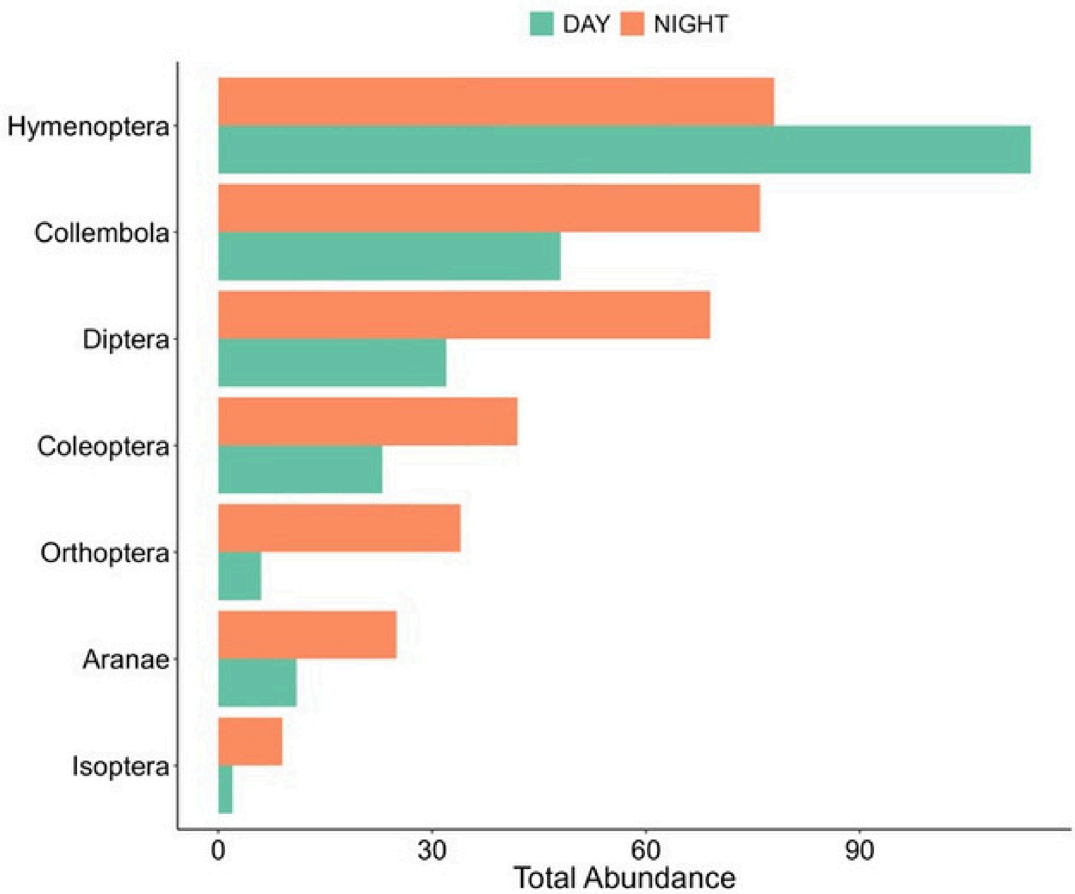


Figure 4: The total abundance of the invertebrates by order during the day and night.

4. Discussion

We found that invertebrate biomass increased with canopy cover, and to some extent soil moisture. However, soil moisture did not vary in the pattern we expected, peaking in middle altitude rather than increasing linearly down the slope. Leaf litter thickness showed the inverse relationship, being highest at the low altitude as we predicted, but lowest in the middle altitude. This pattern may reflect the complex feedback between the leaf litter and soil. Thicker leaf litter may be associated with low moisture conditions via associated low rates of litter decomposition. However, the mechanism also acts in the opposite direction, whereby thicker leaf litter may intercept more rainfall, reducing percolation into the soil. It was surprising that soil moisture was a better predictor of invertebrate biomass than leaf litter thickness, as we expected higher habitat volume and more niche space to promote higher biomass. It is possible that our leaf litter measurements didn't reflect the depth proximal to the pitfall traps as excavation and emptying inevitably disturbed the peripheral litter structure.

The association between higher canopy cover and higher invertebrate biomass may be attributed to differences in radiation reaching the soil layer. High canopy cover may prevent light from reaching the ground, intercepts rainfall, and contributes throughfall of new litter. However, we could not detect a correlation between canopy cover and either leaf litter depth or soil moisture. We recorded a low range of canopy cover, between 92% and 98%. Given this small deviation, we must consider that this effect may be purely correlative until we observe direct interactions between canopy and leaf litter traits. Litter accumulation may be more closely related to surface topography and localised tree species with difference leaf senescence cycles, rather than percentage canopy cover.

We caught more invertebrates from more orders in our night traps than day traps, which could suggest higher invertebrate activity in the dark. Of the top 7 most common orders we recorded, all were found in both day and night, reflecting the fact that these orders are not uniformly nocturnal or diurnal. It fits our understanding that abundance at night is higher, when conditions are cooler, and individuals are less visible to predators. Additionally, insectivorous fauna inhabiting the litter, such as reptiles and amphibians, are overwhelming nocturnal within KNP (Vonesh, 2006), suggesting synchrony between these two trophic levels. We caveat these reflections by adding that day and night periods were of unequal length due to personal safety constraints on forest access during dark hours. Therefore, night periods averaged 16 hours, whilst day periods averaged 8 hours. Additionally, we did not measure environmental characteristics overnight, some of which likely undergo daily cycles such as soil moisture and leaf litter humidity.

The only group with a different response was the order Hymenoptera, which were more abundant during the day. Most hymenopterans sampled were ant species, which occupy a somewhat unique space in forest food webs, acting as mass consumers via their arrangement as 'superorganisms' (Silva and Brandão, 2014). In addition, ants are ubiquitous throughout forest strata, interacting with the canopy, understory and leaf litter via foraging behaviour, and the soil as their colony habitat. Safari ants (*Dorylus* spp.) forage in high numbers, reflected in a case where over 5000 ants, estimated by weight, fell into pitfall traps. These replicates were excluded, as the order of magnitude was too disproportionate to our remaining data.

Future work within this research area may divide specimens into functional groups, which may generate the function-driven picture of leaf communities we aimed to uncover. Detritivores share common strategies but often diverge in their activity, life history, and size. We propose a classification system combining morphological and functional characteristics in addition to food type (detritivores, predators, etc.) for subsequent analyses. A better understanding of the responses of functional groups to environmental conditions could also be applied when evaluating the interactions between invertebrates and trophic levels either side. Leaf litter interfaces with the soil and understory require us to consider the lower trophic level affecting litter invertebrates, namely leaf traits and tree species contributing to litter accumulation. Further spatial resolution could also give an estimate of how widespread certain orders are across the forest. Furthermore, we would recommend an examination of the food web structure between insectivorous leaf litter vertebrates and their prey to better understand the prey niches available in this habitat. Finally, experimental manipulation of leaf litter moisture, experimental wetting (Sayer, 2006), and thickness, throughfall exclusion and addition (Kalbitz et al., 2007), could help inform how invertebrates respond to changing conditions.

We have generated some preliminary information about how environmental characteristics affect leaf litter invertebrate communities on a localised scale. There appears to be a general increase in invertebrate biomass during the night, although our time periods were uneven. Canopy cover and soil moisture are also predictors of invertebrate biomass, whereas leaf litter is not, despite substantial variation between plot locations. There is scope to further analyse the effects of these litter characteristics on the diversity of species and functional groups, since order level richness was not explained by any predictor variables. This information about an important basal trophic level, contributes to our understanding of biodiversity across trophic levels within tropical forest ecosystems.

ACKNOWLEDGMENTS

We would like to thank Graham, the grey colobus, for his advice and support. Thank you to Rosie, Irene, and Frazer for additional wisdom imparted during the planning stages. Our thanks also to the wonderful field guides at MUBFS, Martin and Isaiah, for protecting us from the forest elephants during our field work.

REFERENCES

Guzmán J. B., & Sánchez J. A. (2003). The relationships between litter fauna and rates of litter decomposition in a tropical rain forest. Applied Soil Ecology, 24(1), 91 – 100.

Kalbitz K., et al. (2007). Response of dissolved organic matter in the forest floor to long-term manipulation of litter and throughfall inputs. Biogeochemistry, 86, 301 – 318.

Lieberman, S., & Dock, C. F. (1982). Analysis of the leaf litter arthropod fauna of a lowland tropical evergreen forest site (La Selva, Costa Rica). Revista De Biología Tropical, 30(1), 27–34.

Santana F. D., et al. (2016). Busy Nights: High Seed Dispersal by Crickets in a Neotropical Forest. The American Naturalist, 118(5).

Sayer E. J. (2006). Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biological Reviews, 81(1), 1 – 31.

Silva R. R., Brandão C.R.F. (2014) Ecosystem-Wide Morphological Structure of Leaf-Litter Ant Communities along a Tropical Latitudinal Gradient. PLoS ONE, 9(3).

Vonesh J. R. (2006). Patterns of Richness and Abundance in a Tropical African Leaf-litter Herpetofauna. Biotropica, 33(3), 502 – 510.

Wieder, W.R., Cleveland, C.C. & Townsend, A.R. (2009). Controls over leaf litter decomposition in wet tropical forests. Ecology, 90, 3333-3341.