BIRD'S NEST FERNS AS MODEL SYSTEMS AND CONSERVATION TOOLS

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ABSTRACT

We are in a race against time to understand the response of natural systems to climate change and anthropogenic disturbances, such as large scale land conversion for oil palm expansion. However, natural ecosystems are complex and in reality, it is difficult to quantify multi-trophic biodiversity-ecosystem function (BEF) relationships. Nowhere is this challenge more apparent than in the primary tropical rainforests of Borneo where biodiversity is so highly concentrated. The bird's nest fern (*Asplenium* spp.) is an elegant solution to the problem of studying complex tropical rainforest because the ferns are natural microcosms. The ferns themselves are keystone species in rainforest canopies, and studies have shown that they are hotspots for invertebrate biodiversity and functional processes such as decomposition in the rainforest canopy. Bird's nest ferns are therefore the ideal natural model system, for testing ecological theory, investigating BEF relationships, and performing manipulation experiments to predict the effects of future disturbance. This thesis begins by defining the soil properties that allow bird's nest ferns to regulate their internal microclimate in both rainforest and oil palm plantations. Quantifying the extent to which the ferns buffered extreme climate variation in these habitats revealed why they are such important thermal refuges in both rainforest and oil palm. By defining the ferns' soil properties, it was possible to determine the significant functional role of bird's nest ferns in above ground water storage and natural flood mitigation. Because the ferns are model systems, so too are the animals they support. Cockroaches collected from bird's nest ferns in Borneo and the Eden Project were used to demonstrate the relationship between the oxygen isotopic composition ($\delta^{18}O$) of insect chitin and climate. Revealing that $\delta^{18}O$ in chitin is independent of phylogeny, but entirely a reflection of climate and the way in which the physiological or behavioural traits of a species lead it to interact with its habitat, has paved the way for studies of $\delta^{18}O$ in chitin to quantify species vulnerability or resilience to habitat disturbance and climate change. While cockroaches provided the ideal model animal for quantifying $\delta^{18}O$, centipedes were the ideal group for studying the role of predators in bird's nest ferns. This thesis presents the first study of centipedes in the forest canopy, and the first study of predators in bird's nest ferns. It demonstrated that predation might be more important than competition in structuring communities in forest canopies and that the predators themselves behave in unexpected ways when it comes to using the ferns as a resource. The final chapter revealed that the ferns could indeed be used as conservation tools, to improve habitat connectivity and facilitate the dispersal of animals through oil palm plantations. By transplanting ferns, and their faunal inhabitants, from rainforest to oil palm, it was possible to prime the oil palm landscape with a boost of native biodiversity. This demonstrated that conservation practices in oil palm plantations can improve the landscape for biodiversity, and indeed this is a critical component of the industry's sustainability agenda. In revealing the importance of bird's nest ferns as umbrella species for biodiversity and ecosystem function, this thesis has paved the way for using these ubiquitous epiphytes as a novel tool for conserving biodiversity and improving sustainability within the oil palm landscape.

“IN THE DEPTH OF WINTER, I FINALLY LEARNED THAT
THERE WAS IN ME AN INVINCIBLE SUMMER”
ALBERT CAMUS

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1 INTRODUCTION

1.1 THE TROPICAL RAINFORESTS OF BORNEO

The island of Borneo is situated in the Sundaland hotspot – an equatorial region that covers the western half of the Indo-Malayan archipelago between mainland Asia and Australia (Mittermeier et al., 1999). It supports one of the greatest concentrations of species on Earth, and the species richness of North Borneo in particular resulted in the Sundaland being classified as one of the world's 'hottest hotspots' of biodiversity (Myers et al., 2000). On a global perspective, tropical forests are home to more than two-thirds of all terrestrial plant and animal species (Brooks et al., 2002, Sechrest et al., 2002, Gibson et al., 2011). However tropical forests have long been threatened by conversion for land use, and more than half of the world's primary rainforests have been converted (Asner et al., 2009).

Deforestation has been particularly severe in Southeast Asia (Sodhi et al., 2004, Sodhi et al., 2010) and if current levels of deforestation continue unabated, the region will lose three-quarters of its original forest cover by 2100 (Achard et al., 2002, Gardner et al., 2009, Achard et al., 2014). The lowland dipterocarp forests of Borneo have suffered extensive losses as a result of commercial logging (Richards and Flint, 1994, Flint, 1994, Sodhi et al., 2004) and agricultural expansion for export crops such as rubber (*Hevea brasiliensis*), coconut (*Cocos nucifera*) and oil palm (*Elaeis guineensis*) (Sodhi et al., 2004, Phalan et al., 2013, Laurance et al., 2014). Of these, oil palm is now one of the leading causes of agricultural expansion and subsequent threats to biodiversity (Fitzherbert et al., 2008, Koh and Wilcove, 2008, Barnes et al., 2014).

1.2 THE PALM OIL PARADOX

Oil palm may be considered a 'wonder crop' owing to its high production yield, the highest of all vegetable oil crops. Found in almost everything, from food to detergents, cosmetics, plastics and industrial chemicals (Abdullah and Wahid, 2010, Ruggeri and Samoggia, 2018), palm oil is now the world's most widely consumed vegetable oil (Carter et al., 2007). Palm oil is rich, but odorless and tasteless, with an ability to dramatically increase the shelf life of products, and this makes it a very appealing option to a wide range of manufacturers. The palm oil paradox is this: while the oil palm itself is a wonder crop, its production has driven widespread forest loss, and continued expansion could spell disaster for global biodiversity (Kongsager and Reenberg 2012). However, alternative oils require much larger areas of land to produce the same volume of oil (Sheil et al., 2009), and therefore using an alternative crop to meet vegetable oil demands would only increase land conversion pressures. Indonesia and Malaysia, both in Southeast Asia, are the world's largest producers of palm oil, producing 60 million tonnes of it in 2015 (Pirker et al., 2016). Now oil palm is expanding in other countries including Thailand and Papua New Guinea, as well globally significant forest rich regions such as Colombia and Nigeria (Pirker et al., 2016).

The palm oil industry undeniably promotes economic prosperity, but expansion is frequently linked to deforestation, biodiversity loss and peat degradation (Rival and Levang, 2014). Few development issues generate as much controversy as the expansion of oil palm plantations in forest rich countries (Koh and Wilcove, 2008). The intensity and scope of the ongoing feud between environmental groups and industry representatives over the social and environmental impacts of oil palm (Henson and Chang, 2003, Buckland, 2005) make it difficult to determine 'fact or fiction' on details surrounding the palm oil industry (Sheil et al., 2009). Regardless of the industry's global reputation, this much is true: oil palm has an immense economic value, approximately $60 billion USD per year (Khatun et al., 2017), and demand for palm oil is increasing (Gilbert, 2012, Khatun et al., 2017). It is predicted that consumption of palm oil will triple between 2000 and 2050, and the profitability of this crop is a strong incentive to convert land into oil palm plantations (Laurance et al., 2014, Rival and Levang, 2014). However, expansion without respite will spell disaster for Southeast Asia's biodiversity (Brook et al., 2008, Sodhi et al., 2004) and the subsequent decline in ecosystem services will pose a major threat to human health and wellbeing (Bazzaz et al., 1998, Diaz et al., 2006). We need to take a united stand on the palm oil issue, and demand production through more sustainable means (Teoh, 2010), such as those proposed by the Roundtable on Sustainable Palm Oil (RSPO) (Tan et al., 2009, Laurance et al., 2010, Ivancic and Koh, 2016).

1.3 IMPENDING BIODIVERSITY DISASTER

In regions where primary forest, and even secondary forest are converted into plantation, biodiversity and ultimately ecosystem services are destroyed. Under rapid human population growth and rising demand for food security, the need to ensure efficient production whilst minimising the threat to biodiversity and ecosystem function is an incredible challenge (Tscharntke et al., 2012). In recent decades, agricultural expansion has driven rapid large-scale deforestation (Rival and Levang, 2014), and there is a high degree of uncertainty over how much land has been converted for oil palm plantations (Savilaakso et al., 2014). Recent estimates of land use under oil palm production stand at 18 million hectares (Prescott et al., 2015). However as long as demand continues to rise, production will keep pace and land conversion to oil palm plantation is an inevitable consequence (Koh and Ghazoul, 2010, Laurance et al., 2014). Southeast Asia provides the ideal microclimate for oil palm plantations to thrive (Dufrene et al., 1990), but unfortunately four of the world's most important biodiversity hotspots overlap in Southeast Asia (Myers et al., 2000). When natural ecosystems are transformed into agricultural land much of the original biodiversity is lost (Turner and Foster, 2009, Barnes et al., 2014). This reduction in biodiversity is being increasingly linked with a reduction in ecosystem services (Diaz et al., 2006, Edwards et al., 2014, Clarke et al., 2017). The prolific, large-scale conversion of rainforest to oil palm therefore raises significant concerns, not only for biodiversity, but for ecosystem functioning in the tropics (Phalan et al., 2013, Mori et al., 2017, Gray et al., 2017).

1.4 THE NEED FOR SUSTAINABILITY

In recent years there has been a concerted effort to improve oil palm management in order to achieve sustainable production (Tayleur et al., 2017, Begum et al., 2018). Whilst various 'best practices' have been developed to reduce the industry's environmental impacts (Sheil *et al.,* 2009), there have been few independent assessments of their application and effectiveness (Rupani et al., 2010, Foster et al., 2011, Ghazali et al., 2016). We still have a long way to go before we can understand the true implications of oil palm expansion (Fitzherbert et al., 2008, Khatun et al., 2017). This includes investigating alternative routes to sustainable production (Tan et al., 2009), such as not planting on peat, zero deforestation, maintaining riparian buffers, oil traceability, and the active restoration of biodiversity (Ruysschaert and Salles, 2014, Ivancic and Koh, 2016, Khatun et al., 2017). The Roundtable on Sustainable Palm oil (RSPO) was established in 2004 to promote the growth and use of sustainable palm oil. By imposing a series of principles that companies must follow in order to be certified as a sustainable producer (RSPO, 2016), the RSPO encourages transparency along the supply chain and co-operation between stakeholders. Transparency is key, as policy makers and practitioners can only make the best decisions in land management when they are accurately informed and regularly updated (Turner et al., 2008). Most importantly, truthful, unbiased and accurate information needs to be communicated, if not at least made available, to the public (Laurance et al., 2010). The palm oil industry is after all, driven by consumer demand, therefore consumers should share the responsibility of sustainable development within the industry. However, this can only be achieved through increasing public awareness of the oil palm issue, and by communicating how sustainable practices aid biodiversity conservation (Bateman et al., 2010). When consumers demand— and are willing to pay more—for certified sustainable palm oil (CSPO) products, there is economic incentive for growers and producers to grow sustainably (Bateman et al., 2015). The lack of public awareness on oil palm is a key sustainability issue (Teoh, 2010, van der Ven et al., 2018) and until this is addressed, oil palm expansion will continue to lead towards ecological disaster (Sodhi et al., 2004).

1.5 HABITAT TRANSFORMATION

Most of the concerns regarding the loss of biodiversity, relate directly to the loss of rainforest and the associated habitat transformation. Oil palm plantations are often created through forest clearance, either mechanically or (illegally) with fire. The land is terraced, roads and drainage systems are added and finally young oil palms are planted (Butler, 2011). The conversion process reduces structural complexity and destroys ecological niches associated with the architecturally complex and physically dynamic rainforest (Foster et al., 2011). The canopy is reduced from around 50m in tropical rainforest (Okuda et al., 2003), either to bare-ground, or open canopy just a few meters above the ground in young plantations. Habitat simplification also has a significant effect on the microclimate within the habitat (Luskin and Potts, 2011). Having lost the rainforest canopy's ability to buffer microclimate, oil palm plantations are much harsher environments (Turner and Foster, 2006, Hardwick et al., 2015).

1.6 THE ENVIRONMENTAL FILTER IN PRINCIPLE

Ecological communities are structured jointly by stochastic processes such as random dispersal, and deterministic processes such as interspecific competition (Ellwood et al., 2009, Ellwood et al., 2016). However, as physical conditions deteriorate, competitive interactions are thought to be less important because, regardless of their competitive ability, certain species are winnowed by the environment (Ellwood et al., 2016). It follows that the environmental filtering metaphor (Kraft et al., 2015) could be highly relevant to explain the changes in community assembly and dynamics observed when rainforest is converted to oil palm.

While most taxonomic groups show reduced species richness, abundance and biomass in oil palm plantations, some groups show the opposite trend, increasing in abundance and biomass compared with primary forest (Foster et al., 2011). These important exceptions included beetles, woodlice and cockroaches (Turner and Foster, 2009), animals that are notable for their importance in decomposition and nutrient cycling. However, very little is known of the effect of habitat conversion on predatory groups such as centipedes. Though Turner and Foster (2009) proposed that variability between taxa could be a consequence of species-specific differences in environmental tolerances, they did not go as far as invoking environmental filtering as the process behind the patterns that they observed. This thesis will test whether environmental filtering (Kraft et al., 2015) rather than competition determines the structure of arthropod communities in the physically harsh conditions of oil palm. In doing so, we will be in a better position to quantify how shifts in the diversity-abundance relationships of arthropod decomposers changes ecosystem function (Whittaker, 1960, Swenson et al., 2006, Shipley, 2010, Gray et al., 2017). As well as decomposition and nutrient cycling, insects perform other ecosystem services such as pollination and pest predation, and the increase in abundance of resilient species may provide a functional buffer against the loss of sensitive species (Foster et al., 2011). As well as considering the effects of environmental filtering on decomposers, this thesis will explore the shifts in abundance and diversity of centipedes, a functionally significant, but largely neglected group of predators (Klarner et al., 2017).

1.7 THE ENVIRONMENTAL FILTER IN PRACTICE

Species that are able to endure harsh physical conditions such as those in the rainforest high canopy, and in oil palm, should share traits which enable them to share the same abiotic niche. Under such conditions, phenotypic similarities relating to climatic tolerance should be shared by members of the community (Kraft et al., 2015), and we should observe a higher degree of 'phenotypic convergence' relative to what would be expected by chance (Cornwell et al., 2006, Ackerly and Cornwell, 2007, Kraft et al., 2008, Cornwell and Ackerly, 2009). According to Kraft *et al* (2015) a quantifiable physiological marker of convergence would be crucial to truly detect environmental filtering.

Molecules of water (H_2O) show slight mass variations based on their isotopic composition of oxygen and hydrogen i.e. the different combinations of stable isotopes of oxygen (O^{16}/O^{18}) and hydrogen (H^1/H^2). These mass differences result in molecules of water evaporating and condensing at different rates. When water evaporates, the lighter molecules, containing isotopes of ^{16}O, change phase more rapidly than the heavier molecules (containing ^{18}O). This leaves liquid water with a higher concentration of ^{18}O than atmospheric water vapor because the heavier molecules are slower to change phase. The extent of this exchange is controlled by the bidirectional movement of water between the surface of water bodies and the atmosphere. Therefore the exchange is a function of environmental temperature and relative humidity (RH), and can be described using the Craig Gordon (C-G) model (Craig and Gordon, 1965).

Insect spiracles are functionally equivalent to plant stomata. While their primary function is to permit air diffusion for respiration, spiracles also facilitate water exchange between the body of an insect and the atmosphere (Schimpf et al., 2009). This is why insects and other tracheated arthropods show such a strong response to moisture gradients (Dial et al., 2006). Their haemolymph (blood) can be considered an isolated pool of water, and so it has its own oxygen isotopic composition ($\delta^{18}O$), which can also be defined by the C-G model (Ellwood et al., 2011). Insect haemolymph provides an almost real-time indication of the environmental conditions under which an animal is living, whereas the $\delta^{18}O$ signature of insect chitin ($C_8H_{13}O_5N$) provides an indication of the temperature and humidity of the environment in which the animal created its exoskeleton (Ellwood et al., 2011). The process by which an insect creates its exoskeleton is known as ecdysis or moulting. The specific environmental conditions under which ecdysis takes place are isotopically fixed in the chitin, where it remains unchanged until the animal's next moult (Schimmelmann and DeNiro, 1986). This signature can be quantified using Infrared Spectroscopy (IR) and Mass Spectronomy (MS).

Although the 'physiological marker of abiotic niche' proposed by Kraft *et al* (2015) was purely theoretical, Ellwood *et al* (2011) proposed use of $\delta^{18}O$ could provide a quantitative means for defining the abiotic tolerances of species. Their study showed that the $\delta^{18}O$ of insect tissues could provide a physiological marker of the specific environmental conditions under which an insect has lived. As animals tend to avoid habitats to which they are not climatically suited (Suggitt et al., 2011), the $\delta^{18}O$ composition of insect tissue could provide an early indication of an animal's response to environmental disturbance, either through habitat disturbance or climate change. Widespread application of this method would not only allow us to define the climatic tolerances of species, but to: (1) quantify species vulnerability or resilience to environmental change; (2) determine whether environmental filtering can explain the change in community assemblages when rainforests are disturbed or transformed and (3) develop the appropriate management strategies that will protect or extend the distribution of climatically sensitive, functionally important animals thus maintaining the ecosystem services they provide.

1.8 BIRD'S NEST FERNS AS MODEL SYSTEMS

Bird's nest ferns (*Asplenium* spp.) (**Figure 1.1** (Top) Asplenium nidus (frond diameter >2m) at 45m, and (Bottom) Asplenium phyllitidus in the low canopy of tropical rainforest in Borneo.) are widespread, abundant epiphytes (non-parasitic) that occur throughout the old world tropics (Holttum, 1974). They consist of a rosette of upward facing fronds, and a fibrous root-soil mass, which secures them to their substrate. The leaf bowl traps falling litter, which subsequently decomposes in the root-soil mass, providing nutrients and contributing material for soil formation (Benzing, 1987, Piggott and Piggott, 1988, Turner et al., 2007).

There are two common species, *Asplenium nidus* which dominates the exposed upper levels of the rainforest canopy, and *Asplenium phyllitidus* which occurs in the low canopy (Latiff et al., 1998, Fayle et al., 2009). The two species can usually be distinguished by their leaf morphology (*A. nidus* has a dark mid-vein as well as much larger leaves) and by the position of their spore producing sori (*A. nidus* have sori on every vein that stretch about two thirds of the leaf width, *A. phyllitidus* have sori only on alternate veins that stretch almost to the edge of the leaf) (Holttum and Roy, 1966). Species identification is not always straight forward (Fayle et al., 2009) however, and genetic research has revealed the existence of cryptic species within the *A. nidus* complex (Yatabe and Murakami, 2003, Yatabe et al., 2009, Fayle et al., 2011).

Bird’s nest ferns support a significant proportion of the rainforest’s invertebrate species (Ellwood et al., 2002). The importance of these hanging gardens is such that they double the estimated invertebrate biomass of the rainforest canopy (Ellwood and Foster, 2004). They are natural microcosms (Srivastava et al., 2004) and can be considered islands in a sea of rainforest canopy (Ellwood et al., 2016). While we have developed an understanding of the ecological interactions between species at lower trophic levels in bird’s nest ferns (Ellwood et al., 2009), we know nothing of the higher trophic levels. Although ecological communities are structured by both stochastic and deterministic processes (Ellwood et al., 2009), competition usually goes a long way towards explaining species assemblages. However, in instances where competition does not govern the structure of communities, predation is most likely the dominant ecological force (Menge and Sutherland, 1976).

Bird’s nest ferns are model systems because they can be sampled exhaustively and experimentally manipulated (Ellwood et al., 2002). Ecological models such as the bird’s nest fern provide an elegant means to explore ecological complexities, such as multi-trophic interactions, the role of predation in species assembly, and the relationship between biodiversity and ecosystem function. Not only are bird’s nest ferns functionally significant in primary forest but they persist in logged forests and in oil palm plantations (Turner, 2005). Indeed the ferns are more abundant in plantations, where their functional role may be of greater importance (Fayle et al., 2008). However, the precise role played by bird’s nest ferns in oil palm plantations has yet to be elucidated.

Figure 1.1 (Top) *Asplenium nidus* (frond diameter >2m) at 45m, and (Bottom) *Asplenium phyllitidus* in the low canopy of tropical rainforest in Borneo.

1.9 BIRD'S NEST FERNS AS CONSERVATION TOOLS

Bird's nest ferns are clearly an important microhabitat for arboreal invertebrates (Ellwood and Foster, 2004) and this may be because they permit animals to survive in environments that would otherwise be beyond their climatic tolerance. For example, it was shown that beetles occur at higher abundances in bird's nest ferns during the dry season (Sergeeva et al., 1990). Animals not only utilise canopy microhabitats (such as the ferns) for foraging (Nadkarni and Matelson, 1989), but as climatic refuges when external environmental conditions become unfavourable. Previous work has shown that bird's nest ferns buffer microclimate (Scheffers et al., 2013, Scheffers et al., 2014a, Scheffers et al., 2014c), as well as the microclimate in their immediate vicinity (Turner and Foster, 2006, Freiberg and Turton, 2007). The ferns are consistently cooler than the air around them (Scheffers et al., 2014c) but to date nobody has attempted to explain how or why the ferns are cooler. The ability of bird's nest ferns to buffer microclimate would be even more important in oil palm plantations, where conditions are much harsher than in rainforest. *A. nidus* dominates the high canopy of tropical rainforest and is the only species of *Asplenium* to persist in oil palm plantations (Fayle et al., 2011). In fact, *A. nidus* shows an increase in abundance in oil palm plantations (Turner, 2005), and this raises the question: why does *A. nidus* do so well in oil palm? It is most likely that *A. nidus* evolved to survive in the harsh conditions of the forest high canopy, whilst *A. phyllitidus* favoured the cool shady understory. Consequently, *A. nidus* is pre-adapted to survive the similarly challenging conditions in oil palm, where it may thrive in the absence of competitors.

Bird's nest ferns would logically be the preferred habitat for sensitive fauna (Scheffers et al., 2014c) in both tropical rainforests and oil palm plantations. However, if bird's nest ferns ameliorate the physical stress of the transformation process from natural forest to oil palm (Foster et al., 2011), they would provide a unique opportunity to conserve biodiversity, and improve the ecological outlook of the increasingly common oil palm landscape.

1.10 THE FUNCTIONAL ROLE OF BIRD'S NEST FERNS

Although bird's nest ferns are an important habitat for functionally important invertebrates (Ellwood and Foster, 2004), the functional importance of ferns to decomposition and other processes in the canopy (Turner et al., 2007, Snaddon et al., 2012), is largely attributed to microbes in the ferns' associated suspended soils (Donald et al., 2017a). Decomposition is a fundamental ecological process, not only for the release of nutrients, but also for a build-up of stable humus and its accompanying storage of nutrients (Zheng, 2006). Understanding decomposition is key to understanding nutrient cycling (Fonte and Schowalter, 2004). Although decomposition is mediated by microorganisms, the effects of variation in microbial community composition on decomposition are largely unexplored (Bardgett et al., 2008, Van Der Heijden et al., 2008, McGuire et al., 2010, McGuire and Treseder, 2010, Donald et al., 2018). Recent research by Donald (2018) developed our understanding of the role of microbial communities to ecosystem function in the ferns using a combination of soil microbial community analysis methods such as phospholipid fatty acid (PFLA) analysis, hydrolase and oxidase enzyme assays and MicroResp analysis. These methods have provided a novel approach to study the soil microbial communities of bird's nest ferns and their associated functional profile. While we have a better understanding of decomposition in bird's nest ferns in primary forest (Donald, 2018), little is known of the functional role of these epiphytes in oil palm (Foster et al., 2011, Prescott et al., 2015), and almost nothing is known of the ferns functional processes beyond decomposition.

Despite the broad consensus that biodiversity and ecosystem function are positively correlated (Hooper et al., 2005, Cardinale et al., 2006, Barnes et al., 2014), there are few real-world examples of this relationship (Foster et al., 2011). This is likely because natural ecosystems are complex (Srivastava and Vellend, 2005, Mori et al., 2017, Clarke et al., 2017), and it is very difficult to quantify biodiversity-ecosystem functioning relationships across multiple trophic levels (Barnes et al., 2014). Further to this, our knowledge of the interplay between biodiversity and ecosystem function under land conversion to oil palm is strongly limited, and still we lack the ability to quantify, and compare single measures of ecosystem function (Barnes et al., 2014, Gray et al., 2017, Dislich et al., 2017). This has a knock-on effect for our ability to examine whole-community relationships between species assemblages and their respective functional processes. Using the bird's nest fern as a model system offers an elegant means to study such ecological interactions.

1.11 RESEARCH SITES

1.11.1 THE EDEN PROJECT

Opened in 2001, the Eden Project in St Austell, Cornwall, U.K. (50.36° N,4.74° W) is home to the world's largest indoor rainforest covering an area of 15,590m^2 enclosed within a large biome. The Rainforest Biome (RFB) stands at 50m tall and houses some 1,400 species of plant under controlled climatic conditions (mean ± SD): air temperature (21.7 ± 2.8 °C) and relative humidity (97.4 ± 3.6%) (Donald et al., 2016, Donald et al., 2017a). Arguably, the Eden Project's most unique aspect is that the soils within its biome are artificial, created in partnership with the University of Reading, using sand recycled from the local clay industry, composted bark, green waste from the surrounding area, and lignitic clay as a by-product of Devon's ball clay industry. Despite the artificial origin of its soils, the Eden Project RFB has a functional community of soil microbes and invertebrates (Donald et al., 2017). Consequently, the Eden Project provides a midpoint between sterile laboratory conditions and the full suite of known and unknown variables that characterise tropical fieldwork. It is the ideal model rainforest or 'mesocosm' for studying multi-trophic and environmental interactions in a sealed microbiome.

1.11.2 DANUM VALLEY CONSERVATION AREA

Much of the fieldwork described in this thesis took place in the Danum Valley Conservation Area (DVCA) in Sabah, Malaysian Borneo (4.58° N, 117.48° E). The average annual temperature in the conservation area is 26.7°C, with a mean annual rain fall of 2669 mm (Walsh and Newbery, 1999). The mean annual relative humidity is 94.5% at 0800 hours and 72% at 1400 hours (Walsh, 1990). Mean maximum and minimum temperatures in the primary rainforest surrounding the field centre have been recorded as 28.4 °C and 21.2 °C respectively (Brown, 1993). The DVCA covers approximately 43,000ha, and consists mainly of primary undisturbed lowland evergreen dipterocarp rainforest. Members of the Dipterocarpaceae constitute approximately 80% of the total tree volume (Marsh and Greer, 1992). The Ulu Segama Reserve, which is the forested area surrounding the Danum Valley, contains large tracks of logged forests, exploited for timber extraction from the 1970s through to the early 2000s, as well as forest restoration sites and small scale commercial tree plantations within a agro-forest mosaic (Marsh and Greer, 1992).

1.12 A NOTE ON ANIMAL ETHICS

Ethics are an important aspect of research development and practice (Shamoo and Resnik, 2009) but surprisingly Animal Welfare and Ethics (AWE) have been frequently overlooked in ecological research (Garrett et al., 2012). This is especially true for studies involving invertebrates where there are no legal requirements, and therefore no legal responsibility to consider animal welfare in practice. Although previous AWE discussions have focused on the use of animals in pharmaceutical and medical research (Joffe et al., 2016), the ethical issues faced by biologists, ecologists and conservationists have rarely been discussed in the literature. Whilst AWE is becoming increasingly prominent in contemporary research, and the UK has gone further than almost any other country by implementing the Animals Scientifics Procedures Act 1986 (ASPA), there is still no obligation for research involving invertebrates to consider animal ethics. However, in the interests of accountability and integrity, details of the research conducted for this thesis were sent to UWE Bristol's Animal Welfare and Ethics Committee (R12) for ethical review, where they received approval. Research and export licenses were also obtained from the Danum Valley Management Committee (DMVC Project No: 457) and the Sabah Biodiversity Centre (SaBC Project No:KM/MBS.1000-2/2 JLD.6). Over the duration of this project, an invertebrate collection of 49,759 invertebrates was amassed. It is intended that UWE researchers can continue to derive information from these specimens. Many of the species identified for this thesis will be photographed, and digitally archived in an online open access specimen catalogue. This will not only facilitate knowledge exchange, but create opportunities for future collaborative research.

1.13 RESEARCH OBJECTIVES AND THESIS FORMAT

This PhD thesis has the following objectives:

i. To develop our understanding of the ability of bird’s nest fern to buffer microclimate,
ii. To explore the potential of stable isotopes of oxygen ($\delta^{18}O$) to describe species habitat preference and physical tolerance,
iii. To understand the importance of predation in the bird’s nest fern model system,
iv. To establish the evidence base for bird’s nest ferns as ‘conservation tools’ to not only maintain, but to restore native biodiversity to oil palm plantations,
v. To outline the future direction, and impact beyond academia that this project has generated.

This thesis has been formatted to follow these objectives, and each chapter begins by giving context to the work it presents. Chapter 2 describes the extent to which bird’s nest ferns buffer microclimate, exploring the specific hydro-thermal mechanisms and the ferns capacity to continue buffering microclimate under warming climatic conditions. Chapter 3 details the isotopic composition of chitin in the exoskeleton of cockroaches (Blattodea), collected from the Eden Project, and bird’s nest ferns in Borneo. Using $\delta^{18}O$ in cockroaches as a model for method development, it was possible to explore the potential of $\delta^{18}O$ as: (1) a new direction for stable isotope ecology and (2) a novel means to quantify species physiological tolerances and habitat preferences. Chapter 4 provides not only the first account of the centipedes (Chilopoda) associated with bird’s nest ferns, but the first account of centipedes, and their functional significance in the forest canopy. Chapter 4 details the centipede community composition and structure in ferns throughout the forest canopy, and indicates that the typical rules of ecological engagement do not apply to top predators in the forest canopy. Chapter 5 presents the results of a pioneering experiment that sought to return native biodiversity to the oil palm landscape. A major aim of this thesis was to show that bird’s nest ferns are umbrella species for conservation, and that consideration for the fern itself in conservation practices will have a positive knock on effect for the wider ecological community. Chapter 5 establishes the evidence base for using bird’s nest ferns as conservation tools: (1) to maintain biodiversity and associated ecosystem function as landscapes are altered and (2) to facilitate the restoration and recovery of plantations to a more natural state. Chapter 6 provides a synthesis of the work completed as part of this thesis, with reflections on the originality of the work, and the generation of new knowledge. Chapter 6 also outlines several of the future directives that this project will follow, and highlights some the impact beyond academia that this research has generated.

1.14 SUMMARY

- Although Bornean rainforests are hotspots of species richness and endemism, they are threatened by oil palm expansion.
- The tolerance of invertebrates to such disturbances are poorly understood, but stable isotopes could provide the means to quantify species vulnerability or resilience to habitat disturbance or climate change.
- Bird's nest ferns, which support large numbers of invertebrates in the forest canopy, likely protect inhabitants from climatic extremes, but the underlying mechanisms by which the ferns thermoregulate, and the extent to which they do so is not known.
- Although we have a good understanding of the decomposer community of bird's nest ferns, nothing is known of the predators, or the effect of predation on community structure.
- The importance of bird's nest ferns to biodiversity and ecosystem function in oil palm plantations is poorly understood, and this needs addressing.
- The ferns are discrete, moveable units, therefore they represent the ideal model system. However, they may also provide a unique opportunity to restore native biodiversity to oil palm plantations as conservation tools.

2 TO WHAT EXTENT DO BIRD'S NEST FERNS BUFFER MICROCLIMATE?

CONTEXT

Bird's nest ferns, and the soils associated with them represent one of the most important microhabitats for animals in the canopy. A few studies have shown that bird's nest ferns and other epiphytes regulate their own physical conditions, and that the ferns influence microclimatic conditions in the surrounding canopy. However, no study has explored the mechanisms underpinning the ferns buffering capabilities. The studies which showed that bird's nest ferns buffer microclimate did not go far enough, because not a single study looked at the suspended soils associated with the ferns as the reason for their buffering abilities. Indeed, knowledge of the specific soil properties of bird's nest ferns, and the extent to which these properties determine plant water interactions, is completely lacking. Although bird's nest ferns provide an interface between biodiversity and functional processes in the forest canopy, their importance in processes such as above ground water storage have never been considered. This chapter not only provides an in depth study of the soil properties which underpin the ferns' ability to buffer microclimate, but it considers the extent to which the ferns buffer microclimate in both rainforest canopy, and in anthropogenic habitats such as oil palm.

2.1 INTRODUCTION

2.1.1 FOREST CANOPIES

Tropical forest canopies (Figure 2.1) are one of the most architecturally complex habitats on Earth (Moffett, 1993, Scheffers et al., 2013), and the range of organisms and processes they support are equally diverse (Pedley et al., 2016). Despite a steady increase in canopy science in recent decades, difficulties associated with reaching the canopy (Parker et al., 1995, Anderson et al., 2015), have made progress slow (Lowman et al., 2012). Consequently, the high canopy remains one of the final frontiers for ecological research (Nakamura et al., 2017). Although ecologists have traditionally opted for line insertion techniques and climbing equipment (Maher, 2006), accessing the forest canopy is no easy feat (Anderson et al., 2015). In the case of Bornean lowland rainforest, the canopy frequently exceeds 50m, with the first branches around 30m (Dial and Tobin, 1994, Ellwood and Foster, 2001). Canopy cranes, and remote sensing technologies have become popular means to study canopy processes (Nakamura et al., 2017). While cranes provide ease of access for experimental manipulation (Lowman et al., 2012), remote sensing technology enables extensive data sets to be amassed quickly and effectively over large areas (Frohn and Lopez, 2017). However, the installation of canopy cranes can disturb natural forest (Delvare et al., 1997), and as its name suggests, remote sensing has distracted attention away from the detailed inner workings of forest canopies (Nakamura et al., 2017). As the methods used to study canopy ecosystems have become grander, small-scale studies capable of generating highly refined taxonomic and biological data have declined, which is unfortunate because most organisms in forest canopies are relatively small (Suggitt et al., 2011, Scheffers et al., 2014b). Moreover, small organisms such as insects and microbes are fundamental to functional processes in the rainforest ecosystem, and may be more important in the grand scheme of things than larger more conspicuous animals. To truly understand the way that animals use resources in the canopy, such as the previously unknown resource sharing behaviours of centipedes described in Chapter 4, researchers must be willing to venture into the canopy (Lowman, 2009). Indeed, those rising to the challenge can be rewarded with intimate, highly detailed and minimally invasive studies of the canopy (Mitchell et al., 2002).

Figure 2.1 The structurally dynamic canopy of Bornean lowland rainforest.

Although rainforests are thermally buffered habitats (Foster et al., 2011, Scheffers et al., 2014a, Hardwick et al., 2015, del Pliego et al., 2016), environmental conditions become increasingly variable through the vertical dimension (Dial et al., 2006). In fact, the high canopy is characterised by extreme abiotic (temperature, humidity, solar radiation) conditions (Moffett, 1993, Dial et al., 2006). The resilience of these natural systems will be tested under climate change and increasing levels of disturbance as extreme heat events will become more frequent (Change, 2007, Williams et al., 2008). Although rainforests and their canopies provide a degree of thermal buffering compared with disturbed environments (Hardwick et al., 2015), the large-scale consequences of climate change, and the small-scale shifts in local microclimate caused by disturbance are poorly understood (Nakamura et al., 2017).

2.1.2 THE ROLE OF MICROHABITATS

Several studies have identified that microhabitats will become increasing important under climate change and habitat disturbance (Suggitt et al., 2011, Wardhaugh et al., 2012, Scheffers et al., 2014b, del Pliego et al., 2016). Microhabitats such as bird's nest fern are abundant throughout the forest canopy (Ellwood et al., 2002, Wardhaugh et al., 2014). Not only do microhabitats increase structural complexity (Okuda et al., 2003, Fayle et al., 2009), but they also provide an interface between biodiversity and functional processes in the canopy (Wardhaugh et al., 2014, Donald et al., 2017a). In forest canopies, microhabitats facilitate the maintenance of biodiversity because they ameliorate climatic extremes of the macroenvironment (Keppel et al., 2012). On this basis, microhabitats provide species with an opportunity to circumvent climatic extremes (Scheffers et al., 2014a), and subsequently (for sensitive animals especially) access to the vertical dimension of tropical forests may be entirely dependent on the availability of microhabitats (Scheffers et al., 2014b).

Some microhabitats such as bird's nest ferns, have associated suspended soils (Coxson and Nadkarni, 1995), which form through the assimilation of root material, organic matter and humus (Nadkarni and Matelson, 1989, Bohlman et al., 1995). Many organisms typically associated with the forest floor also occur in suspended soils, including decomposers such as mites (Beaulieu et al., 2010), cockroaches (Chapter 3), springtails, earthworms and millipedes (Ellwood et al., 2002, Wurst et al., 2018), but also large predators such as centipedes (Chapter 4). Perhaps it is unsurprising that suspended soils support animals that are typically associated with the forest floor (Wardhaugh et al., 2014), although these communities often show distinct species separation from ground soils (Wardle, 2002). While suspended soils can accrue in excess of several tonnes per hectare (Coxson and Nadkarni, 1995), their role in carbon storage and other large scale ecosystem processes has yet to be considered.

Bird's nest ferns are the world's largest epiphytes, and they alone can account for around a tonne of dry biomass in a hectare of forest canopy (Ellwood et al., 2002). The ferns are essentially aerial compost heaps (Fayle et al., 2008) because their soils accumulate through the decomposition of litter and humus collected in their leaf baskets (Ellwood et al., 2002, Turner et al., 2007) (Figure 2.2). Individual ferns can grow to 200kg fresh weight, with the bulk of the mass attributed to their associated suspended soil root complex (Ellwood and Foster, 2004). The soil core represents the most important part of the fern, providing a source of nutrients (Snaddon et al., 2012), and moisture (Dial et al., 2006) in the canopy. While the ferns are a harbour of invertebrate biodiversity in the forest canopy (Ellwood et al., 2002, Turner et al., 2007), they are also refuges for climate sensitive vertebrates such as frogs (Scheffers et al., 2013, Scheffers et al., 2014c), geckos and skinks (Donald et al., 2017b). Owing to their size and distribution, the role of bird's nest ferns in biodiversity maintenance and functional processes in the canopy make them keystone species in tropical forests (Ellwood et al., 2002).

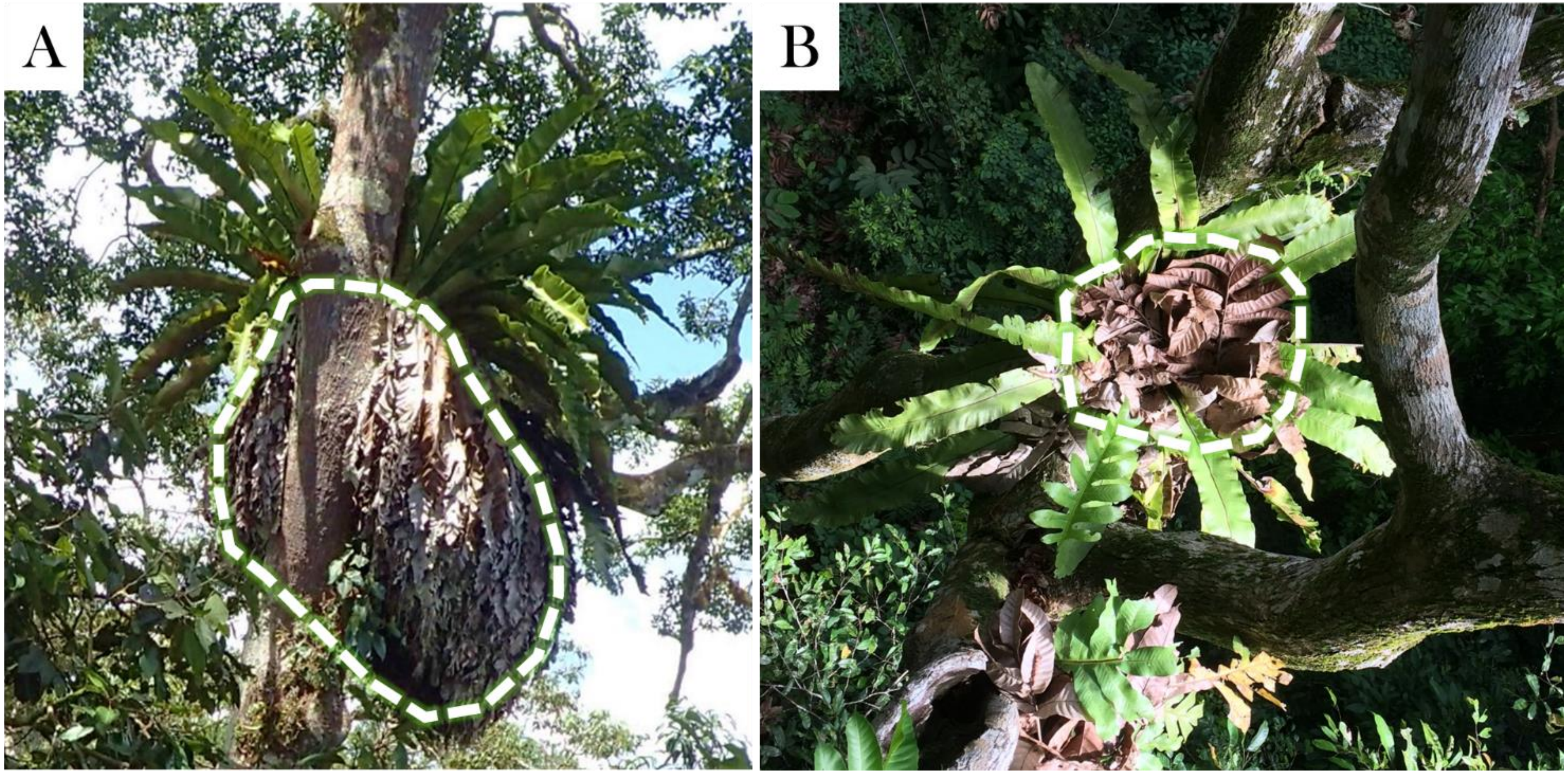


Figure 2.2 (A) Large bird's nest fern in the high canopy of Bornean rainforest, the soil root mass is hidden beneath a skirt of dead leaves. (B) Bird's eye view of a bird's nest fern showing the rosette of fronds intercepting leaf litter from the canopy.

2.1.3 BIRD'S NEST FERNS AS THERMAL BUFFERS

The wide range of organisms that use bird's nest ferns will certainly benefit from the availability of resources such as nutrients (Snaddon et al., 2012). However, the success of any species hinges on their ability to obtain water which is the most important of life's resources (Kramer and Boyer, 1995). The ferns themselves are hardy and drought tolerant (Freiberg and Turton, 2007), but for many of the animals that utilise the ferns, a major benefit will be that they provide a source of moisture, and a microclimatically stable refuge in the forest canopy (Scheffers et al., 2013). In fact, studies have shown that bird's nest ferns influence temperatures and the humidity of the air in their vicinity (Freiberg, 2001, Stuntz et al., 2002, Turner and Foster, 2006). The ability of the ferns to regulate their own temperature regime is such that the ferns influence the microclimate of the canopy around them (Scheffers et al., 2014c). Thermoregulation is dependent on water availability (Kramer and Boyer, 1995, Freiberg and Turton, 2007), and for the ferns to effectively buffer microclimate they must be able to obtain and reserve water (Scheffers et al., 2014c). Although epiphytes obtain moisture from the environment (Nadkarni, 1981, Coxson and Nadkarni, 1995, Bohlman et al., 1995), the suspended soils associated with bird's nest ferns will serve as a water store. Indeed, the ferns are adapted to intercept and funnel rainwater into its soil core (Figure 2.3), although the extent to which ferns store water in the rainforest canopy remains unknown.

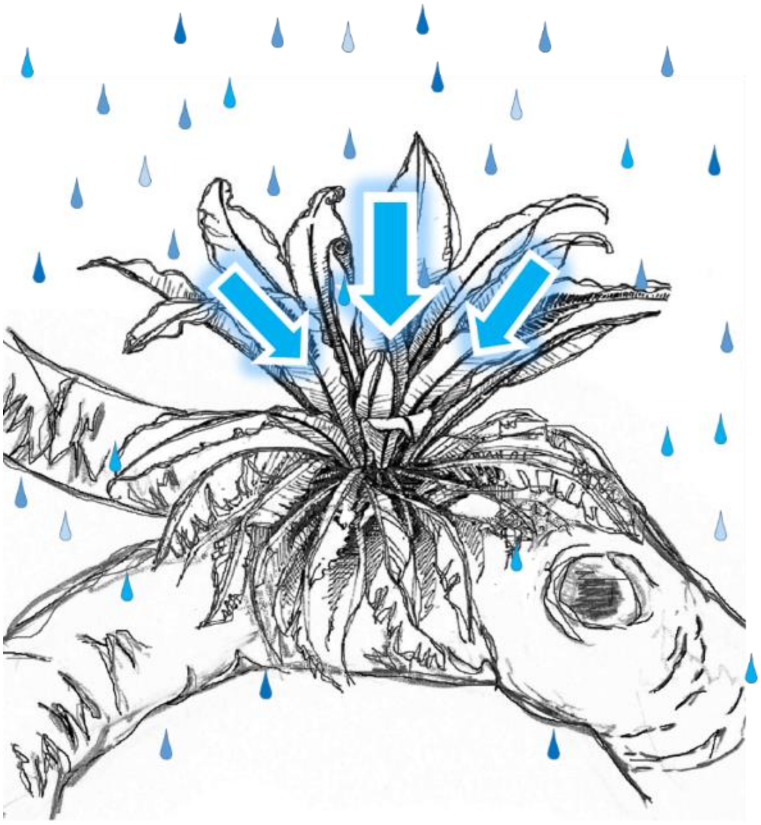


Figure 2.3 The interception and storage of water by a bird's nest fern in the canopy.

The buffering abilities of bird's nest ferns have received some attention (Turner and Foster, 2006, Freiberg and Turton, 2007, Scheffers et al., 2014c), but our understanding of the hydro-thermal properties of these functionally significant plants is far from complete. Studies have shown that areas of forest which support ferns have lower temperatures, and higher humidities, than those without (Turner and Foster, 2006), and also that buffering is dependent on water availability (Freiberg and Turton, 2007, Scheffers et al., 2014c). However, none of these studies considered the importance of the ferns' associated suspended soils. Previous studies of microclimate have collected data using sensors placed in proximity to the ferns (Turner and Foster, 2006, Freiberg and Turton, 2007), or in the fern leaf basket (Scheffers et al., 2014c). Yet remarkably, not a single study inserted probes into the soil core, despite the fact that it is the most important of all the fern sub habitats (Ellwood et al., 2002, Ellwood and Foster, 2004). Further to this, no study has investigated thermal buffering in ferns above 20m in natural forest, even though they occur up to 50m, where physical conditions and climatic fluctuations are most severe (Ellwood et al., 2002, Fayle et al., 2009).

Climate is stratified in the canopy: temperature increases and humidity decreases with distance from the forest floor (Dial et al., 2006). The role of bird's nest ferns as buffered habitats would therefore be more important in the high canopy, but as yet no studies have been conducted on ferns in the highest reaches of the canopy. Interestingly, no in-depth study has been conducted into the ferns' buffering capabilities in disturbed habitats, even though they are abundant in oil palm plantations (Turner, 2005). Crucially, the buffering abilities of the ferns will be entirely dependent on their specific soil properties (Coyne and Thompson, 2006a), yet these properties are also unknown. This chapter will therefore fill key knowledge gaps regarding the buffering capabilities of bird's nest ferns by answering the following questions: (1) What are the specific hydrothermal soil properties of bird's nest ferns? (2) Do bird's nest ferns buffer temperatures in the high canopy of primary tropical rainforest in the same way as in the low canopy? (3) To what extent do bird's nest ferns buffer physical conditions in degraded habitats such as oil palm plantations? And finally, (4) Can we model the fern's ability to buffer microclimate?

2.2 METHODS

2.2.1 STUDY SITES

Line insertion and canopy access techniques (Ellwood and Foster, 2001, Maher, 2006) were used to access bird's nest ferns in the low (4m) and high (40m) canopy of lowland primary tropical rainforest in the Danum Valley Conservation Area in Sabah, Borneo in April 2018 (refer to Chapter 1 for full site information). Although long term measurements of local climate have been taken at the field centre since 1980, the weather station which obtained these measurements was built adjacent to the field centre. Given the development of our understanding of edge effects on climate in tropical forests (Laurance, 1991, Hardwick et al., 2015), it is likely that these measurements are not entirely representative of forest conditions. Microclimatic conditions in bird's nest ferns in oil palm were recorded on the Sabahmas Oil Palm Estate near Lahad Datu in Sabah, Borneo (5.18º N, 118.41 º E) (full site information will be presented in Chapter 5). Although mean annual climatic data were not available for the plantation, nearby Lahad Datu has a mean annual air temperature of 30.1 ºC, and relative humidity of 78% (Climate-Data.org, 2018). Bird's nest ferns used at the Eden Project in Cornwall, UK (50.36 º N, 4.74 º W) (Chapter 1) had been introduced to the rainforest biome more than a year before the study took place. At each study site, the fern selected for inclusion had a leaf rosette diameter of approximately 60 cm (Ellwood et al., 2002). In all experiments, whether in rainforest, oil palm or at the Eden Project fern size was controlled because thermal buffering is linked to water availability, and water storage capacity is linked to volume (Carter and Gregorich, 2008). Selecting ferns of a similar size therefore controlled for any potential systematic buffering effect based on fern size (Scheffers et al., 2014c).

2.2.2 BIRD'S NEST FERN SOIL PROPERTIES

The biotic and abiotic processes that take place in a soil are linked to its specific properties (Coyne and Thompson, 2006a, Coyne and Thompson, 2006b, Carter and Gregorich, 2008). In order to investigate thermal buffering in bird's nest ferns, it was first necessary to quantify the physical properties underpinning soil-water relations. Mean values for water holding capacity (%), bulk density (g/cm^3), total porosity (%), gravimetric water content (g/g), volumetric water content (cm^3/cm^3), air filled porosity (%) and water filled pore space (%) were determined using a soil sample harvested from five different bird's nest ferns, which were naturally occurring in the low canopy in Danum Valley. By using the values calculated for water holding capacity and bulk density, as well as the estimated biomass of bird's nest fern soils (Ellwood et al., 2002), it was possible to calculate the maximum volume of water (in litres) that bird's nests ferns may store in a hectare of forest canopy.

The masses of each of the five fresh, undisturbed soil samples were recorded to the nearest 0.1 g before being placed in a drying oven at 60 °C, until mass became constant (~3-5 hours) (Carter and Gregorich, 2008). The dry sample mass was recorded (g) and its volume determined through water displacement. To do this, the sample was wrapped in plastic and placed in a container with a known volume of water (Robertson et al., 1999). The volume of displaced water was equal to that of the soil sample. The sample was then fully saturated with water, reweighed, and the saturated mass (g) minus the dry mass, determined the mass of the water held in the soil. And because 1 g of water occupies a volume of 1 cm^3, the mass of the water also provided the volume of water contained in the sample. Water holding capacity

(WHC, %) i.e. the maximum proportion of water that a given soil volume can hold, was determined by dividing the mass of the water by the mass of the saturated sample, and multiplying it by 100. Bulk density (BD, g / cm^3), was calculated as the dry mass divided by the dry volume of the sample (obtained through water displacement). Gravimetric water content (θ_g, g/g or %) i.e. the mass of water that could be added per mass of dry soil, was calculated as the mass of water upon saturation, divided by the dry soil mass and multiplied by 100. Volumetric water content (θ_v, cm^3/cm^3 or %) is the volume of water per volume of dry soil, and was determined by multiplying the gravimetric water content by the bulk density.

Total porosity (TP, %) i.e. the proportion of pore space in a given volume of soil that may be filled with air or water, was calculated using bulk density divided by particle density (taken as 1.1 g/cm^3 because fern soils are high in organic material), multiplied by 100 (Brady and Weil, 2000). Soils with a high percentage total porosity hold more air or water within their pore space (Coyne and Thompson, 2006a). Porosity also defines the maximum possible water or air content, because when all available pore spaces are filled with water or air, the soil is saturated. This is an important metric, because the extent to which soils are filled with air or water influences biological processes such as microbial metabolism and invertebrate movement (Kramer and Boyer, 1995). Air filled porosity (AFP, % or cm^3/cm^3) i.e. the proportion of pore space in the fern soil sample filled with air, was the total porosity minus the volumetric water content. Water filled pore space (%) was the proportion of available pore space filled with water at the time of sampling, and calculated as volumetric water content divided by total porosity, multiplied by 100.

2.2.3 DATA LOGGING

To monitor microclimate in the field, Microclimate Monitoring Systems (MMS) were built incorporating: Em50 data loggers (Decagon Devices Inc. USA) housed in waterproof boxes, 5TM soil temperature sensors (-40.0 to 60.0 ± 0.5 ºC), VP4 simultaneous air temperature (AT) and relative humidity (RH %) sensors (-40.0 to 80.0 ± 0.5 ºC, 0.0 to 100.0 ± 2.0 %), PYR solar radiation sensors (0 to 1750 ± 50 Wm^{-2}), and RT1 radiant heat sensors (-40.0 to 80.0 ± 0.5 ºC). Each MMS supported two VP4s, one to record ambient air temperature (AAT) and relative humidity (ARH %), and one to record air temperature and relative humidity immediately adjacent (AT and RH % <1m) to the fern. I mounted the VP4 sensors onto poles ensuring free airflow, and stabilised them with cable ties. The 5TM soil probes were inserted into the fern soil up to 10cm, burying the entire length of the sensor, thus reducing any influence of external temperatures on the thermocouple (Figure 2.4). Radiant heat sensors, henceforth referred to as black bulbs sensors or simply black bulbs, were designed to incorporate the effect of heat transfer from electromagnetic thermal radiation, as well as convectional heat transfer into temperature readings. Thus, the black bulb sensors provided an indication of heat energy transfer processes in the environment. Air movement is also known to influence water exchange processes (Kramer and Boyer, 1995), therefore anemometers were also installed the forest canopy and oil palm plantation to record wind speed (m/s).

Installation of the MMS into the rainforest high canopy required some modification of typical rope access techniques to accommodate a pulley system (Maher, 2006, Anderson et al., 2015). This made it possible to haul the MMS into the canopy. The MMS remained in the rainforest canopy in Danum Valley for 28 consecutive days (between 14/02/2017 and 14/03/2017), after which they were collected, serviced and transferred to the Sabahmas Oil Palm Estate for a further 23 consecutive days (from 21/03/2017 to 12/04/2017). Data from the Eden Project were collected over 4 days in July 2017 (from 05/07/2017 to 09/07/2017). Prior to statistical analyses, all data, which had been recorded each minute, were converted into mean hourly values for each day over the study period. Finally, a single 24 hour cycle representative of each habitat was established using hourly values of each day of data logging. The maximum and minimum, as well as the range in values for each climatic variable were also calculated providing for each day that the MMS collected data. This provided an indication of just how extreme environmental conditions in each habitat could be.

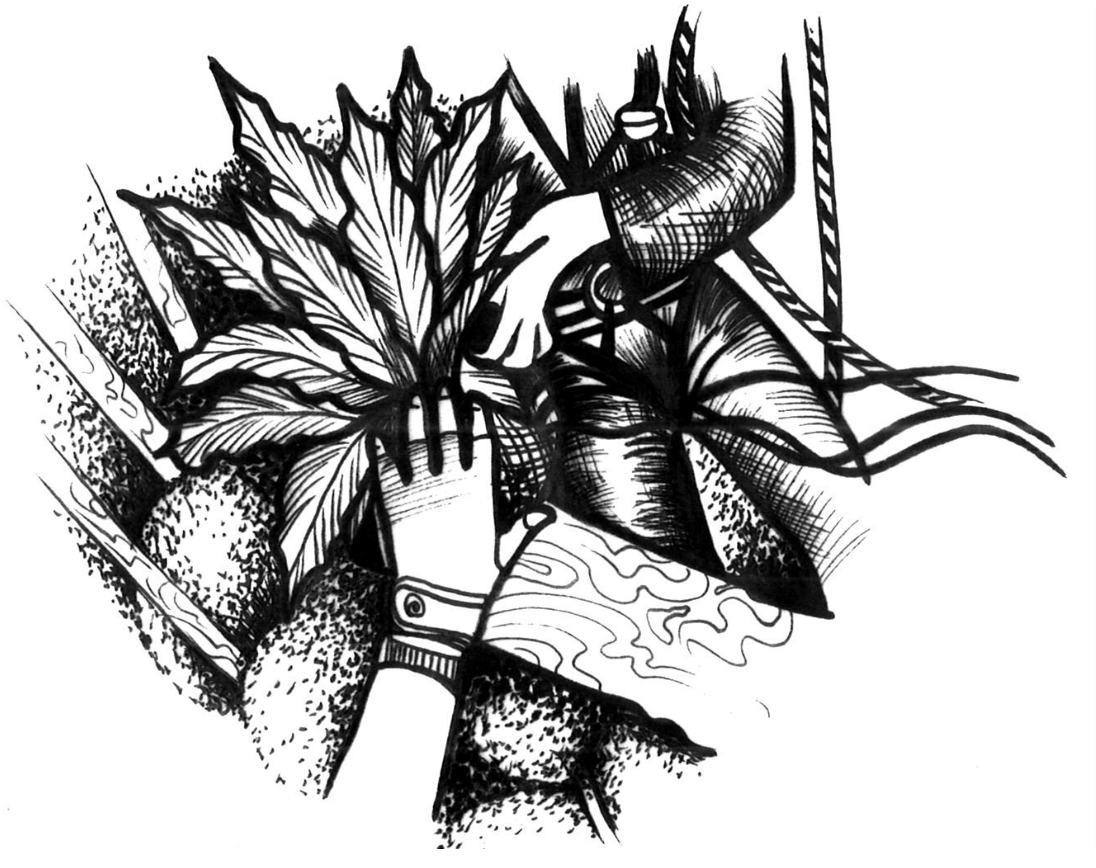


Figure 2.4 The insertion of temperature sensors into a bird's nest fern in the canopy.

2.2.4 STATISTICAL ANALYSES

All data were tested for normality prior to analysis. Non-normal data were normalised using log10 transformations. If upon transformation the data were still not normal, non-parametric statistics were used. Paired *t*-tests were used to analyse percentage mass loss upon drying, and the percentage mass gained upon saturation, to determine whether the fern soil samples were near saturation upon collection. Prior to investigating thermal buffering in the ferns, and whether they influenced their surroundings, differences in ambient conditions between the low canopy, the high canopy, and oil palm were focused on.

Kruskal Wallis (H) tests were used to determine whether differences in (1) ambient relative humidity (ARH%), (2) ambient air temperature (AAT), (3) black bulb (BB) temperature and (4) wind speed over the 24hr cycle occurred between the three habitats. All data values were then separated into day (07:00 – 19:00) and night time (20:00 – 06:00), one way ANOVAs were used to determine whether there were differences in (1) AAT, (2) ARH%, (3) BB temperature, and (4) wind speed between the three habitats by day and night. Additionally, a one way ANOVA was used to determine whether levels of solar radiation differed between the three habitats during the day. Any differences in (1) the range of (AAT_R), maximum (AAT_{MAX}) and minimum (AAT_{MIN}) ambient air temperature, (2) relative humidity ($ARH\%_R$, $ARH\%_{MAX}$ and $ARH\%_{MIN}$), (3) black bulb temperature (BB_R BB_{MAX} and BB_{MIN}) as well as (4) fern soil temperatures (FT_R ,FT_{MAX} and FT_{MIN}) between the habitats were explored using one way ANOVA's.

A Kruskal Wallis test was used to determine whether fern temperature (FT) differed significantly over the 24 hour cycle between the low canopy, the high canopy and oil palm plantation. These values were also separated into day (07:00 – 19:00) and night (20:00 – 06:00), and one way ANOVA's were used to test for differences in FT. General linear models (GLM's) were used to determine whether significant interactions occurred between habitat and recorded climate variables such as (1) FT and AAT's, (2) AAT's and air temperatures less than a metre from the fern (AT < 1m), and (3) ARH% and relative humidity less than a metre from the fern (RH% < 1m).

One way ANOVA's were used to determine whether 'captive ferns' at the Eden Project were able to buffer microclimate, by exploring differences in FT, BB, AAT, AT < 1m and also the temperature of the ground soil (GS). Finally, to determine whether ferns influence the humidity of their immediate surroundings, I used a one-way ANOVA to compare ARH% and RH < 1m away from the captive ferns. All data analyses were carried out using IBM SPSS Statistics Version 25.0.

2.3 RESULTS

2.3.1 BIRD'S NEST FERN SOIL PROPERTIES

Figure 2.5 reveals the mass (in grams) of each bird's nest fern soil sample at the point when it was (1) freshly harvested from ferns in the low canopy i.e. undisturbed, (2) oven dry, and (3) saturated with water. On average, undisturbed soils lost 38.4 ± 6.9g or 27 ± 4.1% of mass as water through drying, and gained 69.1 ± 6g or 40 ± 2.7% of mass as water upon saturation. Undisturbed soils lost significantly less water than dry soils gained (Figure 2.6, $t = 4.15$, df = 4, $p = 0.014$) indicating that undisturbed fern soils were not saturated, therefore not waterlogged upon collection. Table 2-1 reports the mean calculated values for the specific properties of bird's nest fern soils.

Table 2-1 Specific soil property and mean value (± standard error), calculated based on soil analysis of five samples of bird's nest fern soil media ($n = 5$).

Soil Property (Abbrev.)	**Mean Value (± Standard Error)**
Water Holding Capacity (WHC)	40.0 (± 2.7%)
Material Bulk Density (BD)	0.41 (± 0.01 g / cm^3)
Total Porosity (TP)	62.5 (± 1.0%)
Gravimetric Water Content (θ_g)	0.68 (± 0.08 g / g) or 68.1 (± 8%)
Volumetric Water Content (θ_v)	0.28 (± 0.03 cm^3 / cm^3) or 28 (± 3.1%)
Air Filled Porosity (AFP)	34.6 (± 3.1%)
Water Filled Pore Space (WFPS)	44.7 (± 4.9%)

Using the value calculated for water holding capacity (40%), the bulk density of fern soil (0.41 g / cm^3) and the estimated dry mass of soil associated with bird's nest ferns (886 kg ha^{-1}) (Ellwood et al., 2002), it was able to calculate that [1] ~2161000 cm^3 or 2160 litres of soil [volume = mass (886000 g)/ density (0.41 g / cm^3)], and [2] 864 litres of water [volume of water = volume of soil (2160 litres)/ 100 x WHC (40%)], can be held by bird's nest ferns in a hectare of forest canopy. There are 43,000 hectares of rainforest in the Danum Valley Conservation Area (DVCA). This means that the soils associated with bird's nest ferns alone could store as much as 37,152,000 litres of water in the canopy of DVCA (as much water as 15 Olympic sized swimming pools). This estimate does not include water contained within the plant itself nor any debris collected in the leaf basket.

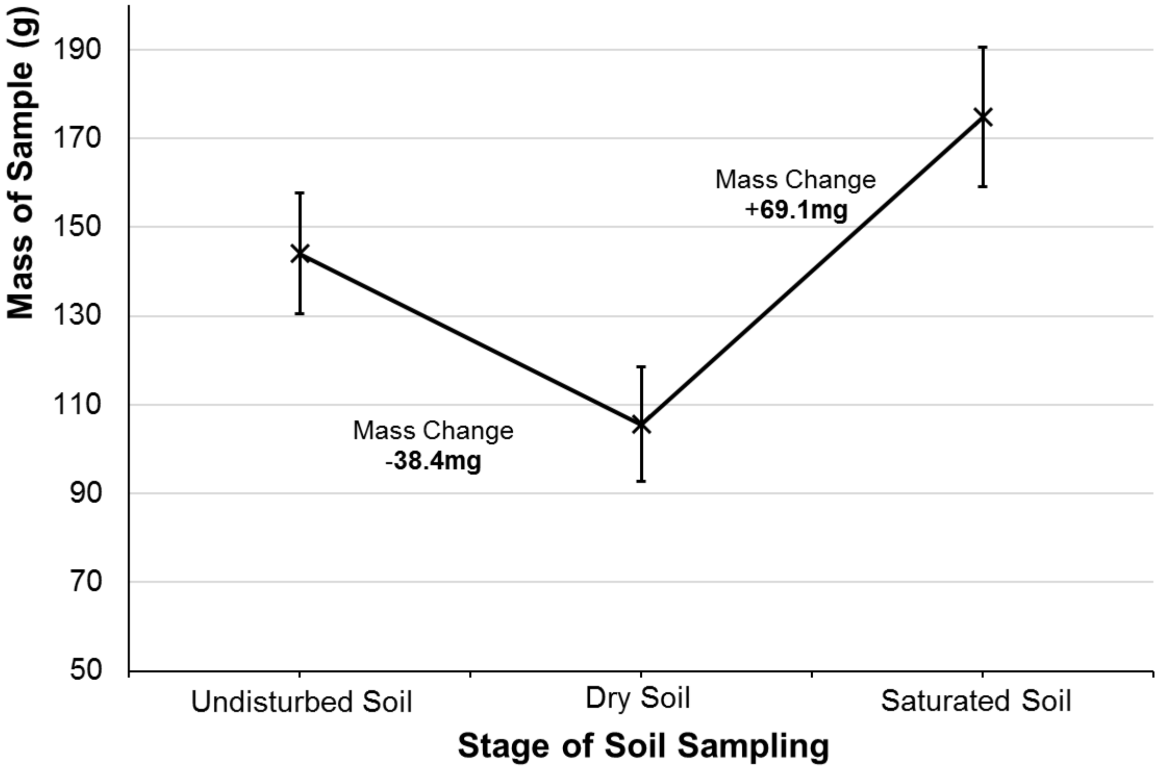


Figure 2.5 The mean mass of fern soil samples (*n* = 5) when recently harvested bird's nest fern soil samples were (1) Undisturbed, (2) Dry and (3) Saturated with water. The mean change in mass of soil sample (through water loss or gain) is also given.

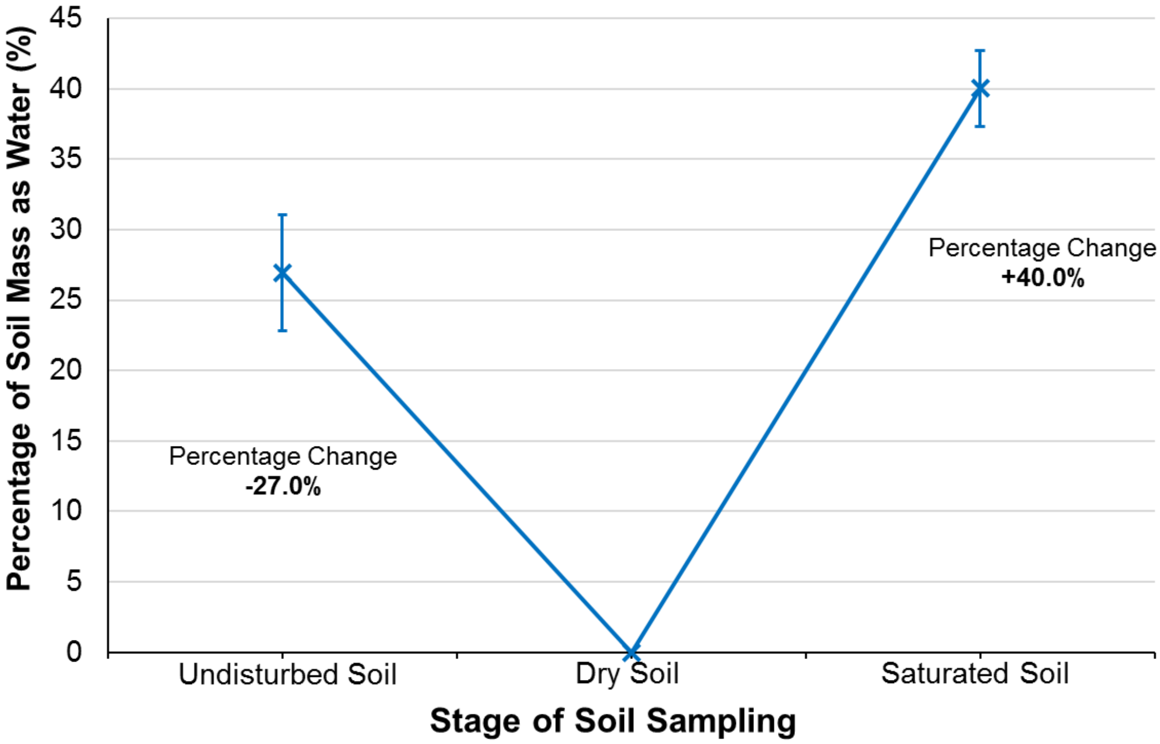


Figure 2.6 The mean calculated percentage of the total mass of recently harvested fern soil samples (*n* = 5) as water when soil samples were (1) Undisturbed, (2) Dry and (3) Saturated with water. The mean change in percentage of soil mass as water is given.

2.3.2 CLIMATIC DIFFERENCES BETWEEN RAINFOREST AND OIL PALM

Figure 2.7 shows the mean fluctuation in ambient air temperature (AAT) and ambient relative humidity (ARH %) in the rainforest low canopy (green), high canopy (yellow) and oil palm (red), over 24 hours based on 28 days of data logging in the rainforest, and 23 days in the oil palm. There were significant differences in ambient conditions between the three habitats, both in AAT's (Kruskal Wallis $H = 13.7$, $p = 0.001$) and in ARH%'s ($H = 36.9$, $p < 0.001$). The oil palm plantation was the hottest (26.6 ± 0.5°C) and driest (83.7 ± 1.2%), followed by the high canopy, which was significantly cooler (24.6 ± 0.4 °C) (Games Howell, $p = 0.02$), but not significantly drier (86.7 ± 1.6%) ($p = 0.304$) than oil palm. AAT's in the high canopy were not significantly different to those in the low canopy ($p = 0.840$), which had the lowest mean temperature (24.3 ± 0.3 °C) and highest ARH% (96.5 ± 0.8%). These results confirmed that the low canopy was the coolest and most humid of the three habitats. Although the high canopy did not differ from the low canopy in terms of temperature, it was significantly drier. Black bulb (BB) temperatures also differed between the habitats ($H = 11.8$, $p = 0.003$, Figure 2.8). While the oil palm BB was significantly hotter (27.6 ± 0.8 °C) than the low canopy (24.5 ± 0.3 °C), it did not significantly differ to the high canopy (25.3 ± 0.5 °C) ($p = 0.059$). Table 2-2 details the mean value over 24 hours, and during the day and night, for each microclimate variable recorded in each habitat using the MMS.

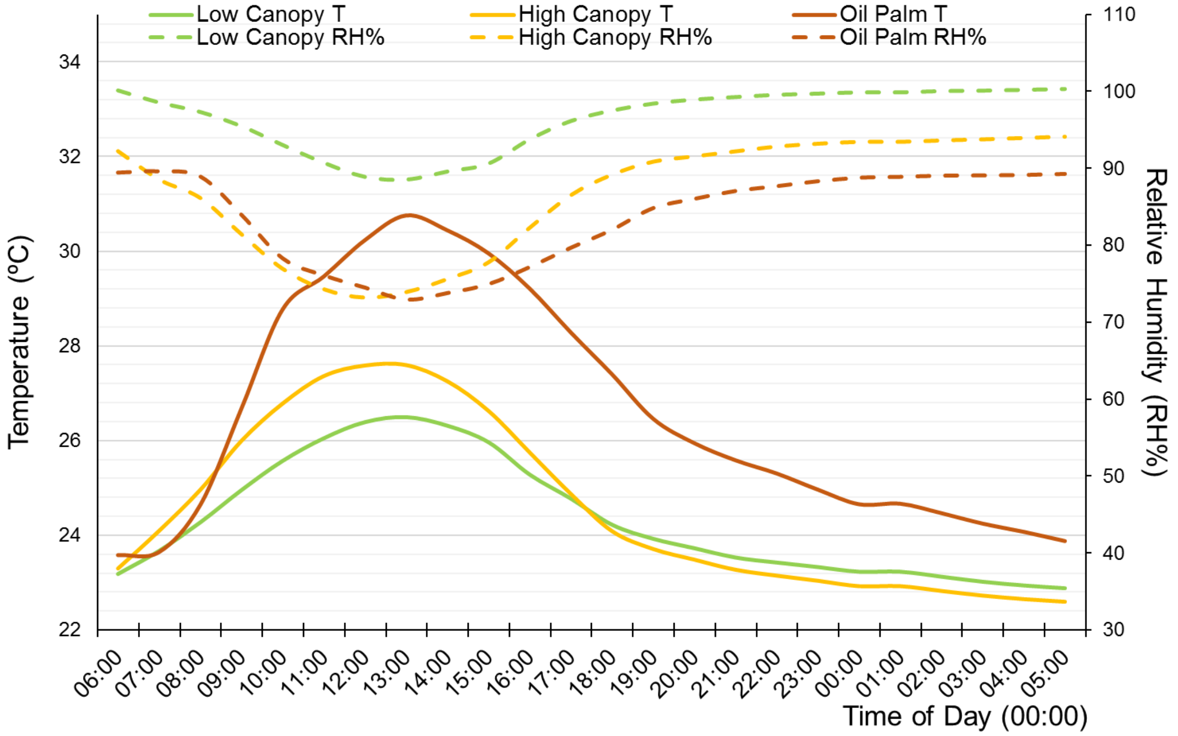


Figure 2.7 Mean hourly fluctuation in temperature (T) and relative humidity (RH %) in the low canopy (green), high canopy (yellow) (both $n = 28$) and oil palm plantation (red) ($n = 23$).

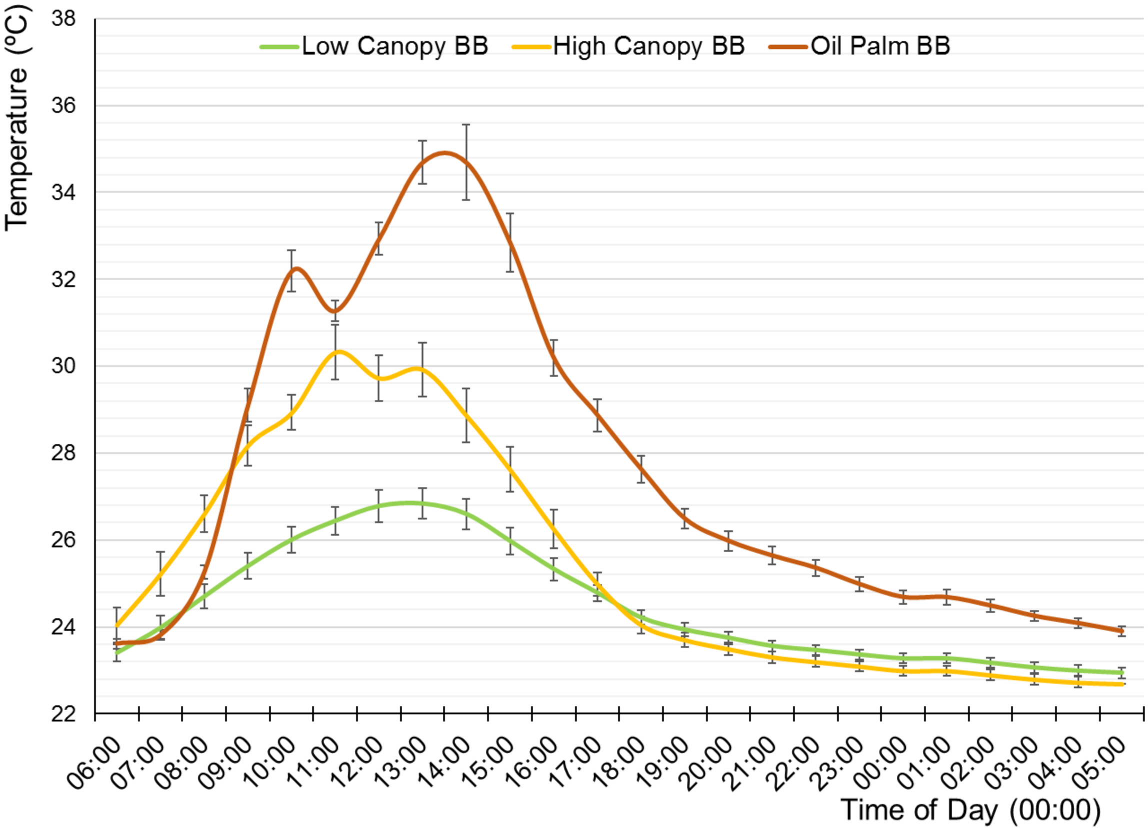


Figure 2.8 Mean hourly fluctuation (with S.E) in black bulb (BB) temperatures (T°C) in the low canopy (green), high canopy (yellow) (both *n* = 28) and oil palm plantation (red) (*n* = 23).

During the day [07:00 – 19:00], AAT in the oil palm plantation (27.9 ± 0.6 °C) was higher than both the low (25.1 ± 0.3 °C) and high canopy (25.7 ± 0.4 °C) (One Way ANOVA, *F* = 11.4 $p < 0.001$). However, AAT's were not significantly different between the low and the high canopy (Tukey HSD $p = 0.608$). ARH% also differed significantly between the three habitats ($F = 26.1$, $p < 0.001$), with the low canopy remaining more humid (94.1 ± 1.0 %) than both the high canopy (82.0 ± 1.8%) and the oil palm (80.2 ± 1.8%). However, ARH% was not significantly different between the high canopy and the oil palm (Tukey HSD $p = 0.663$). BB temperatures were also significantly different between the three habitats during the day ($F = 11.0$, $p < 0.001$), with temperatures highest in the oil palm (30.0 ± 1.0 °C), followed by the high canopy (27.3 ± 0.6 °C) and low canopy (25.4 ± 0.3 °C).

Solar radiation was an order of magnitude lower in the low canopy (15.7 ± 2.6 w/m^2) than both the high canopy (123.9 ± 24.3 w/m^2) and the oil palm (130. 2 ± 31.7 w/m^2) ($F = 7.77$, $p = 0.002$, Figure 2.9). However, solar radiation did not differ significantly between the high canopy and oil palm (Tukey HSD, $p = 0.98$). Average wind speed also differed significantly between the three habitats ($F = 91.9$, $p < 0.001$, Figure 2.10). Again, the low canopy (0.02 ± 0.002 ms^{-1}) received an order of magnitude less wind than the high canopy (0.43 ± 0.04 ms^{-1}). This time, however, there were no significant differences between conditions in the oil palm (0.09 ± 0.009 ms^{-1}) and conditions in the low canopy (Tukey HSD $p = 0.08$).

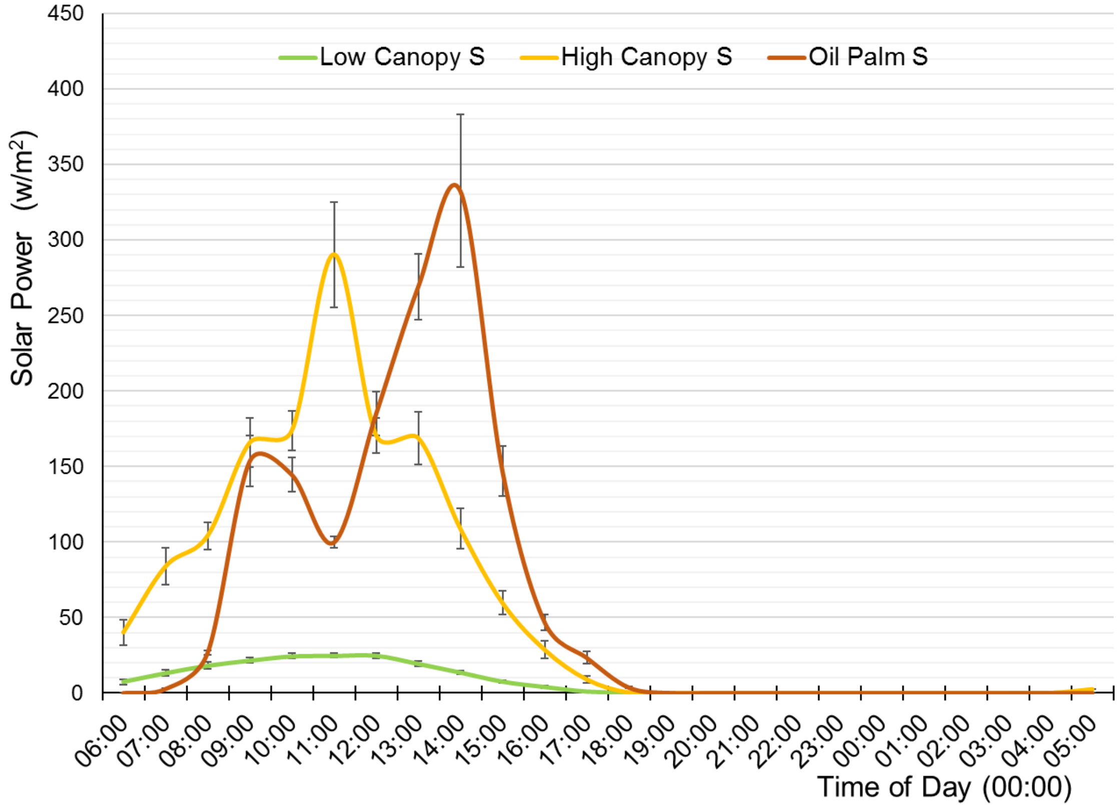


Figure 2.9 Mean hourly fluctuation (with S.E) in solar power (S) in the low canopy (green), thigh canopy (yellow) (both *n* = 28) and in the oil palm plantation (red) (*n* = 23).

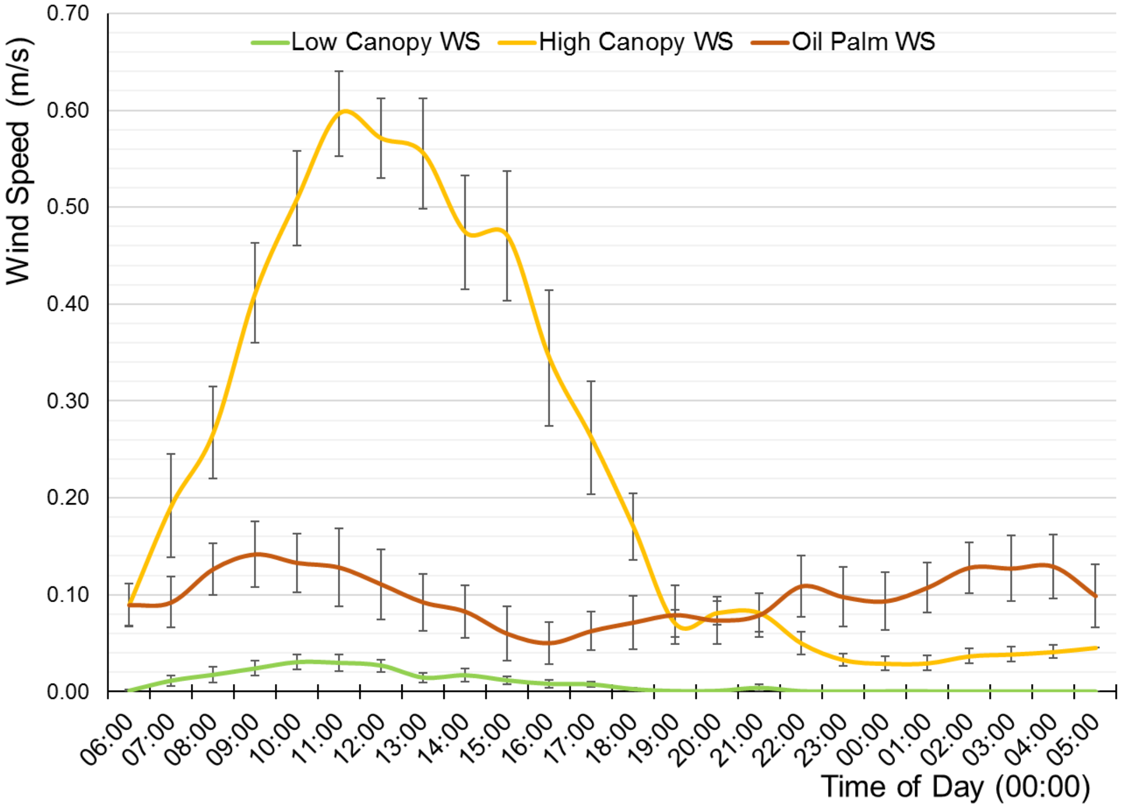


Figure 2.10 Mean hourly fluctuation (with S.E) in wind speed (WS) in the low canopy (green), thigh canopy (yellow) (both *n* = 28) and in the oil palm plantation (red) (*n* = 23).

Table 2-2 The mean with standard error (S.E) of each climate variable recorded by the MMS over a 24 hour cycle, as well as during the day and night. These values are based on 28 days of data logging in the low canopy and the high canopy (both $n = 28$) and 23 days in the oil palm plantation ($n = 23$).

Climate Variable (Abbrev.)	Mean ± S.E								
	24 hour			Day time (07:00 – 19:00)			Overnight (20:00 – 06:00)		
	Low Canopy	High Canopy	Oil Palm	Low Canopy	High Canopy	Oil Palm	Low Canopy	High Canopy	Oil Palm
Ambient air temperature (AAT)(ºC)	24.3 ± 0.3	24.6 ± 0.4	26.6 ± 0.5	25.1 ± 0.3	25.7 ± 0.4	27.9 ± 0.6	23.2 ± 0.1	23.0 ± 0.1	24.7 ± 0.2
Ambient relative humidity (ARH%) (%)	96.5 ± 0.8	86.7 ± 1.6	83.7 ± 1.2	94.1 ± 1.0	82.0 ± 1.8	80.2 ± 1.5	99.8 ± 0.1	93.1 ± 0.3	88.4 ± 0.3
Black Bulb Sensor (BB) (ºC)	24.5 ± 0.3	25.4 ± 0.5	27.6 ± 0.8	25.4 ± 0.3	27.3 ± 0.6	30.0 ± 1.0	23.3 ± 0.1	23.1 ± 0.1	24.7 ± 0.2
Solar Power (w/m^2)	n/a	n/a	n/a	15.7 ± 2.6	123.9 ± 24.3	130 ± 31.7	n/a	n/a	n/a
Wind Speed (ms^{-1})	n/a	n/a	n/a	0.02 ± 0.00	0.43 ± 0.04	0.09 ± 0.01	n/a	n/a	n/a
Air temperature less than 1m from the fern (AT < 1m)	24.4 ± 0.3	24.7 ± 0.4	26.5 ± 0.5	25.4 ± 0.3	26.0 ± 0.4	28.0 ± 0.6	23.3 ± 0.1	23.2 ± 0.1	24.7 ± 0.2
Relative humidity less than 1m from the fern (RH% <1m)	98.7 ± 0.9	94.8 ± 1.6	83.9 ± 1.1	95.7 ± 1.2	89.3 ± 1.8	80.4 ± 1.3	102.3 ± 0.1	101.3 ± 0.2	87.1 ± 0.4
Fern Temperature (FT)	24.2 ± 0.1	24.9 ± 0.2	24.9 ± 0.4	24.5 ± 0.2	25.5 ± 0.3	25.9 ± 0.4	24.0 ± 0.1	24.1 ± 0.2	23.6 ± 0.1

Overnight [20:00 – 06:00] AAT's remained higher in the oil palm (24.7 ± 0.2 °C), than in the low (23.2 ± 0.1 °C) and high canopy (23.0 ± 0.1 °C) ($F = 42.1$, $p < 0.001$), although AAT's in the low and high canopy were not significantly different (Tukey HSD, $p = 0.475$). The oil palm was significantly less humid (88.4 ± 0.3 %) than the low (99.8 ± 1.8 %) and the high canopy (93.1 ± 0.2 %) ($F = 528.2$, $p < 0.001$). Overnight, BB temperatures were also significantly higher in the oil palm (24.7 ± 0.2 °C) than the low (23.3 ± 0.1 °C) and high canopy (23.1 ± 0.1 °C) ($F = 32.3$, $p < 0.001$) with BB temperatures homogeneous between the latter two ($p = 0.628$).

Table 2-3 reveals the mean maximum, minimum and range for each variable recorded by the Microclimate Monitoring Stations (MMS) across the three habitats. AAT_{MAX}, AAT_{MIN} and AAT_{R} differed significantly between the three habitats. AAT_{MAX} (31.0 ± 0.3°C), AAT_{MIN} (23.5 ± 0.1°C) and AAT_{R} (7.4 ± 0.3°C) were all significantly higher in the oil palm than in the high canopy (AAT_{MAX}, 28.2 ± 0.3°C, AAT_{MIN} 22.4 ± 0.1°C and AAT_{R}. 5.8 ± 0.3°C) and the low canopy (AAT_{MAX}, 26.9 ± 0.3°C, AAT_{MIN}, 22.6 ± 0.1°C and AAT_{R}, 4.3 ± 0.4°C) ($\text{AAT}_{\text{MAX},}$ $F = 41.8$, $p < 0.001$, AAT_{MIN}, $F = 24.2$, $p < 0.001$ and AAT_{R}. $F = 25.5$, $p < 0.001$). Although AAT_{MIN}'s in the low and high canopy were not significantly different ($p = 0.378$).

$\text{ARH\%}_{\text{MAX}}$ differed significantly between the habitats ($F = 1189.2$, $p < 0.001$). On average, the $\text{ARH\%}_{\text{MAX}}$ in the low canopy was 100.7% (± 0.2), this was significantly higher than $\text{ARH\%}_{\text{MAX}}$'s in both the high canopy (94.4 ± 0.2%) and the oil palm (89.7 ± 0.1). $\text{ARH\%}_{\text{MIN}}$'s also significantly differed between the three habitats ($F = 38.2$, $p < 0.001$) with $\text{ARH\%}_{\text{MIN}}$ in the low canopy (86.2 ± 1.6%) more than 10% higher than $\text{ARH\%}_{\text{MIN}}$ in the high canopy (70.3 ±1.5%) and the oil palm (71.8 ±1.0%). Although $\text{ARH\%}_{\text{MIN}}$'s were not significantly different between the high canopy and the oil palm ($p = 0.735$). $\text{ARH\%}_{\text{R}}$ differed between the habitats ($F = 13.5$, $p < 0.001$). The high canopy had the highest $\text{ARH\%}_{\text{R}}$ (24.1 ± 1.4%) although, interestingly the range in ARH%'s of the low canopy (14.5 ± 1.5%) and oil palm (17.8 ± 1.0%) were not significantly different ($p = 0.222$). BB_{MAX} temperatures differed significantly between the low canopy (27.4 ± 0.3 °C), high canopy (31.6 ± 0.5 °C) and oil palm (35.9 ± 0.6 °C) ($F = 70.3$, $p < 0.001$). BB_{MIN} was also significantly different between the habitats ($F = 22.4$, $p < 0.001$). BB_{MIN} was highest in the oil palm (23.6 ± 0.1°C), while BB_{MIN}'s in the low (22.7 ± 0.1 °C) and high canopy (22.5 ± 0.1 °C) were not significantly different ($p = 0.213$). BB_{R}'s were also significantly higher in the oil palm (12.3 ± 0.7 °C) than the high (9.1 ± 0.5 °C) and low canopy (4.6 ± 0.3 °C) ($F = 60.0$, $p < 0.001$).

Table 2-3 Mean daily maximum, minimum and range of values with standard error (S.E), of each climate variable recorded by the MMS over 24 hours. These values are based on 28 days of data logging in the low canopy and the high canopy (both *n* = 28) and 23 days in the oil palm plantation (*n* = 23).

Climate Variable (Abbrev.)	Mean Over 24hrs ± S.E								
	Maximum (MAX)			Minimum (MIN)			Range (R)		
	Low Canopy	High Canopy	Oil Palm	Low Canopy	High Canopy	Oil Palm	Low Canopy	High Canopy	Oil Palm
Ambient air temperature (AAT) (ºC)	26.9 ± 0.3	28.2 ± 0.3	31.0 ± 0.3	22.6 ± 0.1	22.4 ± 0.1	23.5 ± 0.1	4.3 ± 0.4	5.8 ± 0.3	7.4 ± 0.3
Ambient relative humidity (ARH%) (%)	100.7 ± 0.2	94.4 ± 0.2	89.7 ± 0.1	86.2 ± 1.6	70.3 ± 1.5	71.3 ± 1.0	14.5 ± 1.5	24.1 ± 1.4	17.8 ± 1.0
Black Bulb Sensor (BB) (ºC)	27.4 ± 0.3	31.5 ± 0.5	35.9 ± 0.6	22.7 ± 0.1	22.4 ± 0.1	23.6 ± 0.1	4.7 ± 0.3	9.1 ± 0.5	12.2 ± 0.7
Fern Temperature (FT) (ºC)	25.2 ± 0.1	28.3 ± 0.3	28.9 ± 0.5	23.3 ± 0.1	22.4 ± 0.1	22.9 ± 0.1	1.9 ± 0.1	5.9 ± 0.2	6.1 ± 0.5

2.3.3 BIRD'S NEST FERNS AS THERMAL BUFFERS

While AAT's significantly differed between the three habitats, fern temperatures (FT), did not significantly differ between the low canopy (24.2 ± 0.1 °C), high canopy (24.9 ± 0.2 °C) and oil palm (24.9 ± 0.4 °C), ($H = 0.778$, $p = 0.678$). The average temperature of the soil core of the bird's nest fern over 24 hours was almost identical in the high canopy and oil palm (to 0.1 of a degree, both 24.9 °C). During the daytime [07:00 – 19:00] there was a significant difference in temperature between the ferns ($F = 5.1$, $p = 0.011$, Figure 2.11). The oil palm fern (25.9 ± 0.4 °C) was significantly warmer than the fern in the low canopy (24.6 ± 0.2 °C) (Tukey HSD $p = 0.01$), although the oil palm fern was not significantly warmer than the high canopy fern (25.9 ± 0.4 °C) ($p = 0.630$). Similarly, the high canopy fern was not significantly warmer than the low canopy fern ($p = 0.086$). Overnight [20:00 – 06:00] FT's did not significantly differ between the three habitats ($F = 3.02$, $p = 0.064$). Although FT's in the oil palm were lower (23.6 ± 0.1 °C) than both the high (24.1 ± 0.1 °C) and low canopy (24.0 ± 0.1 °C).

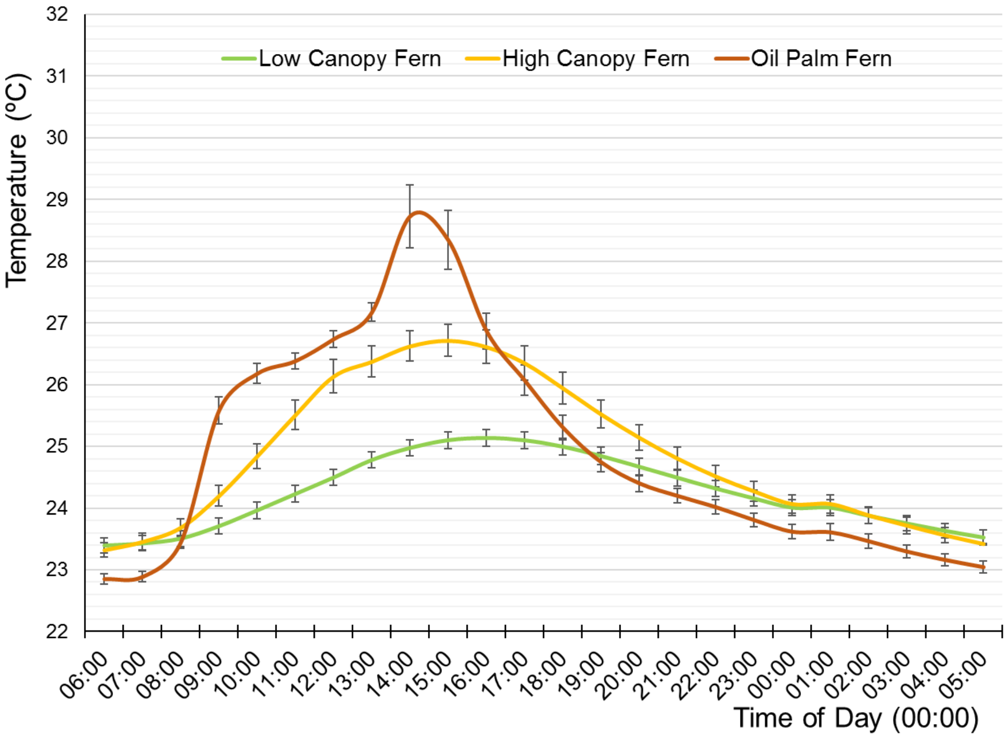


Figure 2.11 Mean hourly fluctuation (with S.E) in temperature of bird's nest fern soils in the low canopy (green), high canopy (yellow) (both $n = 28$) and oil palm plantation (red) ($n = 23$).

While mean FT's did not differ significantly between the habitats over a 24 hour cycle, FT_{MAX}, FT_{MIN} and FT_R all showed significant differences. FT_{MAX}'s were significantly higher in the oil palm (28.9 ± 0.5 °C), than the low (25.2 ± 0.1°C) and the high canopy (28.3 ± 0.3 °C) ($F = 38.5$ $p < 0.001$). However, FT_{MAX} was not significantly different in the high canopy and in the oil palm plantation (Tukey $p = 0.413$). FT_{MIN} also differed significantly between the habitats

($F = 14.33$ $p < 0.001$), with significantly lower temperatures recorded in the oil palm fern (22.9 ± 0.1 °C) than the low canopy fern (23.3 ± 0.1 °C) ($p < 0.001$). However, FT_{MIN}'s in the low and in the high canopy (22.4 ± 0.1 °C) did not significantly differ ($p = 0.07$), neither did FT's in the high canopy, and in the oil palm ($p = 0.23$). FT_R's also differed between the three habitats ($F = 60.2$, $p < 0.001$), with the lowest FT_R in the low canopy (1.9 ± 0.1 °C). FT_R's in the oil palm (6.1 ± 0.5 °C) and high canopy (5.9 ± 0.2 °C) did not differ ($p = 0.945$).

Figure 2.12 illustrates the significant two-way interaction between AAT's and FT's over 24 hours across the three habitats (General Linear Model (GLM) $F = 4.87$, df = 2, $p = 0.009$). The ferns in the oil palm plantation clearly buffered microclimate to the extent that FT's in oil palm were not significantly different to FT's in both the high ($p = 0.970$) and the low canopy ($p = 0.175$), as well as AAT's in the high ($p = 0.430$) and low canopy ($p = 0.204$). The interaction between habitat and climate variable was also significant during the day ($F = 3.70$, df = 2, $p = 0.03$, Figure 2.13) with AAT's in the oil palm plantation being significantly higher (Tukey $p < 0.001$) than all other recorded variables. AAT's and FT's were otherwise homogeneous during the day. FT's in the low canopy were significantly lower than FT's in the oil palm ($p = 0.032$). Figure 2.14 reveals the significant interaction between habitat, AAT's and FT's overnight ($F = 3.70$, df = 2, $p < 0.001$). Overnight FT's did not significantly differ between the habitats, although interestingly temperatures were lowest in the oil palm fern.

While bird's nest ferns significantly buffered their own temperatures, they did not appear to influence air temperatures in their immediate vicinity over the 24 hour cycle. Figure 2.15 shows that there were no significant diurnal interactions between habitat, AAT and AT < 1 m ($F = 0.05$, df = 2, $p = 0.95$). Similarly, there were no significant interactions by day ($F = 0.09$, df = 2, $p = 0.91$, Figure 2.16) or night ($F = 0.08$, df = 2, $p = 0.92$, Figure 2.17). Although the fern did not influence AT's < 1 m, they did appear to affect relative humidity, with a significant interaction between ARH%'s and RH%'s < 1 m over 24 hours ($F = 5.08$, df = 2, $p = 0.007$, Figure 2.18). By day the significant interaction ($F = 3.58$, df = 2, $p = 0.033$, Figure 2.19) was driven largely by the difference between RH% < 1 m and ARH% in the high canopy (Tukey $p = 0.004$). ARH% in the high canopy was not significantly different to either ARH% ($p = 0.918$) or RH% < 1 m ($p = 0.987$) in the oil palm. In the oil palm, ARH%'s and RH%'s <1 m were equally low ($p = 0.99$). Finally, there was no significant difference in ARH% and RH% <1 m in the low canopy because relative humidities remained high ($p = 0.37$). Overnight, the interaction between habitat, ARH% and RH% < 1 m was highly significant ($F = 78.95$, df = 2, $p < 0.001$, Figure 2.20). In fact, the only non-significant difference occurred between ARH% in the low canopy and RH% < 1 m in the high canopy (Tukey $p = 0.34$), all other interactions were highly significant ($p < 0.001$).

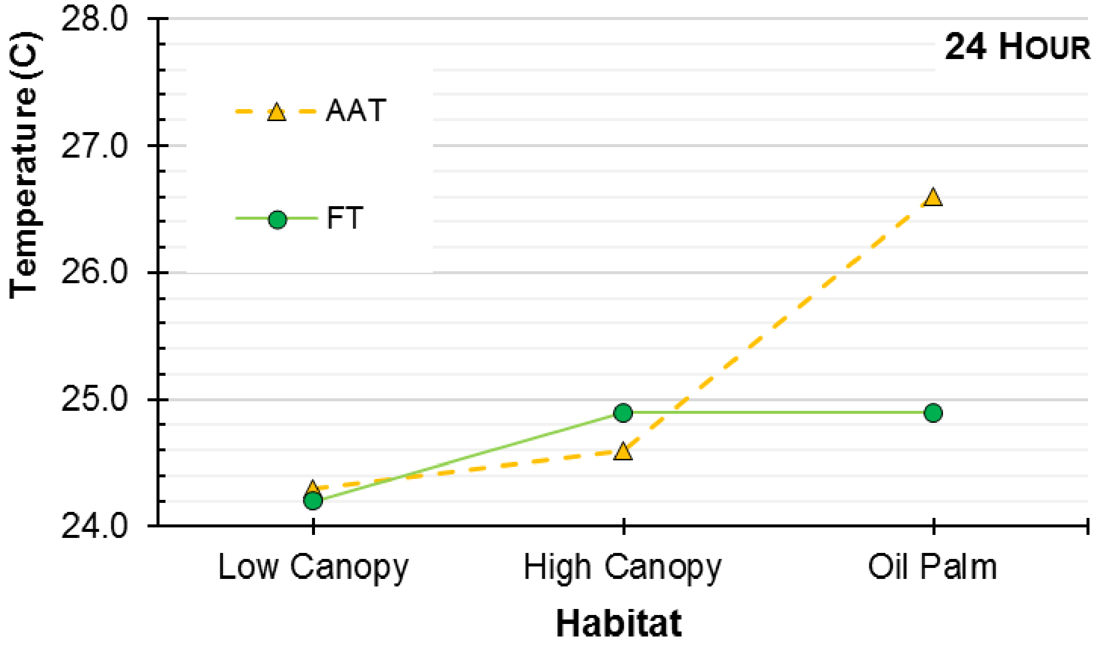


Figure 2.12 Interaction between fern temperature (FT) and ambient air temperature (AAT) over 24 hours in the low canopy, high canopy and oil palm ($p = 0.009$).

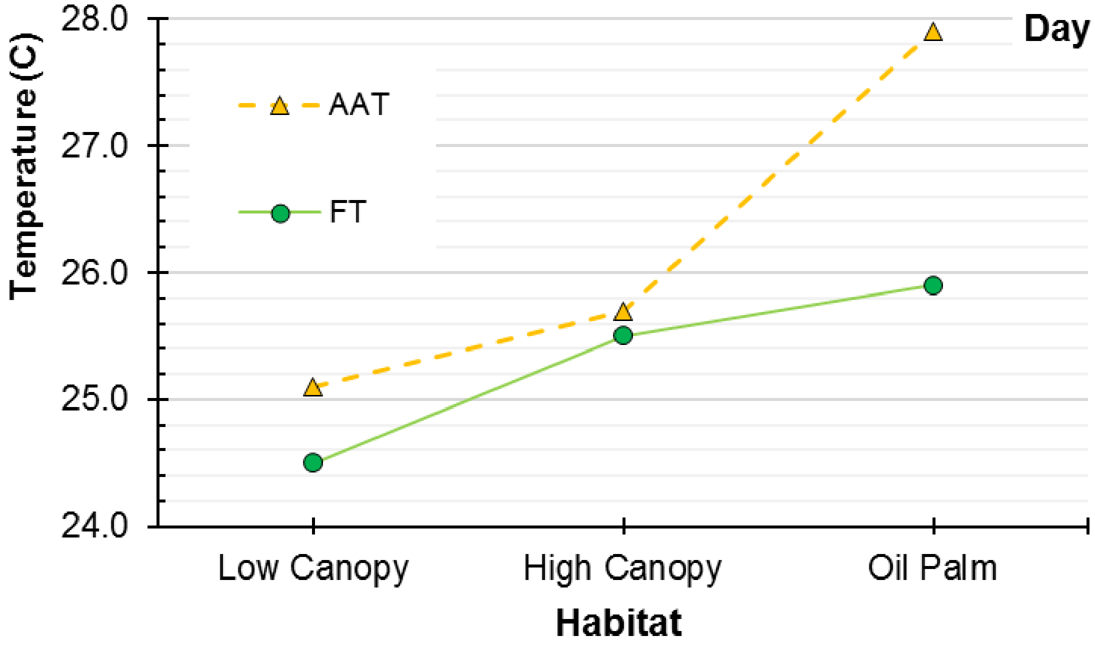


Figure 2.13 Interaction between daytime fern temperature (FT) and ambient air temperature (AAT) in the low canopy, high canopy and oil palm ($p = 0.03$).

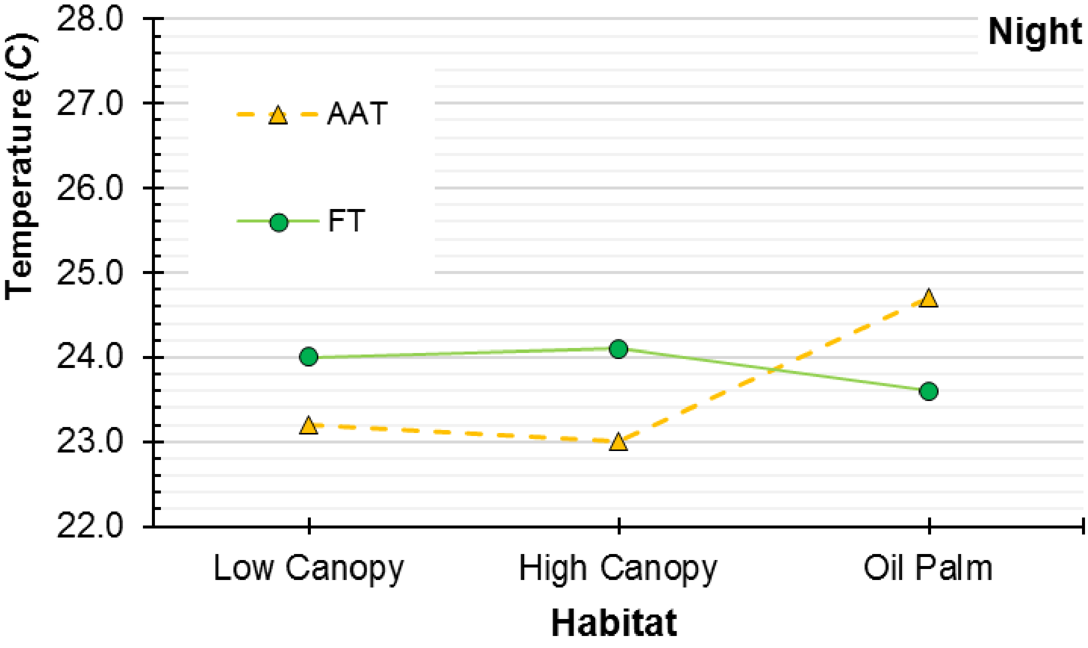


Figure 2.14 Interaction between night time fern temperature (FT) and ambient air temperature (AAT) in the low canopy, high canopy and oil palm ($p < 0.001$).

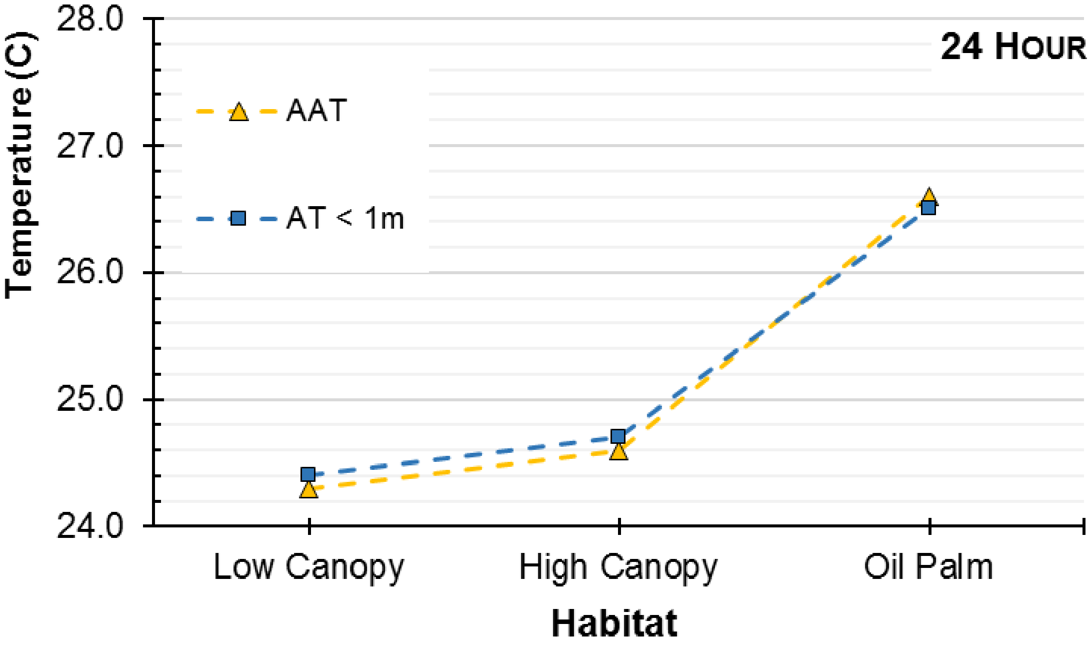


Figure 2.15 Interaction between air temperature less than 1m from the fern (AT < 1m) and ambient air temperature (AAT) over 24 hours in the low canopy, high canopy and oil palm ($p = 0.95$).

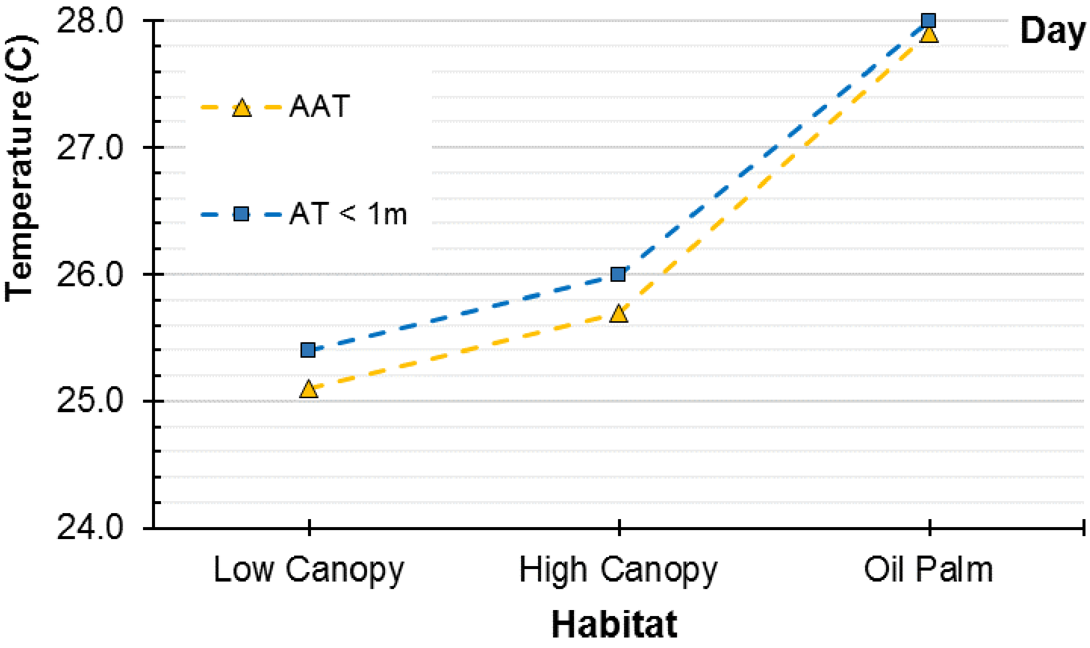


Figure 2.16 Interaction between daytime air temperature less than 1m from the fern (AT < 1m) and ambient air temperature (AAT) in the low canopy, high canopy and oil palm (p = 0.91).

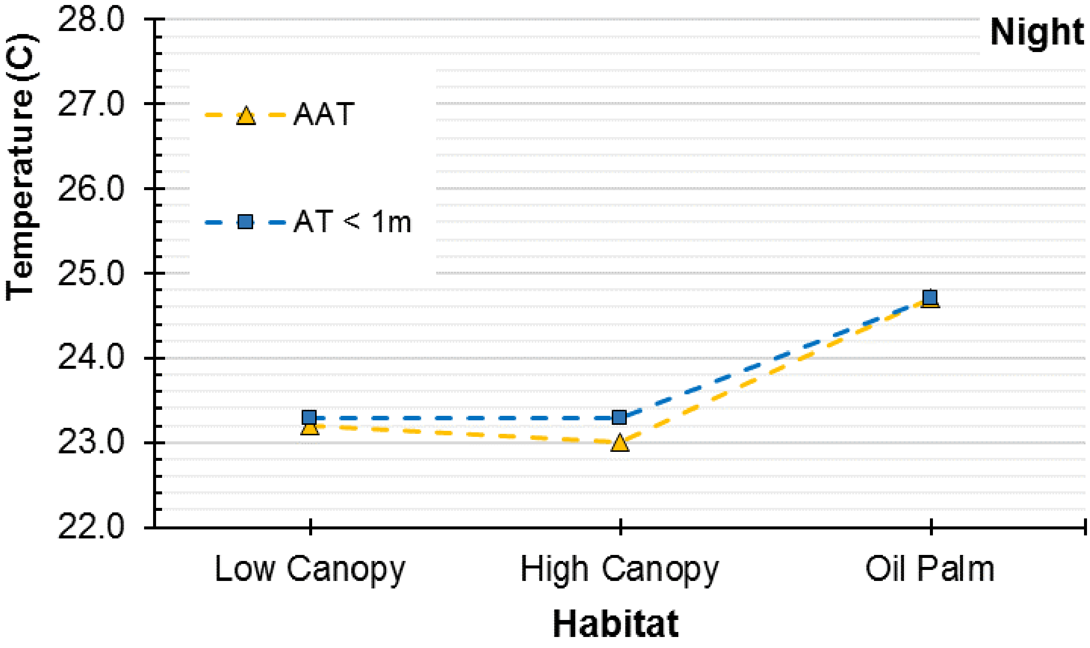


Figure 2.17 Interaction between night-time air temperature less than 1m from the fern (AT < 1m) and ambient air temperature (AAT) in the low canopy, high canopy and oil palm (p = 0.92).

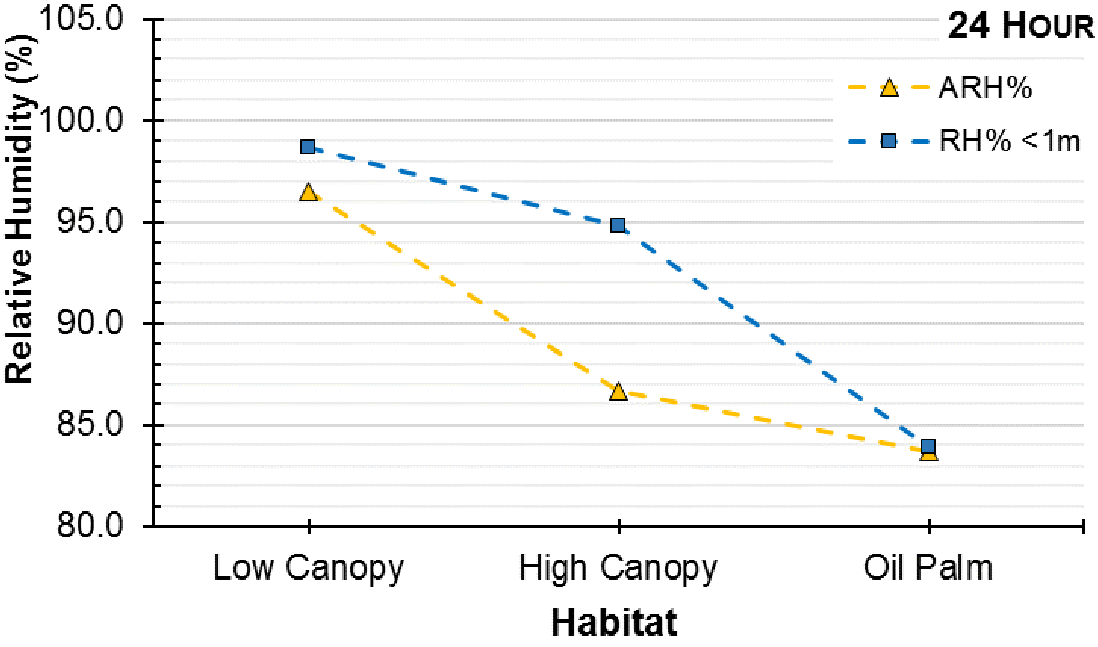


Figure 2.18 Interaction between relative humidity less than 1m from the fern (RH% < 1m) and ambient relative humidity (ARH %) over 24 hours in the low canopy, high canopy and oil palm (*p* = 0.007).

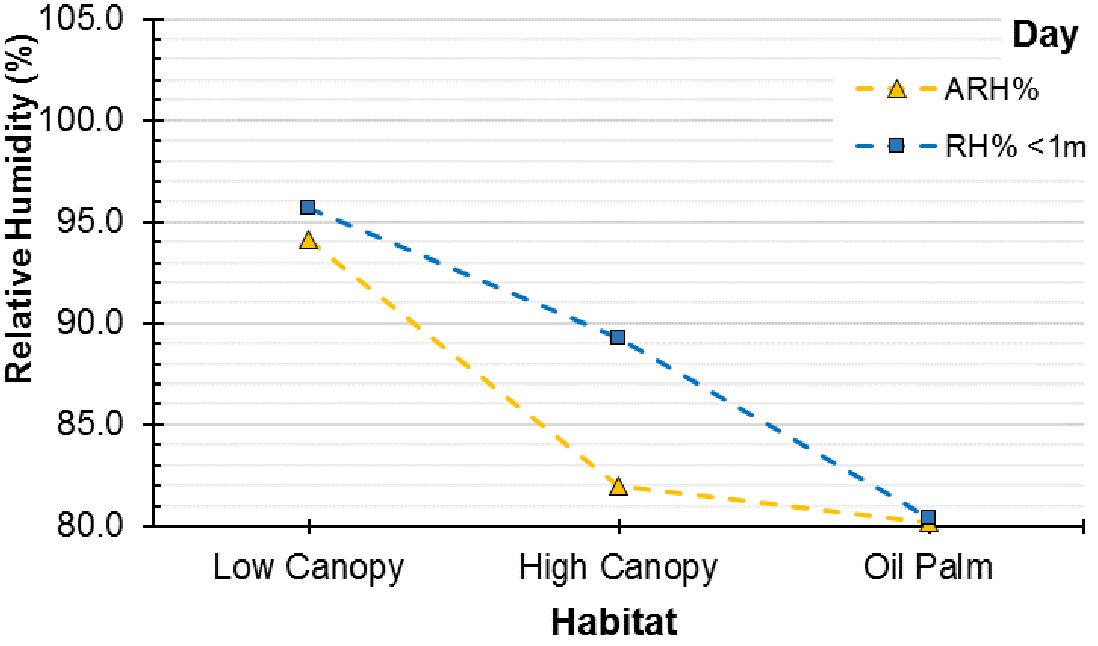


Figure 2.19 Interaction between daytime relative humidity less than 1m from the fern (RH% < 1m) and ambient relative humidity (ARH %) in the low canopy, high canopy and oil palm (*p* = 0.033).

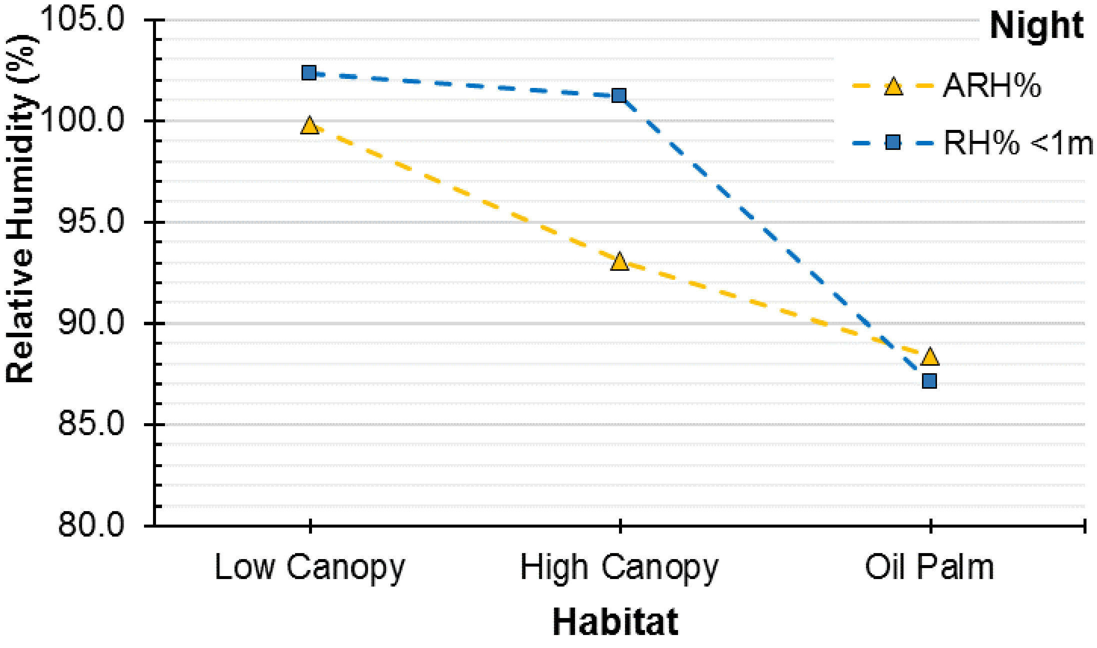


Figure 2.20 Interaction between night-time relative humidity less than 1m from the fern (RH% < 1m) and ambient relative humidity (ARH %) in the low canopy, high canopy and oil palm ($p = 0.004$).

2.3.4 MODEL BIRD'S NEST FERNS AT THE EDEN PROJECT

Figure 2.21 illustrates the diurnal temperature regime of the FT, AAT, AT <1m, BB and ground soil (GS) in the rainforest biome of the Eden Project. FT's were the lowest (25.1 ± 0.7 ºC), followed by AT's < 1m (25.7 ± 0.7 ºC), AAT's (26.6 ± 0.9 ºC), BB's (27.5 ± 1.3 ºC) and GS's (28.7 ± 1.2 ºC) over the 24 hour cycle, although these differences were not significant (Kruskal Wallis $H = 6.72$, $p = 0.152$). However, there was a significant difference in the range of temperatures recorded from the variables ($F = 5.2$, $p = 0.005$), with AT's < 1m (9.9 ± 1.0 ºC) showing the lowest range in temperatures, followed by FT's (10.2 ± 1.1 ºC), AAT's (12 ± 1.2 ºC), GS's (14.8 ± 1.9 ºC) and BB's (18.3 ± 2.0 ºC).

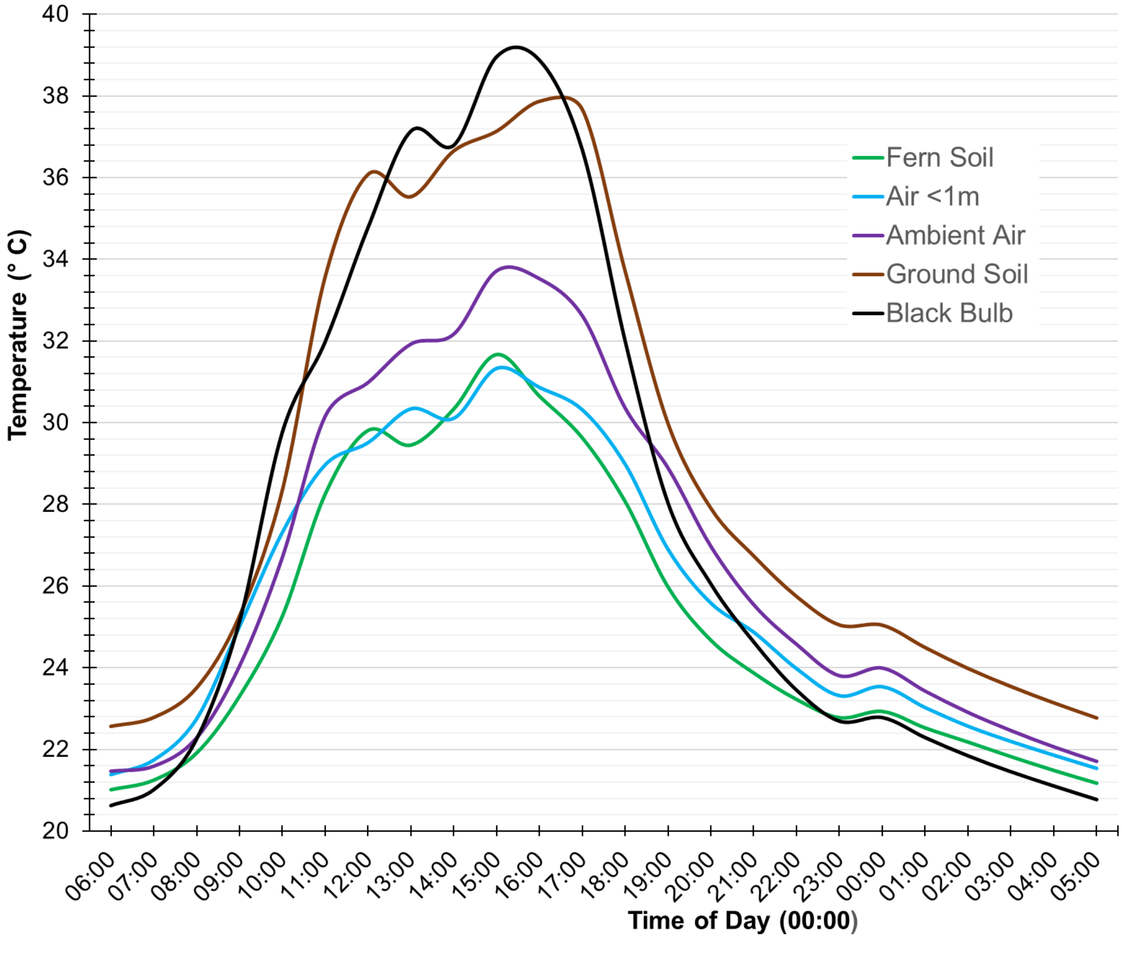


Figure 2.21 Mean hourly fluctuation over four days ($n = 4$) of temperature in fern soil (FT, green), air temperature less than 1m from the fern (Air < 1m, blue), ambient air temperature (AAT, purple), ground soil (GS, brown) and black bulb sensor (BB, black) at the Eden Project.

By day FT's, AT's < 1m away, AAT's, GS and BB temperatures were significantly different (One Way ANOVA $F = 2.95$, $p = 0.026$). FT's remained significantly cooler (27.1 ± 0.9 ºC), than AAT's (29.0 ± 1.1 ºC), BB (31.4 ± 1.6 ºC) and GS (31.9 ± 1.5 ºC). AT's < 1m (27.8 ± 0.8 ºC) and FT's were not significantly different (Tukey $p = 0.289$) providing evidence of the ferns buffering effect. Similarly, AT < 1m was significantly lower than GS ($p = 0.023$), BB ($p = 0.034$) and AAT ($p = 0.049$). Overnight, significant difference still occurred ($F = 5.12$ $p = 0.02$) with GS remaining significantly warmer (24. 3 ± 0.4 ºC), than AT <1m (22.8 ± 0.3 ºC), FT (22.3 ± 0.3 ºC), AAT (22.3 ± 0.4 ºC) and BB (22.2 ± 0.4 ºC). However, temperatures were less variable overnight, relative to the daytime, FT's were not significantly different to AT's <1m (Tukey $p = 0.693$), AAT's ($p = 0.289$) or BB temperatures ($p = 0.057$). The greatest difference overnight existed between GS and BB ($p < 0.001$), although through the hottest part of the day (12:00 – 17:00) these temperature regimes were fairly similar (Figure 2.21). Figure 2.22 highlights the mean difference in temperature between the bird's nest fern soil and each of the other microclimate variables recorded over four days ($H = 24.9$, $p < 0.001$).

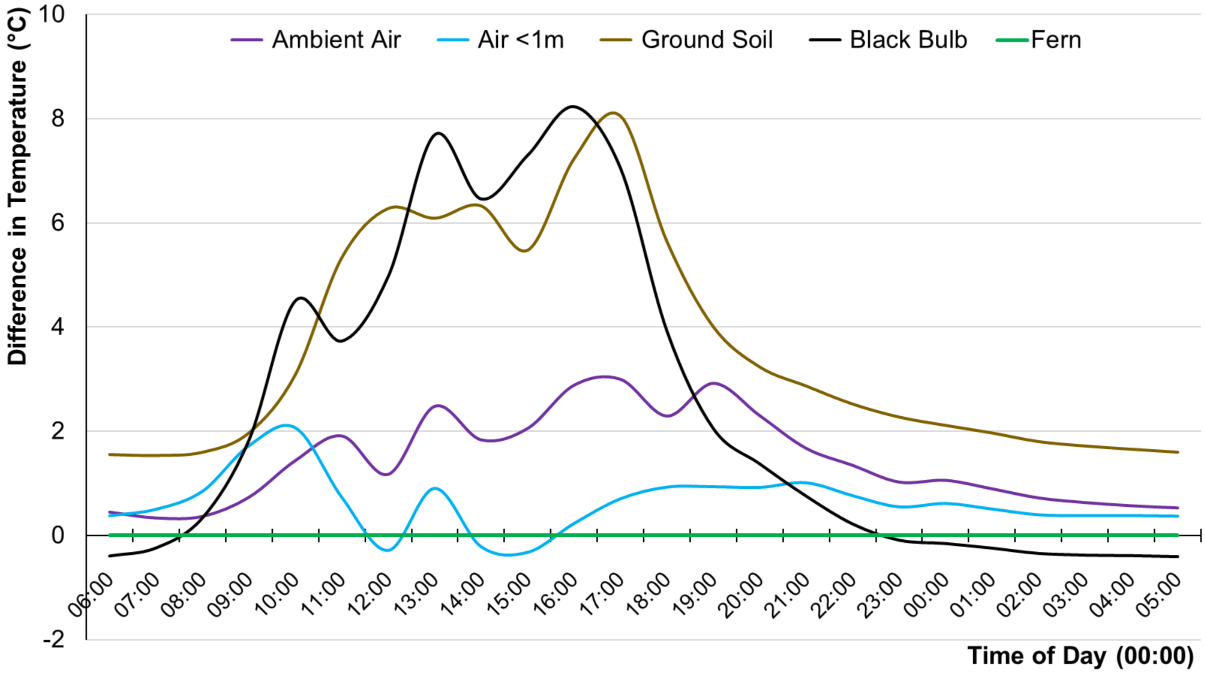


Figure 2.22 Mean hourly temperature difference between fern soils (green) and (1) ambient air (AAT, purple), (2) air less than 1m from the fern (Air < 1m, blue), (3) ground soil (GS, brown) and (4) black bulb (BB, black) over four days ($n = 4$). Positive values illustrate that media was warmer than the fern, negative values denote that media was cooler than the fern soil.

Figure 2.23 highlights the relationship between (1) AAT and ARH% (2) AT<1m and RH% <1m and (3) FT over the 24 hour cycle. During the day, RH% <1m away was higher (61.6 ± 8.7%) than ARH% (58.8 ± 9.5%), although the difference between the two was not significant ($H = 0.57$, $p = 0.45$). The same was true overnight ($H = 1.6$, $p = 0.21$), although again RH% <1m was higher (83.4 ± 3.1%) than ARH% (81.7 ± 2.7%).

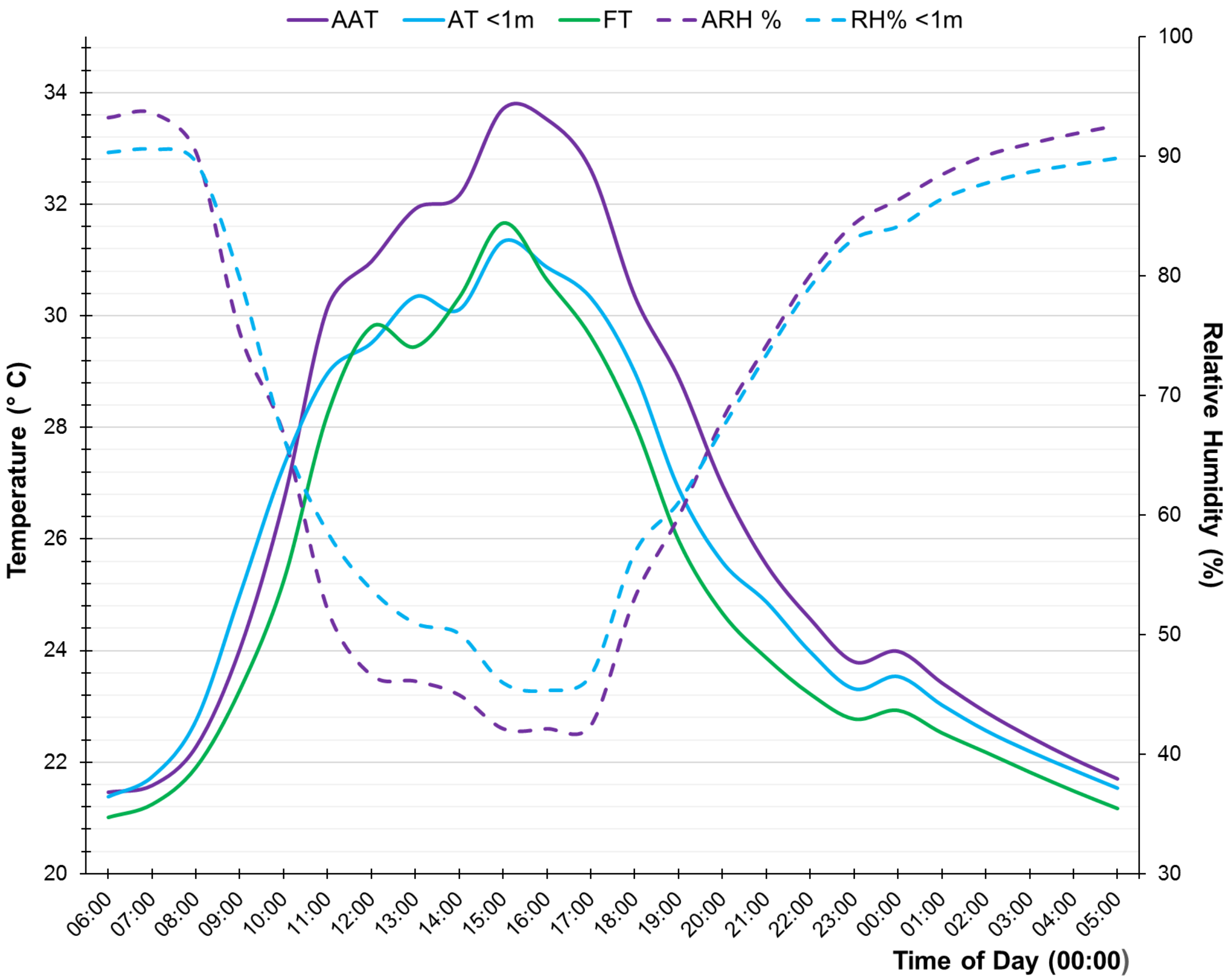


Figure 2.23 Mean hourly fluctuation in (1) ambient air temperature (AAT, purple line), (2) air temperature less than 1m from the fern (AT <1m, blue line), (3) fern temperature (green line), (4) ambient relative humidity (ARH %, purple dash line) and (5) relative humidity less than 1m from the fern (RH% <1m, blue dash line).

2.4 DISCUSSION

Previous studies of bird's nest ferns and microclimate (Turner and Foster, 2006, Scheffers et al., 2014c, Freiberg and Turton, 2007) have neglected the role that the suspended soils associated with the ferns play in thermal buffering. This chapter represents the first investigation of the climatic regimes of bird's nest fern soils, revealing the extent to which ferns mitigate climate extremes in both natural and disturbed habitats. Additionally quantifying the specific hydro-thermal properties which underpin the buffering capabilities of the ferns, and determining the significance of the ferns in above ground water capture. This chapter has taken important steps towards fulfilling our understanding of the role of bird's nest ferns as (1) climate contingent refuges for animals, and (2) water capture systems. While the former evidences the importance of the ferns in biodiversity maintenance, the latter delivers a quantifiable numeric value for the fern's role in ecosystem function.

The results reveal that despite significant differences in the macroclimate between oil palm, the high canopy, and the low canopy, temperatures in the soil core of bird's nest ferns did not differ significantly across the habitats. Consistent with other studies (Foster et al., 2011, Hardwick et al., 2015), the oil palm plantation was hottest (26.6 ± 0.5 °C) with low humidities (83.7 ± 1.2%). On average, the plantation was 2.3 °C hotter than the rainforest low canopy, but by 13:00 (the hottest part of the day) that temperature difference rose to 4.3 °C. Although the maximum recorded temperature differences between the forest and oil palm was still 2.1°C lower than those which have been reported by other studies (Hardwick et al., 2015). The low canopy itself is thermally buffered, with consistently low ambient air temperatures (24.3 ± 0.3 °C) and high humidity (96.5 ± 0.8%). Ambient air temperatures increased somewhat through the vertical dimension, although the average increase of 0.3 °C in air temperatures in the high canopy (24.6 ± 0.4 °C) was not statistically significant. This temperature difference increased to 1.1 °C at the hottest part of the day, but while air in the high canopy is constantly in flux, air becomes trapped in the low canopy, and is warmed through solar heating. This leads to the homogenisation of air temperatures in the high and low canopy (Dial et al., 2006).

The range of ambient air temperatures recorded in the high canopy (22.4 °C - 28.2 °C) overlapped with those recorded in the oil palm plantation (23.5 °C - 31.0 °C). On average, however, temperatures in the high canopy (24.6 ± 0.4 °C) were 2 °C lower than the oil palm plantation, increasing to 3.1 °C at the hottest part of the day. Despite temperature differences between the two habitats, with relative humidities of 83.7 ± 1.2% in the oil palm, and 86.7 ± 1.6% in the high canopy, the 3% difference in humidity was not significant between the two habitats. The oil palm plantation and the high canopy showed greater variation in both temperature and humidity than the low canopy, which over 24 hours had the lowest fluctuation in both temperature (4.3 °C) and in relative humidity (14.5%). The oil palm plantation showed greater temperature fluctuation (7.4 °C) than the high canopy (5.8 °C). However, the high canopy fluctuated in relative humidity (24.1%) to a greater extent than the oil palm plantation (17.8%). While it was unsurprising to record such extreme climatic variation in the oil palm plantation (Luskin and Potts, 2011, Foster et al., 2011), it was somewhat unexpected to observe such large fluctuations in the forest high canopy. Although previous studies have shown that conditions become increasingly variable in the forest canopy as height increases (Dial et al., 2006, Hardwick et al., 2015), no study has examined climatic conditions over 20m, in the highest reaches of the forest.

The rainforest canopy is a high-energy environment, characterised by solar powered turbulence. During the day, solar radiation levels in the rainforest high canopy (123.9 ± 24.3 w/m^2) were an order of magnitude greater than the low canopy (15.7 ± 2.6 w/m^2). As solar radiation penetrates the canopy, it heats the air and any surfaces it encounters; these surfaces absorb and in turn release heat. The black bulb sensors were designed to provide an indication of these unseen heat exchange processes (Moran et al., 2001). On average, the black bulb temperatures were 1.9 °C warmer in the high canopy (27.3 ± 0.6 °C) than those in the low canopy (25.4 ± 0.6 °C), although at the hottest part of the day this difference increased to 3.5°C. The greater extent of heat exchange processes at the top of the canopy, as indicated by the black bulb sensor, would cause turbulence. Indeed, the high canopy was characterised by a greater degree of air movement, as revealed by average wind speeds (0.43 ± 0.04 m/s) which were 20 times higher than in the low canopy. In fact, there was very little air movement in the low canopy (0.02 ± 0.002 m/s). Wind speed and air movement relate directly to humidity (Ephrath et al., 1996). Air movement ensures that the air is constantly mixing, preventing the build-up of humidity, which would explain the greater degree of variability in relative humidity in the high canopy. By comparison, the little air movement occurring in the low canopy provides only a fraction of the mixing, and consequently relative humidity remains consistently high.

With the exception of the black bulb sensor, many of the climatic conditions recorded in the highest reaches of the rainforest canopy were quite similar to those recorded in the oil palm plantation. On average in the oil palm, the black bulb sensor (30.0 ± 1.0 °C) was 2.7 °C hotter than in the high canopy, and 4.6 °C hotter than the low canopy. However, at the hottest part of the day, the difference in temperature increased to 7.9 °C between the oil palm and the low canopy, and 4.4 °C between the oil palm and the high canopy. In oil palm plantations the height of the canopy is greatly reduced, and much of the ground is exposed soil. Levels of solar radiation were highest in the oil palm plantation (130.2 ± 31.7 w/m^2) and as such a higher proportion of sunlight is able to heat the surface of the exposed ground soil. This would in turn lead to greater heat exchange transfer between the bare ground and the air, thus explaining the greater degree of warming of the black bulb sensor in the oil palm plantation. While wind speed was higher on average in the oil palm (0.09 ± 0.01 m/s) compared with the low canopy, there was relatively little air movement, which probably resulted in hot air build up from reduced air flux.

At the hottest part of the day, the ferns buffered external air temperatures by 3.6 °C in the oil palm, 2.0 °C in the high canopy, and 1.2 °C in the low canopy. Although bird's nest ferns are known to buffer climatic conditions (Turner and Foster, 2006, Scheffers et al., 2013), the extent to which the suspended soils associated with the ferns buffered microclimate was surprising. The fact that fern temperatures were not significantly different between the three habitats, to the extent that the high canopy and oil palm ferns were both 24.9 °C, was unexpected. Ambient air temperatures in the oil palm plantation were 2.3 °C hotter than the high canopy, yet on average the fern soil was just 0.7 °C warmer than the low canopy ferns at 24.2 °C. The ferns were far more climatically stable than their respective habitats. They showed less fluctuation in their temperature regime over 24 hours than their respective habitats, with a range in fern soil temperatures of 6.1 °C, 5.8 °C and 1.8 °C compared with a range in ambient air temperatures of 7.4 °C, 5.9 °C and 4.3 °C in the oil palm, high canopy and low canopy, respectively. The mean maximum temperatures reached by the low canopy fern (25.2 °C) were however still more than 3 °C lower those of the high canopy (28.3 °C) and oil palm (28.9 °C) fern. Most likely this was a symptom of the lower ambient air temperatures in the low canopy, and the fact that the low canopy environment was less energetic. As such, conditions in the low canopy were less challenging than those presented in the high canopy and the oil palm plantation. This means that those ferns in the low canopy did not need to buffer microclimate to the same extent as those in the high canopy and the oil palm plantation, and consequently the ferns temperature regimes were far less variable.

In addition to the thermal buffering within the fern soils, this study revealed that the ferns were also capable of influencing climatic conditions in their vicinity. Previous studies have shown that epiphytes influence conditions in the surrounding canopy (Freiberg, 2001, Stuntz et al., 2002), and that areas of forest which supported ferns were more humid than those without (Turner and Foster, 2006). However, the ferns used in this study were of a much smaller size than ferns used in previous studies (Turner and Foster, 2006, Freiberg and Turton, 2007, Scheffers et al., 2013, Scheffers et al., 2014c). In the study by Freiberg and Turton (2007), the *Asplenium* fern studied had a leaf bowl diameter of around 2m, almost an order of magnitude larger than the ferns used in this study. For the ferns, size is related to thermal buffering (Scheffers et al., 2014c), with larger ferns better able to buffer microclimate. This is probably because size determines volume of soil, and the volume of soil determines the volume of water that a fern is capable of storing. Certainly, we would expect large ferns to buffer microclimate more efficiently, and therefore to influence their surroundings to a greater extent. More than half of the ferns in a hectare of forest are of an intermediate size (Ellwood et al., 2002), meaning that intermediate-sized ferns represent a large proportion of the microhabitat space available for animals in the canopy. I therefore felt that studying intermediate sized ferns was appropriate, given that they represent a substantial portion of the fern population.

Air temperatures less than a metre (AT's < 1m) from the fern were not significantly lower than ambient air temperatures (AAT's) in this study. This means that the ferns used in this study had no statistically significant influence on air temperatures in their vicinity. Indeed, there was no temperature difference between AT < 1m from the fern, and ambient air temperatures in the high canopy (both 27.6 °C) at 13:00. However, at 13:00 in the low canopy AT's <1m from the fern were 0.1 °C lower than AAT's, and in the oil palm this difference rose to 0.6 °C. It seems that despite a non-significant difference in temperature between the two, the ferns did influence temperature in their vicinity to some extent. However, it is perhaps unsurprising that AT's <1m from the ferns are only fractionally lower than ambient air temperatures. The buffering capabilities of the ferns are dependent on hydrothermal processes, and latent heat of evaporation in particular. Water stored in the fern soil core is heated as a result of heat exchange with the environment, and heat energy is dissipated from the fern as water is vaporised. On this basis, an important indication of the fern's buffering capabilities is the effect on humidity of the air in proximity to the fern. In this study, we observed a significant difference in relative humidity less than a metre from the fern and ambient relative humidity in the environment. At 13:00, when ambient air temperatures were at their highest, we would expect the fern to be dissipating heat energy in the form of latent heat to the greatest extent. Indeed, in the high canopy there was a difference of 12.6% in relative humidity between ambient relative humidity and that of the air less than a metre away from the fern. Although it was not to such an impressive extent as in the high canopy, we also observed differences in relative humidity in the oil palm (3.7%) and in the low canopy (3.6%). Interestingly, in the oil palm overnight, ambient relative humidity was marginally higher than that of the air less than a metre from the fern. This inversion can be explained by the fact that the oil palm plantation was much drier than the rainforest, and the ferns are epiphytic, meaning that they actively absorb moisture from the air. Given that conditions in oil palm plantation would be more energetically expensive during the day, oil palm ferns will have greater water requirements and so may actively absorb water from the air overnight.

Bird's nest ferns at the Eden Project also significantly buffered microclimate in the same way as their wild counterparts in Borneo. On average, the fern was 1.5 °C cooler than ambient air temperatures, 2.4 °C cooler than the black bulb sensor, and 3.6 °C cooler than ground soil temperatures. However, at the hottest part of the day, which was 15:00 at the Eden Project, temperature differences increased to 2.0°C, 7.3°C and 5.4°C respectively. Environmental conditions at the Eden Project were somewhat more variable than in Borneo, which was unsurprising given that the rainforest biome is an anthropogenically established and enclosed environment. Fern temperatures were also more variable at the Eden Project compared with Borneo, with a mean 24 hour cycle temperature variation of 10.5 °C in the fern soils, and up to 12 °C in ambient air temperatures. However, the range of ambient air temperatures in the biome (21.7 °C – 33.7 °C) was not beyond those experienced by the ferns across the Bornean habitats. As in Borneo, air temperatures less than a meter from the fern were lower than ambient air temperatures, although at the Eden Project, these differences were significant.

During the day, air temperatures less than a metre from the fern were on average 1.2 °C cooler than ambient air temperatures, but this difference rose to 2.4 °C at 15:00.

At the Eden Project, the ambient relative humidity of the air (58.8%) was lower than that of the air less than a metre from the fern (61.6%), although in contrast with Borneo the difference was not significant. Ambient relative humidity at the Eden Project was far more variable than any of the Bornean habitats, with an ambient diurnal fluctuation of 49.5%, although similarly to Borneo, at the hottest part of the day (15:00) the air less than a metre from the fern was 3.8% more humid than ambient conditions. As in the oil palm plantation, at the Eden Project a similar inversion of humidity was observed overnight as the air less than a metre from the fern became less humid than ambient conditions. Again, this is suggestive that the ferns absorb moisture from the air overnight to compensate for any potential deficits that arise through the daytime buffering regime.

This investigation of the soil properties of bird's nest ferns provided the first quantitative measure of the ferns contribution to above ground water storage in the rainforest canopy. This study revealed that the soils associated with bird's nest ferns have a naturally high water holding capacity (WHC, 40%). This places the fern soil media between a clay (39.1%) and a loam soil (42.5%) (Paul, 2014), and this is important because soils which have higher water holding capacities are less likely to lose nutrients through leaching (Walczak et al., 2002). This means that the ferns are not only well adapted to hold water in above ground forest strata, but that they are adapted to retain nutrients for slow release from the forest canopy. The fact that the fern soil media also has a naturally high total porosity (62.5%) suggests that even when the fern becomes fully saturated with water, it will never become waterlogged and anaerobic. This would be critically important for the fern's faunal inhabitants for several reasons. Firstly, it means that heavy rainfall would not necessitate evacuation of the fern by the inhabitants, which would be important if animals were nesting in the ferns (Chapter 4) and secondly, it means the soils will never become anaerobic, a critically important feature for the aerobic bacteria driving decomposition (Sommers et al., 1981) and again, for the animals residing in the ferns.

Generally, soils with high water holding capacity also have high organic matter content (Walczak et al., 2002). The ferns likely have a high organic matter content, given that they are assimilated through the decomposition of humus collected in their leaf basket (Turner et al., 2007, Donald et al., 2017a). Further evidence that the fern soils will be high in organic matter stems from their low bulk density ($0.41 g/cm^3$), which is quite similar to that of a peat soil (Walczak et al., 2002). Soils which are high in organic matter represent critically important carbon storage systems (Brown and Lugo, 1982), and given that the ferns are essentially aerial compost heaps (Fayle et al., 2008), they likely contribute to carbon sequestering in forest canopies. However, to date there has been no consideration for the role of bird's nest ferns in carbon cycling in forest canopies. Given the impressive contribution of the ferns to above ground water storage (~865 L ha^{-1}), it is highly likely that the role of the ferns in other major cycling systems in the rainforest have also been grossly underestimated.

Although this study did not include organic matter content analysis for the fern soils, it can be assumed that the ferns have a high organic matter because they are largely made of humus. Organic matter content analysis will enable specific heat capacity to be calculated for the fern soils (Abu-Hamdeh and Reeder, 2000), i.e. the amount of energy required to raise temperatures in the fern by one degree. This will be the next step towards fulfilling our understanding of the hydrothermal dynamics of bird's nest ferns, and will allow us to parameterise a microclimate model capable of predicting the internal temperatures of the fern under climate change scenarios. While this study has shown that bird's nest ferns can climatically buffer against the conversion of rainforest to oil palm plantation, it is now imperative that we determine the extent to which the ferns can mitigate the effects of climate change and protect sensitive fauna. Therefore the importance of a model that can predict the ability of bird's nest ferns in thermal buffering against the effects of climate change for sensitive species cannot be overstated.

To determine the soil properties of bird's nest ferns, samples of bird's nest fern soils were obtained from easily accessible low canopy ferns. This was to ensure that fern soils were as fresh as possible for processing in the lab. However, it is possible that suspended soil properties show vertical stratification through the forest canopy. Low canopy ferns have a reduced need to buffer microclimate, and as such they may have reduced water holding capacity compared with high canopy and oil palm ferns. Ferns from harsher environments would require more water for thermoregulation, necessitating a greater water storage capacity. Indeed, when bird's nest ferns were subjected to water stress in greenhouse experiments, the ferns focused growing efforts on root, rather than shoot development (Ainuddin and Najwa, 2009). This would likely give rise to altered soil-root properties. Ferns of similar leaf diameter also tend to have greater biomasses in plantations compared with forest ferns (Turner, 2005), this would support the notion that ferns put more effort into assimilating their root-soil complex under harsh conditions. An increase in soil biomass may result in increased water storage. This would suggest that bird's nest ferns in plantations and the high canopy would be even better at storing water, and their contribution to above ground water storage would increase. Given their ability to capture and store water in above the ground, the ferns are likely an underappreciated flood defence. As flooding is a major concern in oil palm plantations (Turner et al., 2008), actively increasing the density of ferns in plantations may provide a degree of natural flood mitigation.

2.5 SUMMARY

- The suspended soils associated with bird's nest fern have a high water holding capacity (40%), low bulk density (0.41g/cm^3) and high total porosity (62.5%). These physical properties are biologically significant and indicate that fern soils would never become waterlogged or anaerobic.
- Based on the ferns' specific soil properties and biomass in the forest canopy, I calculated that the bird's nest fern store ~865L of water per hectare of forest canopy.
- The ferns regulate their temperatures by dissipating heat energy to their environment through latent heat, this was evident because relative humidities were higher in proximity to ferns.
- Bird's nest ferns in oil palm plantations buffer microclimate to such an extent that animals residing in oil palm ferns would experience similar temperatures as those in ferns in primary rainforest, consequently the ferns should be considered a critically important microhabitat in oil palm plantations.
- Captive ferns at the Eden Project also buffered microclimate. This suggests that we can model the evolutionary adaptations of ferns to thermoregulate in order to predict their role in thermal mitigation under climate change.

3 THE POTENTIAL OF INSECT CHITIN IN STABLE ISOTOPE ECOLOGY

CONTEXT

Stable isotopes were first applied to ecological studies in the 1970s, and since then their applications have grown extensively. From enabling scientists to disentangle deep ocean food webs, track animal migrations across continents, and trace ocean pollutants back to their source, as our understanding of naturally abundant isotopes in the environment has improved, so too have the impact and opportunities for stable isotope ecology. The multidisciplinary nature of this field means that as scientists continue to pioneer new applications, the isotopic toolbox continues to expand. This chapter considers an isotopic application which has tremendous potential for studying the ecology and behaviour of arthropods, but has yet to receive the attention it deserves. That is the use of oxygen isotopes in arthropod exoskeletons to define their habitat preferences and physiological tolerances. Just two studies have shown that the isotopic signature of oxygen in the chitinous exoskeletons of insects is derived from respiratory vapour exchange with the atmosphere. When an arthropod moults, this atmospheric signature is fixed into the animal’s new exoskeleton. Despite their functional significance, and the fact that invertebrates account for nearly 90% of global biodiversity, the majority of stable isotope studies have focused on large animals such as elephants or whales. As is so often the case, invertebrates have been largely neglected in this scientific field. Today, invertebrate populations are suffering in the face of anthropogenic disturbance and climate change. A marker of abiotic tolerance in invertebrates could provide the urgently needed metric for those trying to predict the fate of these populations under future change. In this chapter, the relationship between climatic conditions and insect isotopic signatures is quantified, using cockroaches, an ecologically important and widespread group of insects.

3.1 INTRODUCTION

3.1.1 STABLE ISOTOPES AND OXYGEN

While some isotopes are radioactive, stable isotopes are not. These naturally occurring species of given elements have different numbers of neutrons contained within their nuclei. This gives rise to slight differences in their mass numbers compared with those species typically displayed on the periodic table (Peterson and Fry, 1987). Indeed, most elements of biological interest have stable isotopes, including hydrogen (^{1}H, ^{2}H), carbon (^{12}C, ^{13}C), nitrogen (^{14}N, ^{15}N) and oxygen (^{16}O, ^{17}O and ^{18}O). In the past few decades, it has become a major focus of research to describe the relative ratios of these isotopes in various geochemical and biological processes (Rundel et al., 2012). The isotopic composition of a given sample is measured as a ratio of stable isotopes relative to the common species, and typically expressed using the delta notation (δ) (Peterson and Fry, 1987). Fractionation, caused by various biological and chemical processes, leads to variation in the ratio of isotopes present (Gat, 1984). When liquid water becomes vapour, isotopic fractionation occurs, because water molecules contain different ratios of stable isotopes of oxygen (H_2O^{18}/ H_2O^{16}). As a result, water molecules have different vapour pressures proportional to their masses (Dansgaard, 1964). Because of their slight mass differences, these different molecules of water evaporate and condense at different rates. As water evaporates the lighter molecules, which contain isotopes of ^{16}O rather than the heavier ^{18}O, require less energy to change phase, and so do so more rapidly than the heavier molecules containing ^{18}O (Figure 3.1). Consequently, liquid water is left with a higher proportion of ^{18}O (in H_2O molecules) relative to the lighter ^{16}O (in H_2O molecules). The liquid water that remains is said to be enriched with ^{18}O, while atmospheric water vapour is comparatively depleted in ^{18}O (because it contains relatively more ^{16}O). However, the exchange of water vapour between the surface of a body of water and the atmosphere is bidirectional, and this controls the extent of ^{18}O enrichment in the liquid water. The Craig-Gordon (C-G) model defines the ^{18}O isotopic composition ($\delta^{18}O$) of a water body as a function of temperature and relative humidity (RH) (Craig and Gordon, 1965).

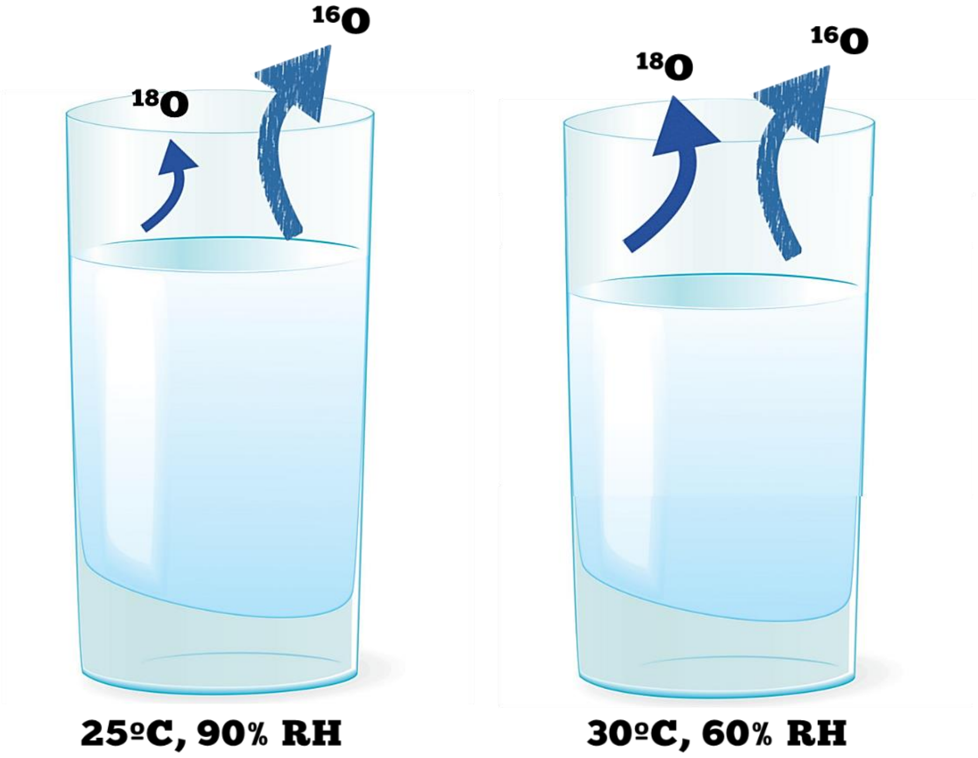


Figure 3.1 Model illustrating the evaporation of lighter water molecules from a body of water under less energetic conditions, and the relative increase in evaporation of the heavier water molecules as environmental conditions become hotter and more energetic.

The majority of stable isotope studies have shown that the isotopic composition of oxygen and hydrogen in plant and animal tissues correlate with that of the precipitation from the environment in which they live and grow (Vander Zanden et al., 2016). However, the isotopic ratios of oxygen ($\delta^{18}O$) from insect tissues respond specifically to the atmospheric conditions under which an animal has lived (Ellwood et al., 2011). The isotopic composition of rainwater itself is dependent on temperature, and this means that independent of biological processes, the isotopic composition of organisms have unique isotopic signatures reflecting the precipitation in a given location (Rundel et al., 2012). Studies have shown that it can be difficult to determine the provenance of the ^{18}O isotopic composition of some samples, because signatures may also be derived from metabolic food processes, or CO_2 (Post, 2002, Rundel et al., 2012). However, $\delta^{18}O$ in insect chitin reflects atmospheric water vapour and not that of the precipitation taken into the insect as drinking water (Ellwood et al., 2011). As such, the $\delta^{18}O$ signature of chitin provides a precise physiological marker of the climatic conditions under which all insects and other tracheated arthropods (e.g. centipedes, millipedes, spiders) have lived (Ellwood et al., 2011, van Bergen et al., 2016).

3.1.2 INSECTS AND THERMAL TOLERANCE

All insects and other tracheated arthropods, such as centipedes (Chapter 4), respire through spiracles, which are the faunal equivalent of plant stomata (Figure 3.2). As with stomata, the major function of spiracles is to facilitate the diffusion of oxygen and carbon dioxide into and out of the organism during respiration, while regulating the exchange of water vapour between the organism and the atmosphere (Schimpf et al., 2009). Desiccation is the major risk for terrestrial invertebrates, which explains why populations show a strong response to moisture gradients (Dial et al., 2006). In harsh environments, such as the rainforest high canopy, or in oil palm plantations (Chapter 2), there is a serious risk of death by desiccation.

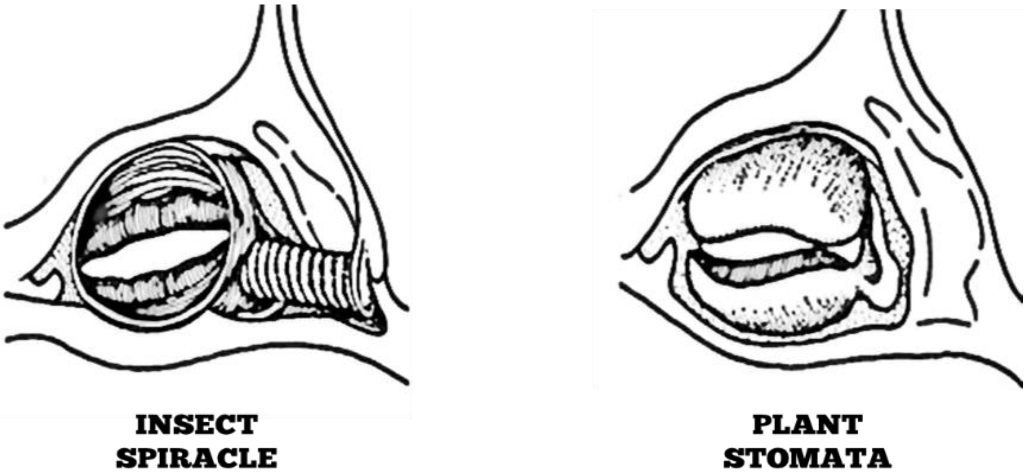


Figure 3.2 Visual comparison of an insect spiracle and plant stomata.

Insect haemolymph (blood) gives a real-time indication of the environmental conditions under which the animal is living (Ellwood et al., 2011) (Figure 3.3). However, the ^{18}O isotopic composition of the chitin ($C_8H_{13}O_5N$), which composes the insect's exoskeleton, correlates with the mean humidity of the environment under which the animal was living when it established its exoskeleton (Ellwood et al., 2011, van Bergen et al., 2016). In order to grow, an insect must moult and replace its chitinous exoskeleton, with a larger one (Schimmelmann, 2011). At this point, the ^{18}O isotopic signature of the insect's haemolymph is transferred to the chitin of the new exoskeleton (Ellwood et al., 2011), where it becomes fixed, and does not change until the next moult (Schimmelmann and DeNiro, 1986).

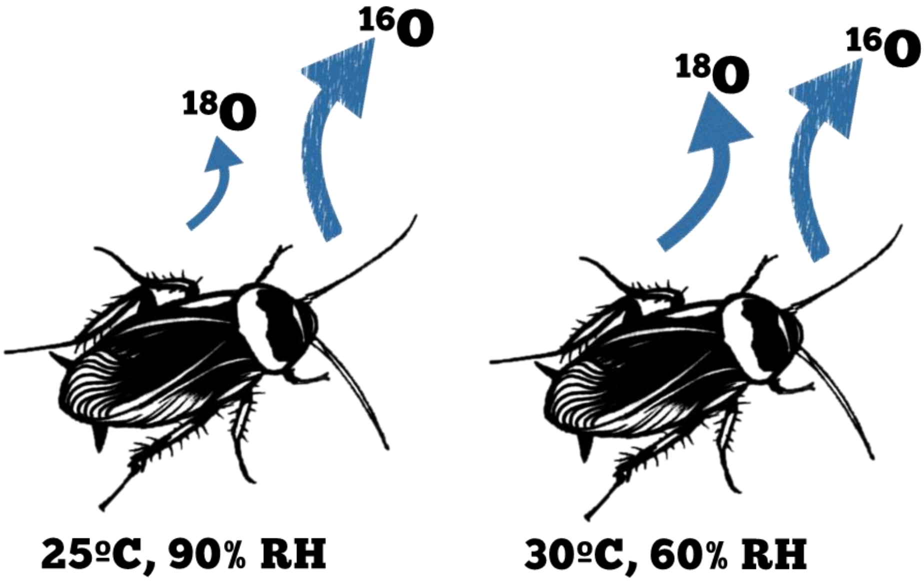


Figure 3.3 Model illustrating the evaporation of lighter water molecules from haemolymph under less energetic conditions, and the increase in evaporation of heavier water molecules, as environmental conditions become more energetic.

Insect haemolymph is analogous to an isolated pool of water, because it so readily exchanges water vapour with the atmosphere (Figure 3.3). And as a body of water, the $\delta^{18}O$ of insect haemolymph can be defined by the C-G model, because the extent of vapour exchange is related directly to environmental temperature and relative humidity (Ellwood et al., 2011). Therefore insect chitin is a physiological marker of ambient abiotic conditions. Given that evaporation favours water molecules containing the lighter ^{16}O isotope because they more readily change phase, haemolymph becomes enriched in the heavier ^{18}O isotope during respiration. Individuals which experience conditions of low humidity, and therefore higher rates of evaporation prior to moulting, will show higher values of $\delta^{18}O$ in their exoskeleton (Ellwood et al., 2011, van Bergen et al., 2016). When the insect sheds its exoskeleton, haemolymph floods to the newly exposed chitin, and as the exoskeleton hardens, the isotopic signature of the environment is fixed in the chitin (Ellwood et al., 2011) (Figure 3.4).

Figure 3.4 Ecdysis (moulting) process photographed in *Periplaneta australasiae* (Australian cockroach).

As the $\delta^{18}O$ signature of insect chitin is a reflection of atmospheric conditions, it provides a physiological marker of the environmental conditions under which the animal has lived (Ellwood et al., 2011). Studies have suggested that a physiological marker of an organism's abiotic niche would help us to understand the long term implications of climate change, because we would be in a better position to identify species that are vulnerable or resilient to environmental change (Turner and Foster, 2009). Traditionally, studies of thermal tolerance in insects have used thermostat incubation, i.e. the lethal temperature method (Uvarov, 1931, Hutchinson, 1979). This rather unethical method involves placing animals into thermostatically controlled chambers, recording behavioural change with temperature, and ultimately the point at which point death occurs (Hutchinson, 1979). Studies continue to use the lethal temperature method today because there is no other way to quantify physiological tolerance (Pincebourde and Casas, 2015). The first study to offer an alternative means to outline abiotic tolerance in tracheated arthropods comes from Ellwood *et al* (2011), who revealed that the $\delta^{18}O$ composition of insect haemolymph responds almost simultaneously to environmental conditions change, while chitin reflects the mean conditions under which the animal lived. A recent study built on Ellwood *et al* (2011) and showed that the $\delta^{18}O$ of chitin of mycalescine butterflies was indicative of the atmospheric humidity under which they developed from larvae to adult forms, rather than the environment that they migrated to upon maturity (van Bergen et al., 2016).

Because animals tend to avoid habitats to which they are not climatically suited (Suggitt et al., 2011), the $\delta^{18}O$ of chitin could provide an outline of an animal's tolerance range, and give early indications of its' response to climate change. For example, species A consistently shows low $\delta^{18}O$ signatures (indicative of high humidities), and species B shows a broad range of $\delta^{18}O$ signatures. It would seem likely that species A would be more susceptible to dry conditions, whereas species B would be tolerant of a range of conditions. On this basis, we would predict that species A would be at higher risk of extinction under disturbance or climate change, whereas species B, would show a degree of resilience.

With more than 1.5 million described species, insects represent a major proportion of global biodiversity (Gardner et al., 2008). If tropical regions, which are biodiversity hotspots (Myers et al., 2000) become even hotter and drier under climate change (Williams et al., 2008, Scheffers et al., 2014a), this may be fatal for many species of insects. Given the relationship between biodiversity and ecosystem function (Barnes et al., 2014), if functionally important populations continue to suffer under environmental uncertainty, then eventually human health will suffer as invertebrate driven processes collapse (Sodhi et al., 2004, Mori et al., 2017). If the $\delta^{18}O$ composition of chitin can provide a robust means to estimate species vulnerability or tolerance towards climatic change, it would put us in a much better position to identify species for conservation priority. Ultimately, this knowledge could enable conservationists to develop management strategies that protect or even extend the distributions of vulnerable, but functionally significant animals, thus maintaining the ecosystem services that they provide.

3.1.3 MODEL ANIMAL IN A MODEL ECOSYSTEM

Cockroaches (Order: Blattodea) were used by Ellwood *et al* (2011) to show that the $\delta^{18}O$ composition of chitin is a reflection of environmental conditions. In natural ecosystems, cockroaches represent major functional contributors to decomposition and nutrient cycling (Bell et al., 2007). However, their persistence and prevalence in anthropogenic environments such as greenhouses and food stores, has firmly established them as pests worldwide (Kramer and Brenner, 2009). The identification of cockroaches as pest animals is perhaps unfair given that, of the 3500 described species, just 30 or so are considered pests (Bell et al., 2007). The majority of these synanthropic pests originate from tropical and subtropical regions (Stejskal et al., 2015) where anthropod diversity is at its highest (Mittermeier et al., 1999).

Centuries ago, the Australian cockroach, *Periplaneta australasiae* (Fabricius, 1775) (Figure 3.5) began its global colonisation as a stowaway on cargo ships (Rehn, 1945). Today, *P. australasiae* is a major pest in botanical greenhouses where it damage plants and seedlings (Schal et al., 1984, Stejskal et al., 2015). Of course for tropical cockroaches, tropical greenhouses provide optimal living conditions (Stejskal et al., 2003), as is also the case with the Suriname cockroach, *Pycnoscelus surinamensis* (Linneus, 1758). *P. surinamensis* is one of the most prevalent invasive cockroach species, because they do well in anthropogenic landscapes, such as oil palm plantations, but they also thrive in undisturbed habitats (Peck and Roth, 1992, Pellens and Grandcolas, 2002) where they may displace native species. However, their prevalence across a range of habitats, and persistence in anthropogenic environments, make pest cockroaches the ideal model insect (Stejskal et al., 2015). Such cockroaches can be sampled exhaustively, with minimal detriment to the environment.

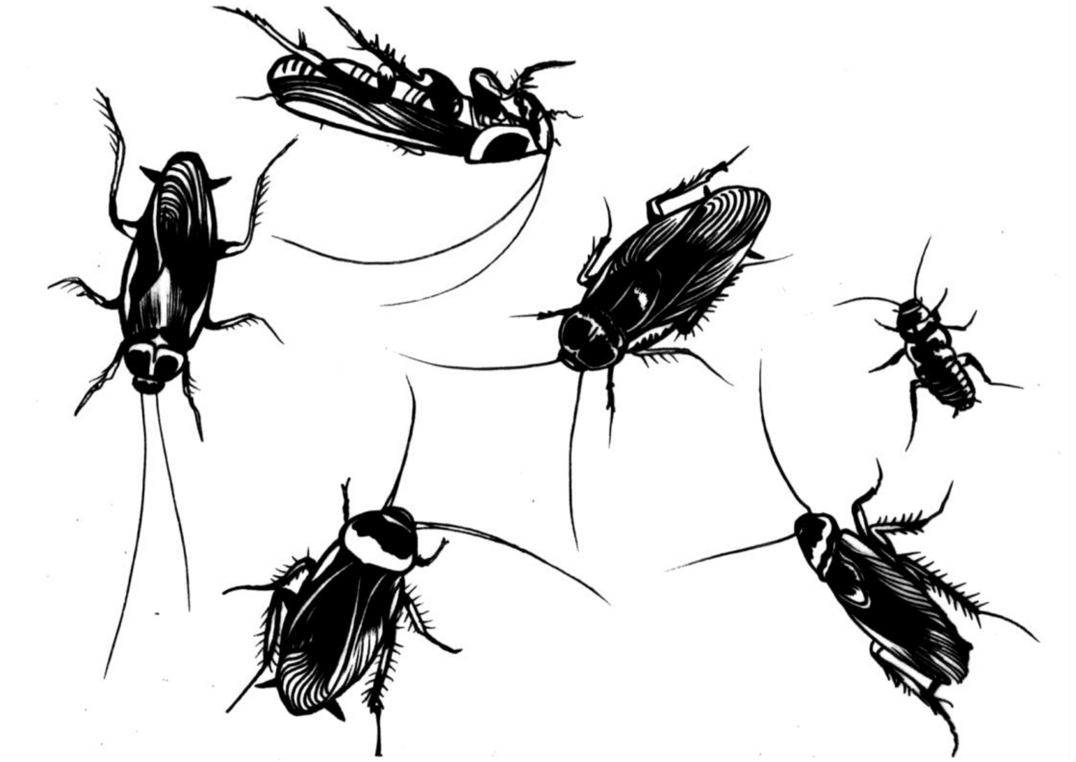


Figure 3.5 Adult and nymph *Periplaneta australasiae* (Australian cockroach).

This chapter will develop our understanding of the relationship between climatic conditions and the $\delta^{18}O$ in chitin by examining the $\delta^{18}O$ signatures within and between cockroach species, in both natural and anthropogenic habitats. In order to fill key knowledge gaps, answers for the following questions will be provided: (1) To what extent does microclimate influence $\delta^{18}O$? (2) How much variation in the $\delta^{18}O$ signature of chitin is there within a species? (3) To what extent does fractionation occur across the exoskeleton? (4) To what extent does $\delta^{18}O$ differ between species? And finally, (5) Are $\delta^{18}O$ signatures in insect chitin indicative of phylogenetic relatedness, or phenotypic convergence?

3.2 METHODS

3.2.1 STUDY SITES

The Eden Project's Rainforest Biome (RFB) (described in Chapters 1 and 2) provided the perfect mesocosm (Donald et al., 2018) for developing our understanding of the interplay between δ^{18}O in insect chitin and climatic conditions. In the biome, mean air temperature is 21.7 ºC (± 2.8), and relative humidity is 97.4% (± 3.6) (Donald et al., 2017a), although as Chapter 2 revealed, these conditions can be highly variable. The RFB covers 15,590 m^2, housing a wide range of plants across different thematic areas (Donald et al., 2016). These different biogeographic themes, and the various types of greenery that they support, give rise to a range of microhabitats and microclimatic conditions. Both *Periplaneta australasiae* (Australian cockroach) and *Pycnoscelus surinamensis* (Suriname cockroach), are abundant in the RFB (Treseder et al., 2011) and will experience different microclimates depending on their location in the biome. Differences in microclimatic conditions across the biome should generate differences in the δ^{18}O signatures of cockroaches collected from these microhabitats. Conversely, cockroaches inhabiting climatically similar sites in the RFB should show convergence in their δ^{18}O signatures.

Having already shown in Chapter 2 that bird's nest ferns buffer microclimate to the extent that conditions within the ferns are constant throughout the forest and between habitats, it was hypothesised that cockroaches collected from within bird's nest ferns would show isotopic convergence. In order to show that the δ^{18}O composition of chitin would converge when cockroaches shared an abiotic niche, cockroaches were obtained from a previous study of five large bird's nest ferns in the rainforest high canopy in Danum Valley (Ellwood et al., 2002, Ellwood and Foster, 2004). These cockroaches, which had all lived within the bird's nest fern, should have experienced climatically similar conditions, and as such, there should be isotopic convergence of the δ^{18}O composition of their chitin.

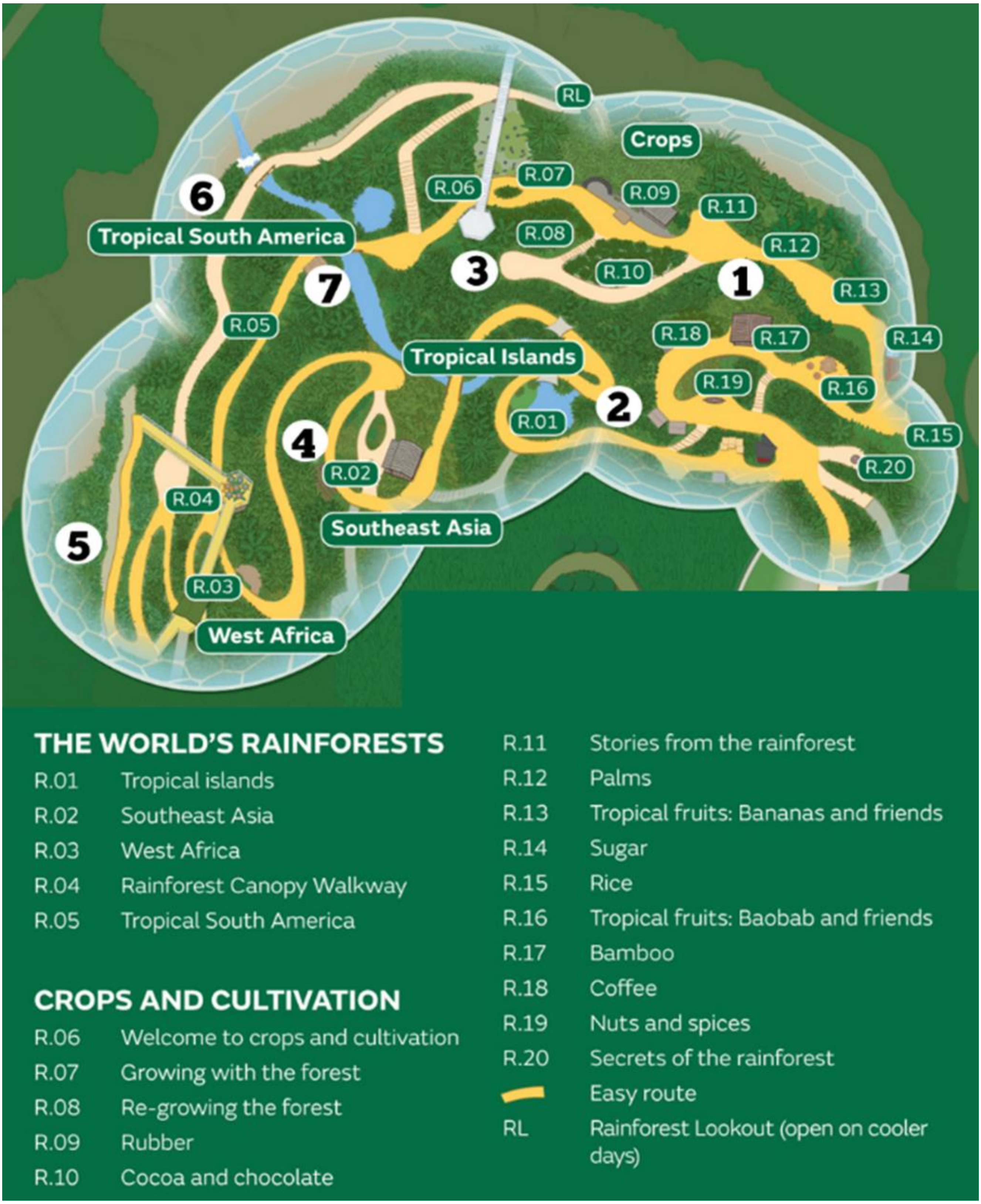
3.2.2 DATA LOGGING

To determine the extent to which different sites across the RFB provided different microclimatic conditions, data loggers (as described in Chapter 2) were used to continuously record conditions over four days in the RFB (96 hours: 56 daytime hours, 40 night time hours). Data loggers, each supporting a VP4 simultaneous air temperature and humidity sensor (-40 to 80 ± 0.5 ºC and 0.0 to 100.0 ± 2.0 %), were distributed to each of the seven sites across the RFB. Figure 3.6 provides an illustration of a typical site, the Malaysian Garden (Site 4). The name and number of each of the study sites are provided in Table 3-1, and their distribution around the biome are shown in Figure 3.7. As in Chapter 2, prior to analysis of the microclimate data, all variables were converted into mean hourly values, so that for each site, the mean climatic conditions over 24 hours could be compared.

Table 3-1 Site number (illustrated on map in Figure 3.7), site name (with thematic area in biome), as well as number of cockroaches collected from each site.

Site *n* (map)	**Site Name (thematic area of biome)**	***n* cockroaches**
1	Oil Palm (Palms)	55
2	Banyan Tree (Tropical Islands)	22
3	Dipterocarp (Re-growing the Forest)	23
4	Malaysian Garden (Southeast Asia)	7
5	Elephant Grass (Canopy Walkway, Biome Edge)	13
6	Cliff Top (Rainforest Lookout)	27
7	Amazon Waterfall (Tropical South America)	38
	Total	**198**

Figure 3.6 The Malaysian garden (Site 4) in the Eden Project's Rainforest Biome.



THE WORLD'S RAINFORESTS

R.01	Tropical islands
R.02	Southeast Asia
R.03	West Africa
R.04	Rainforest Canopy Walkway
R.05	Tropical South America

CROPS AND CULTIVATION

R.06	Welcome to crops and cultivation
R.07	Growing with the forest
R.08	Re-growing the forest
R.09	Rubber
R.10	Cocoa and chocolate
R.11	Stories from the rainforest
R.12	Palms
R.13	Tropical fruits: Bananas and friends
R.14	Sugar
R.15	Rice
R.16	Tropical fruits: Baobab and friends
R.17	Bamboo
R.18	Coffee
R.19	Nuts and spices
R.20	Secrets of the rainforest
▬	Easy route
RL	Rainforest Lookout (open on cooler days)

Figure 3.7 Map of the thematic areas in the Eden Project's Rainforest Biome (RFB) with bold black numbers with white circles to mark the location of each of the study sites.

3.2.3 COCKROACH COLLECTION

Baited no-exit traps cockroach traps were selected (Figure 3.8) over other invertebrate collection techniques such as pitfall or sticky traps (Leather, 2008), deploying three traps to each of the seven sites (Table 3-1, Figure 3.7). Traps were baited with a concoction of sweet scented food waste, and the sites were visited every morning to collect any cockroaches that had been caught in the traps overnight. By using live traps, and checking them each morning, it was possible to ensure that only targeted species were collected. Upon collection, the traps were opened in no-grip high walled containers, target species were removed and placed into bottles of clean 95% ethanol solution. Each bottle was labelled with the site name and stored in a freezer at -20°C until chitin samples were extracted for analysis.

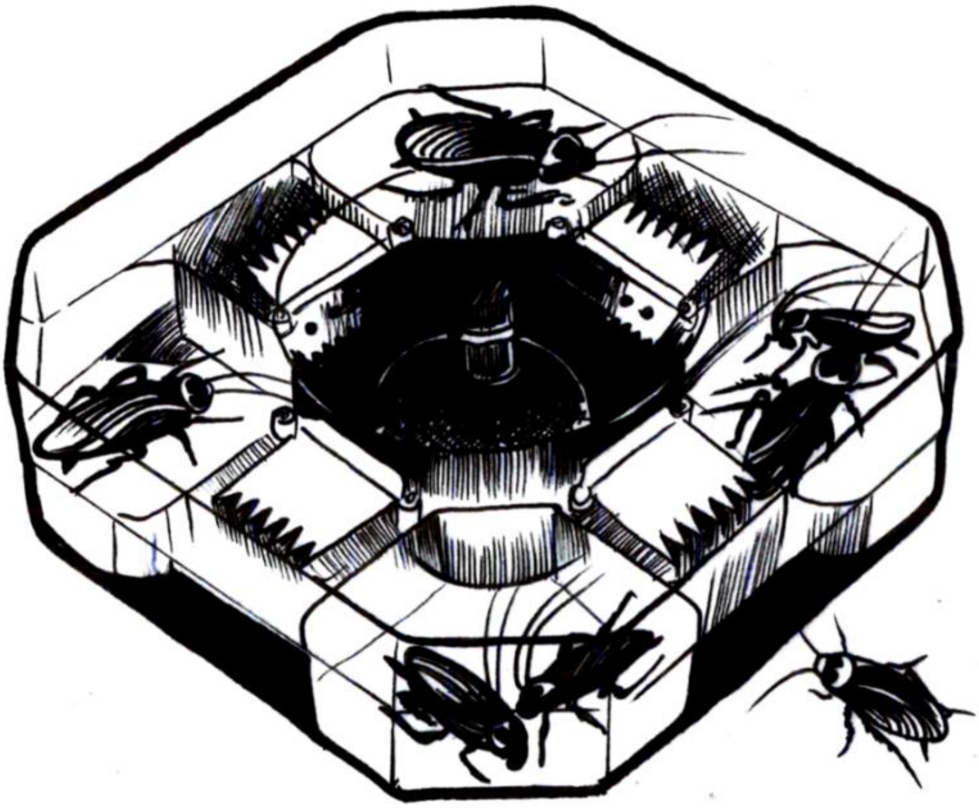


Figure 3.8 Baited, no-exit cockroach traps used to collect live cockroaches at the Eden Project.

A total of 198 cockroaches (Table 3-1) were collected over 4 nights in August 2017 from the RFB. In the lab at UWE Bristol, *Periplaneta* cockroaches were sorted by development stage: (1) young nymphs (Moult/Instar 1-3), (2) older nymphs (Moult/Instar 4-5) and (3) adults. Gender was also determined for adult cockroaches, however adult males were discounted from the study as only four were collected. As per Ellwood *et al* (2011), the $\delta^{18}O$ composition of chitin was determined from a cockroach's hind right tibia. To ascertain whether isotopic fractionation occurred across the body of a cockroach, five egg-laying adult female cockroaches into separated into their constituent body parts (six individual legs, outer wings, inner wings, body and egg), and the pieces were analysed separately. From each of the sites in the RFB, up to 10 individuals of each developmental stage were sent for isotopic analysis, although some life stages were absent from particular sites. Very few of the subterranean *Pycnoscelus* cockroaches were caught in the traps. Therefore, 10 adult females were caught by hand from the Oil Palm site (Site 1) and sent for analysis. In total, 135 cockroaches (125 *Periplaneta* and 10 *Pycnoscelus*) were sent for analysis from across the biome.

Of the 837 cockroaches collected from five large bird's nest ferns in Danum Valley (Ellwood et al., 2002, Ellwood and Foster, 2004), a subsample of 99 adults and nymphs were sent for isotopic analysis. The cockroaches sent belonged to seven recognisable taxonomic units (RTU's) across three families (see Results, Table 3.6). Although a great number of species were recorded from these rainforest ferns, only the most common cockroaches were sent for analysis. This was to ensure that a representative sample of both adults and nymphs from across all five large ferns were analysed. Prior to sampling the chitin, these cockroaches were stored in 95% ethanol solution at Oxford University Museum of Natural History (OUMNH).

3.2.4 STABLE ISOTOPE ANALYSIS

A NERC 'Grant-in-Kind' award of £32,245 funded the stable isotope analysis of oxygen of the Borneo cockroaches for this study (Project no. EK291-14/17). The chitin $\delta^{18}O$ analysis of these cockroaches was completed on bulk samples at the NERC Life Sciences Mass Spectrometry Facility (LSMSF) in East Kilbride. The isotopic signature of the samples was calculated as the ratio of stable isotopes of oxygen-18 (^{18}O) and oxygen-16 (^{16}O), and defined in parts per thousand (‰):

$$\delta^{18}\mathrm{O} = \left(\frac{\frac{18\mathrm{O}}{16\mathrm{O}}\,\mathrm{sample}}{\frac{18\mathrm{O}}{16\mathrm{O}}\,\mathrm{standard}} - 1 \right) \mathrm{x}\ 1000‰$$

where the standard was the Standard Mean Oceanic Water (SMOW) international isotopic standard. The preparation of all samples took place at UWE Bristol ahead of shipment to a mass spectrometry facility for isotopic analysis. Sample specimens were removed from their preserving alcohol and air dried, before the hind tibia was removed, weighed and encapsulated. The Borneo cockroaches were encapsulated in silver and sealed in 96 well plates to protect them during shipping. Isotopic analysis of the Eden Project cockroaches was supported by a UWE Bristol QR Funding award of £13,000. These cockroaches were processed by Iso-Analytical Limited in Crewe, UK. The Eden cockroach samples, and the five specimens that were divided for fractionation analysis, were placed in labelled plastic Eppendorf Tubes® and shipped to Iso-Analytical.

3.2.5 STATISTICAL ANALYSES

One way ANOVA's were used to determine whether significant differences occurred over 24 hours, during the daytime (06:00 - 20:00) and night time (21:00 - 05:00) in ambient air temperatures (AT) and relative humidity (RH%) across the RFB study sites. Similarly, one way ANOVA's were used to quantify differences in the $\delta^{18}O$ of cockroach chitin between (1) study sites, (2) life stages and (3) cockroach species in the RFB. Spearman's Rho correlations were used to determine which microclimatic variable best described the differences in $\delta^{18}O$ of cockroaches between sites. Paired differences *t*-tests were used to determine the extent of isotopic fractionation of $\delta^{18}O$ in chitin across the cockroach body, and whether $\delta^{18}O$ signatures were transferred during egg production.

For the Bornean cockroaches, one way ANOVA's were used to test for differences in $\delta^{18}O$ signature of cockroaches between (1) the five large ferns, (2) cockroach life stage, (3) cockroach species and (4) cockroach family and behavioural strategy. General Linear Models were used to determine whether there were significant interactions of (1) cockroach life stage and fern and (2) cockroach life stage and species, on the $\delta^{18}O$ of cockroach chitin. All *p* values were significant at the level of 0.05. All data analyses were carried out using IBM SPSS Statistics Version 25.0.

3.3 RESULTS

3.3.1 MICROCLIMATE IN THE RAINFOREST BIOME AT EDEN

Sites 5 (Elephant Grass) and 6 (Cliff Top) were much hotter than any other sites in the early afternoon, giving excellent microclimatic separation (Figure 3.9). Unsurprisingly, there were significant differences in air temperatures (AT) between sites across the RFB over 24 hours (One-way ANOVA $F = 14.853$, df = 6, $p < 0.001$). Site 6 (Cliff Top, 27.8 ± 0.8 °C) and Site 5 (Elephant Grass, 27.0 ± 0.9 °C) were the hottest locations, while Site 2 (Banyan, 21.7 ± 0.2°C) and Site 4 (Malaysian Garden, 23.9 ± 0.3 °C) were the coolest. There was a difference of 6.1 °C between the hottest site (Site 6, 27.8 °C) and the coolest site (Site 2, 21.7 °C). There were also dramatic fluctuations in relative humidity (RH%), revealing clear and significant differences in RH% between the sites (One-way ANOVA $F = 93.945$, df = 6, $p < 0.001$, Figure 3.10). A difference of 43.9% in relative humidity was recorded between driest (Site 6 - Cliff Top, 54.5 ± 3.1%) and most humid site (Site 7 - Amazon Waterfall, 98.4 ± 0.3%).

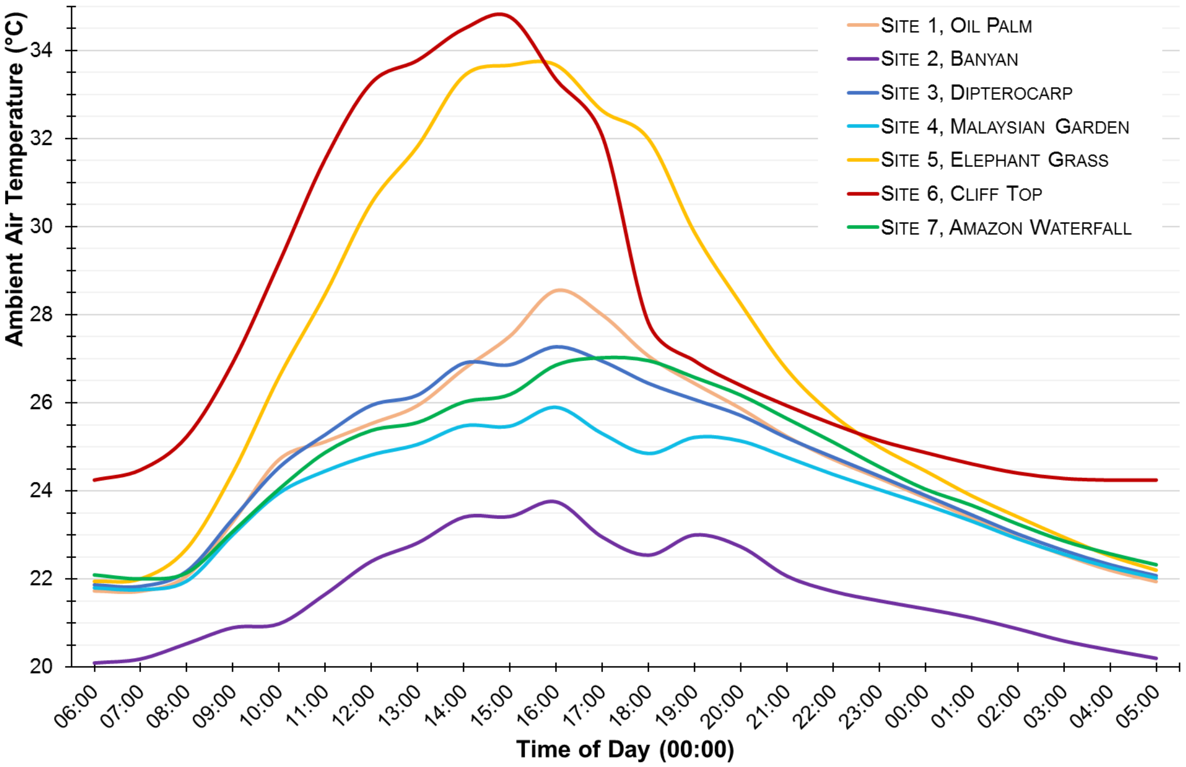


Figure 3.9 Mean hourly fluctuation in air temperature (AT) based on 96 hours of data logging over four days (*n* = 4) across cockroach collection sites in the Eden Project's rainforest biome.

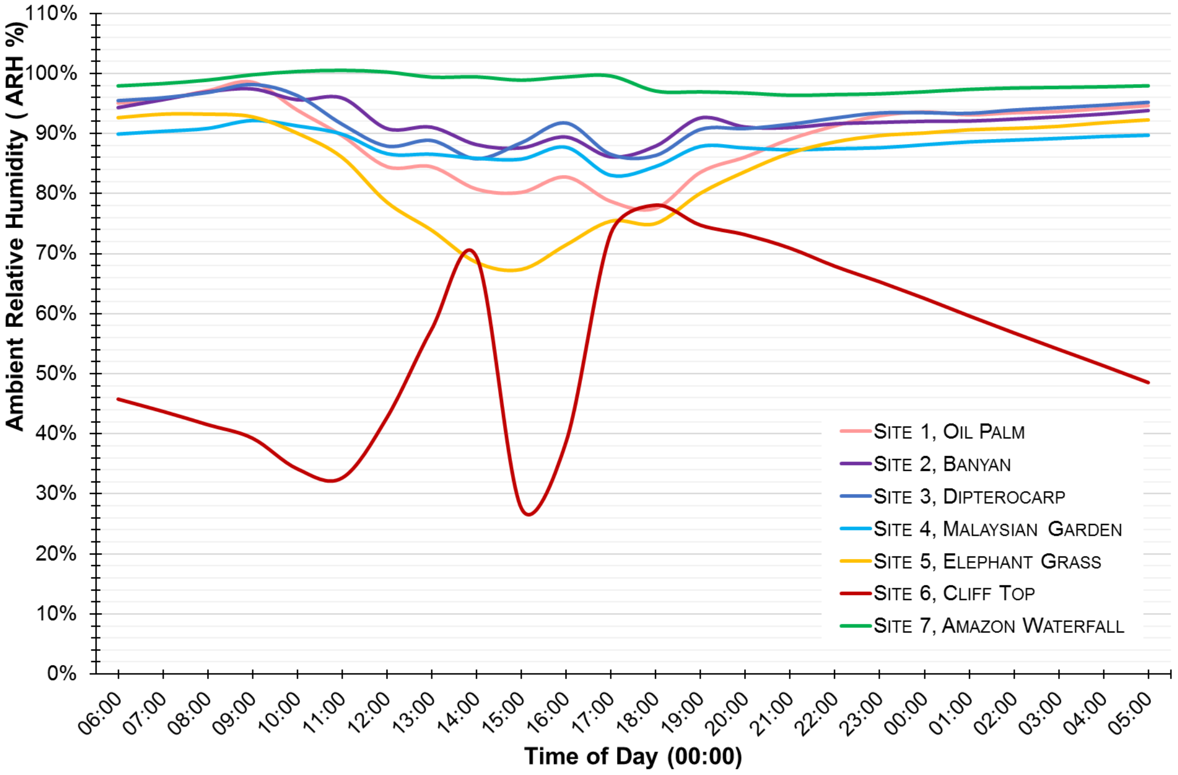


Figure 3.10 Mean hourly fluctuation in relative humidity (RH%) based on 96 hours of data logging over four days (*n* = 4) across cockroach collection sites in the Eden Project’s rainforest biome.

During the day (06:00 - 20:00), climatic differences between the sites were prominent with significant differences in AT (*F* = 14.53, df = 6, *p* <0.001; Figure 3.11) and RH % (*F* = 50.94, df = 6, *p* <0.001; Figure 3.12). Again, the greatest differences in AT occurred between Site 6 (29.6 ± 1.0 °C) and Site 2 (22.1 ± 0.3 °C), with a difference of 7.5 °C. As well as the highest recorded daytime temperatures, Site 6 was also the driest, with the lowest RH % (51.3 ± 4.6%). On average Site 6 was 47.6% less humid than Site 7, which was the most humid (98.9 ± 0.3%).

There were significant differences in climatic conditions between the sites overnight (21:00 - 05:00) (AT, One-way ANOVA *F* = 10.7, df = 6, *p* <0.001; Figure 3.13) (RH%, One way ANOVA *F* = 150.2, df = 6, *p* <0.001; Figure 3.14). As per the daytime, Site 2 was the coolest overnight, and AT's were significantly lower (21.1 ± 0.2 °C) than the other sites. AT's seemed to be homogenous between all of the other sites overnight. Similarly, as per the daytime, Site 6 was the driest (59.7 ± 2.6%), and was significantly less humid than any of the other sites. Site 7 remained the most humid overnight (97.2 ± 0.2%).

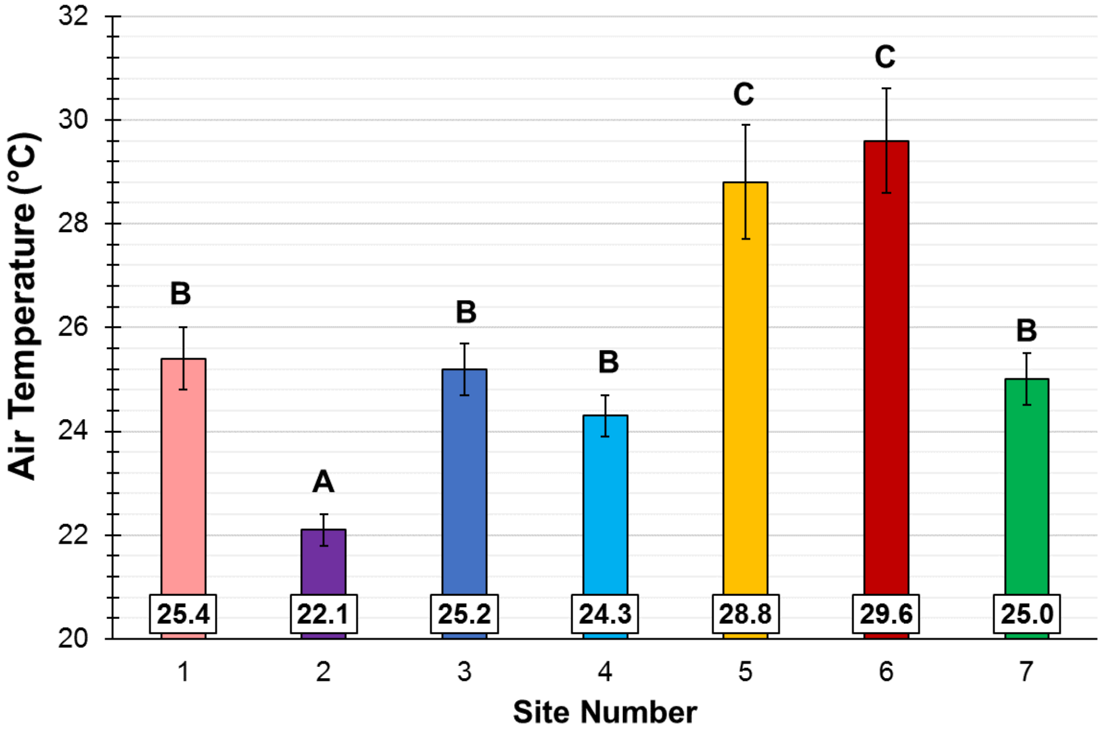


Figure 3.11 Mean daytime [06:00-20:00] air temperature (with error bars) of each of the seven collection sites in the Eden Project RFB based on 56 hours of daytime data logging (*n* = 56). Sites which share a letter are not significantly different from one another (A *p* = 0.052, B *p* = 0.92, C *p* = 0.98).

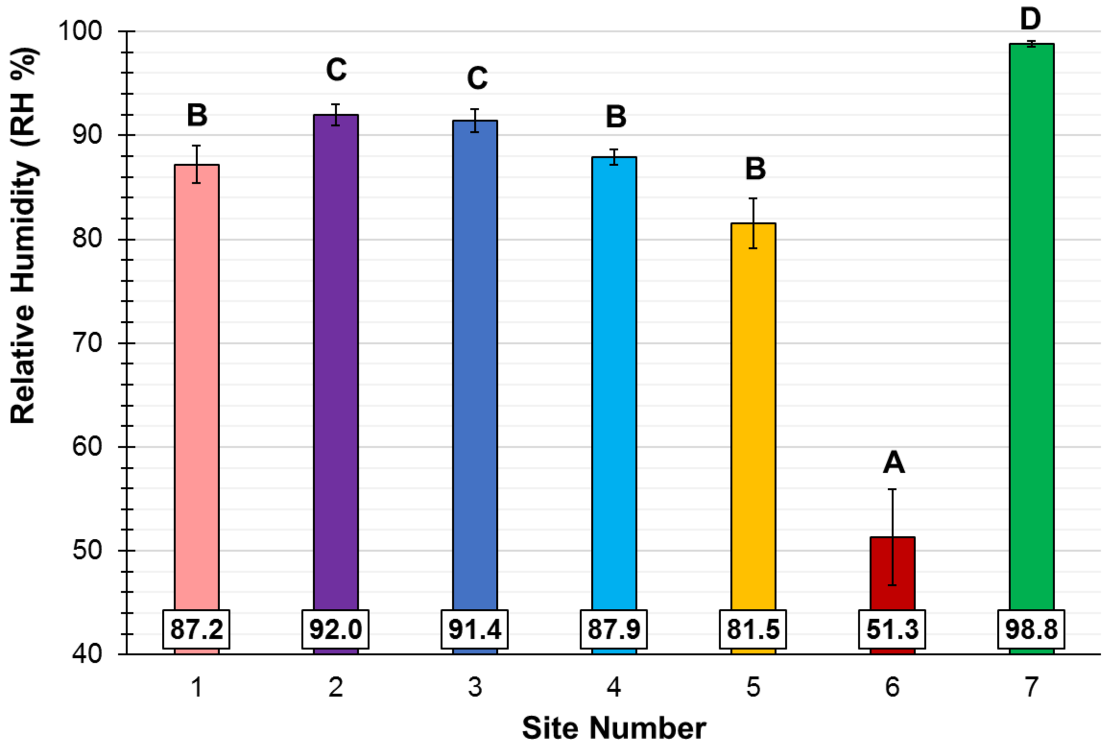


Figure 3.12 Mean daytime [06:00-20:00] relative humidity (with error bars) of each of the seven collection sites in the Eden Project RFB based on 56 hours of daytime data logging ($n = 56$). Sites which share a letter are not significantly different from one another (A $p = 1.0$, B $p = 0.35$, C $p = 0.707$, D $p = 0.18$).

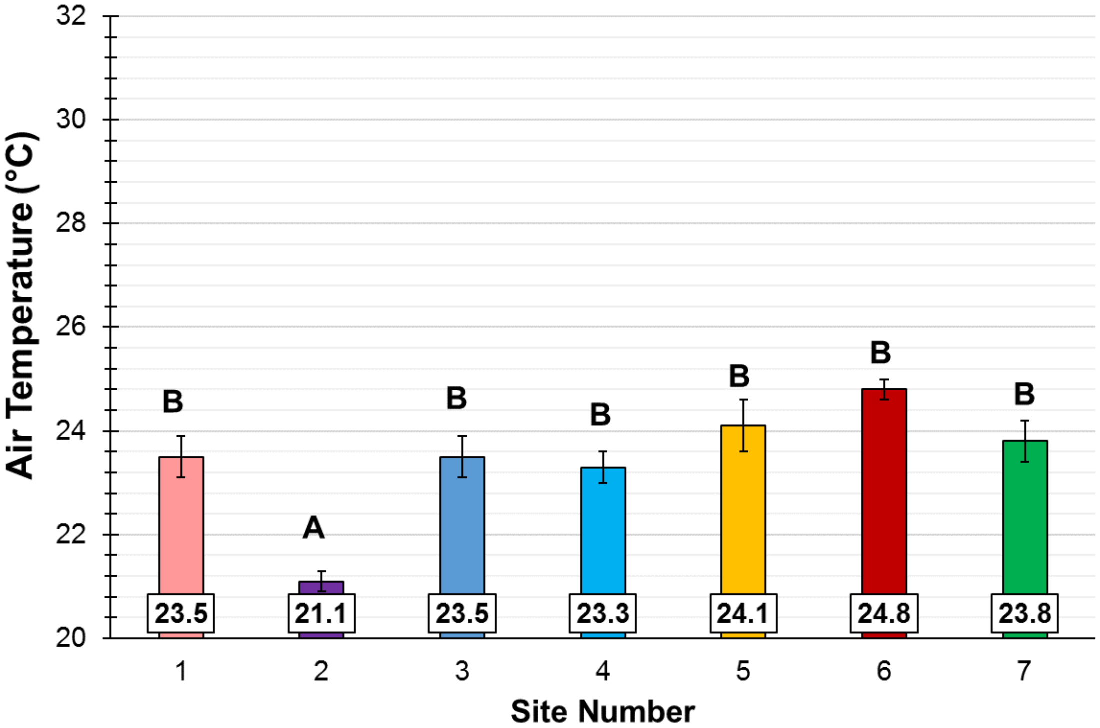


Figure 3.13 Mean night time [21:00-05:00] air temperature (with error bars) of each of the seven collection sites in the Eden Project RFB based on 40 hours of night time data logging ($n = 40$). Sites which share a letter are not significantly different from one another (A $p = 1.0$, B $p = 0.063$).

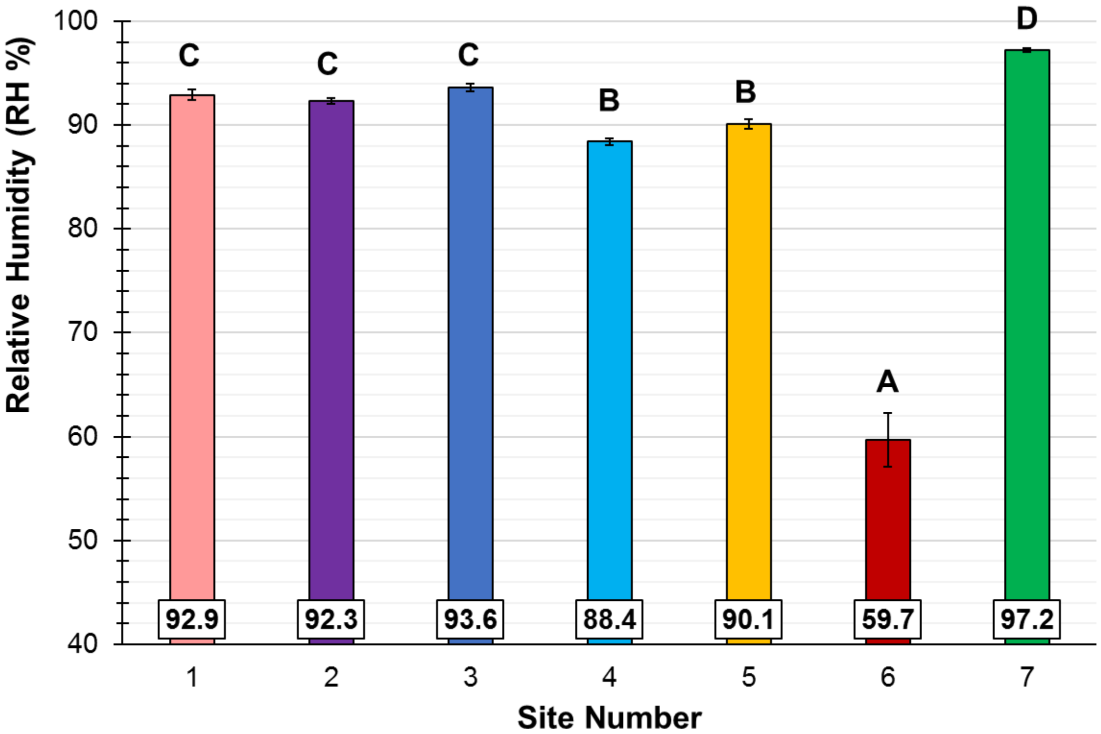


Figure 3.14 Mean night time [21:00-05:00] relative humidity (with error bars) of each of the seven collection sites in the Eden Project RFB based on 40 hours of night time data logging (n = 40). Sites which share a letter are not significantly different from one another (A p = 1.0, B p = 0.129, C p = 0.242, D p = 0.65).

3.3.2 EDEN PROJECT COCKROACHES

Oxygen isotopic signatures ($\delta^{18}O$) were successfully determined for 124 *Periplaneta australasiae* out of the 125 samples sent (Table 3-2). The mean $\delta^{18}O$ signatures of these cockroaches differed significantly between the collection sites (One Way ANOVA F = 15.12, df = 6, p <0.001, Figure 3.15). As was hypothesised, the $\delta^{18}O$ signature of *Periplaneta* from Site 7 (Amazon Waterfall, 20.48 ± 0.17‰), which was the most humid environment, were the most depleted, while the most enriched signatures were recorded from the hottest and driest site in the biome, Site 6 (Cliff Top, 22.48 ± 0.18‰). The $\delta^{18}O$ values ranged from 19.21‰ to 24.93‰, equating to a difference of 5.72‰ between the most enriched and depleted chitin signatures recorded.

Table 3-2 The number (*n*) of *Periplaneta cockroaches* of each life stage collected from each site in the rainforest biome, and their mean $\delta^{18}O$ signature with standard error.

Site	***n* of each life stage analysed ($\delta^{18}O$ ± S.E)**			Total
	Young Nymph	**Late Nymph**	**Adult**	
1	10 (22.09 ± 0.12)	8 (22.49 ± 0.34)	10 (22.55 ± 0.31)	28 (22.43 ± 0.28)
2	0	8 (21.32 ± 0.32)	10 (22.16 ± 0.40)	18 (21.78 ± 0.28)
3	0	8 (21.33 ± 0.31)	10 (22.13 ± 0.21)	18 (21.80 ± 0.21)
4	0	0	7 (22.51 ± 0.26)	7 (22.51 ± 0.26)
5	5 (21.69 ± 0.44)	8 (21.69 ± 0.25)	0	13 (21.67 ± 0.19)
6	10 (22.57 ± 0.27)	10 (23.14 ± 0.19)	0	20 (22.85 ± 0.17)
7	10 (21.45 ± 0.25)	10 (21.09 ± 0.17)	0	20 (20.48 ± 0.18)
Total	35 (21.45 ± 0.25)	52 (21.87 ± 0.25)	37 (22.29 ± 0.15)	**124**

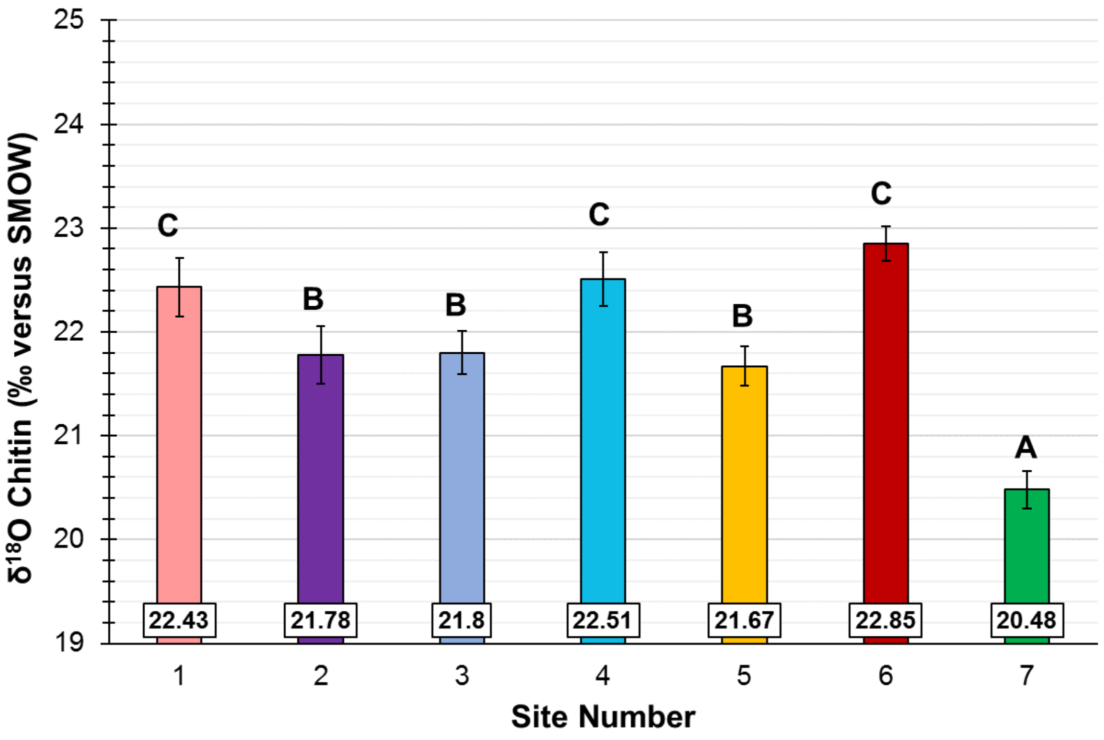


Figure 3.15 Mean $\delta^{18}O$ signature (with error bars) of *Periplaneta australasiae* from each collection site. Sites which share a letter are not significantly different from one another (A $p = 1.0$, B $p = 0.12$, C $p = 0.841$)

The δ^{18}O of *Periplaneta* cockroaches were found to significantly differ according to life stage (F = 5.11, df = 2, p = 0.007) (Figure 3.16). The δ^{18}O signature of adult cockroaches were significantly more enriched (22.29 ± 0.15‰) than those of young nymphs (21.45 ± 0.25‰) (Tukey p = 0.005). However, they were not significantly different to the δ^{18}O signatures of late nymphs (21.87 ± 0.15‰) (p = 0.203). Similarly, the δ^{18}O signatures of late nymphs did not differ significantly to those of the young nymphs (p = 0.226).

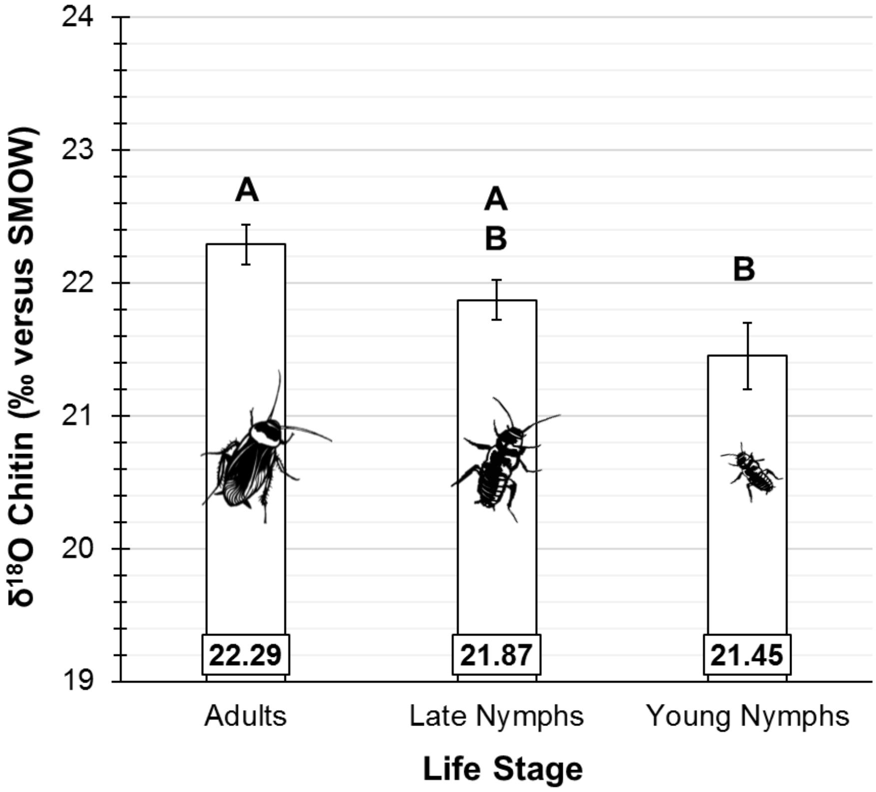


Figure 3.16 Mean δ^{18}O signature (with error bars) of cockroaches at different life stages. Sites which share a letter are not significantly different (A p = 0.203, B p = 0.226).

The δ^{18}O signatures of adult cockroaches were not significantly different between collection sites around the biome (F = 0.51 df = 3, p = 0.679, Figure 3.17). However, those of late (F = 10.47, df = 5, $p < 0.001$, Figure 3.18) and young nymphs (F = 26.72, df = 3, $p < 0.001$, Figure 3.19) were significantly different between sites. In each instance, the greatest differences in the δ^{18}O signature were recorded between the hottest, driest site (Site 6, Cliff top) and the most humid site (Site 7, Amazon Waterfall) in the biome. In the late nymphs this difference amounted to 2.05‰ (Site 6, 23.14‰ - Site 7, 21.09 ‰), and 2.70 ‰ in young nymphs (Site 6, 22.57‰ – Site 7, 19.87‰).

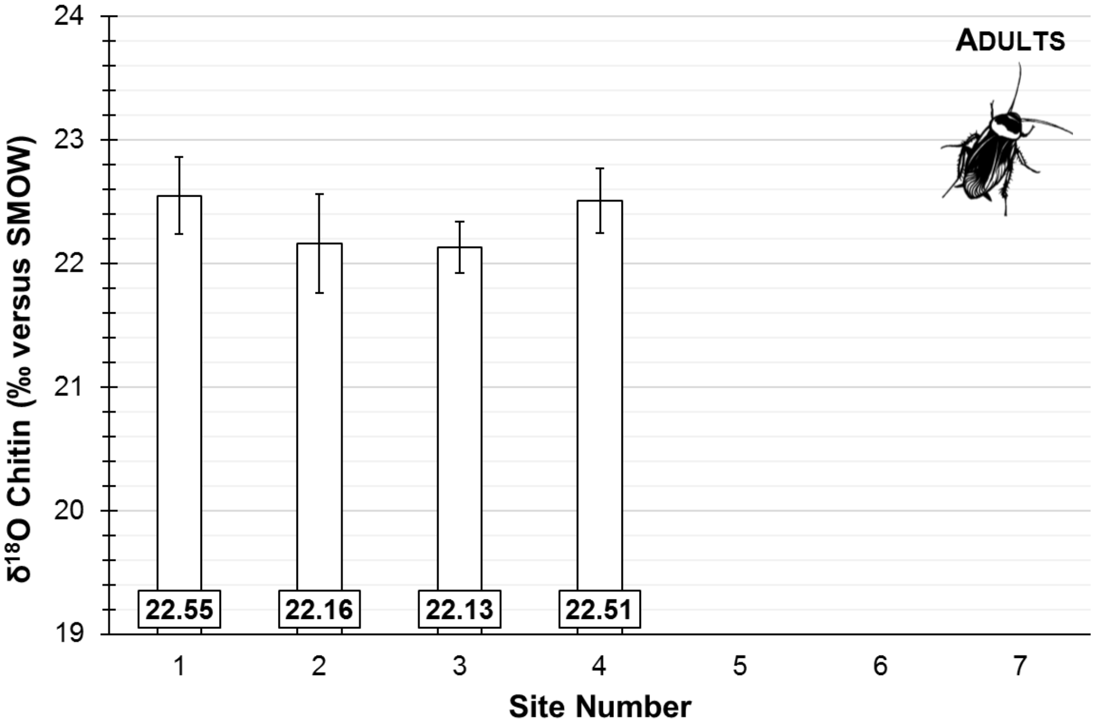


Figure 3.17 Mean δ^{18}O signature (with error bars) of adult cockroaches from each of the collection sites across the rainforest biome (p = 0.679). No adult cockroaches were collected from Site 5, Site 6 or Site 7.

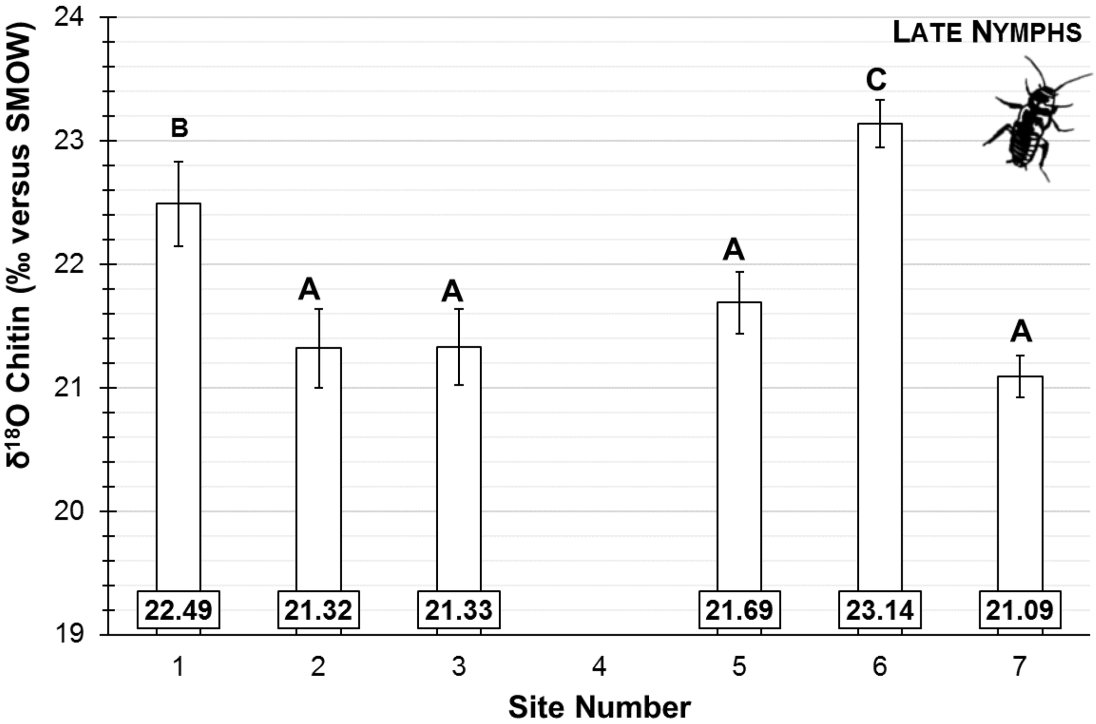


Figure 3.18 Mean δ^{18}O signature (with error bars) of late nymph cockroaches from each of the collection sites across the rainforest biome. No late nymph cockroaches were collected from Site 4. Sites which share a letter are not significantly different (A p = 0.588, B p = 1.0, C p = 1.0).

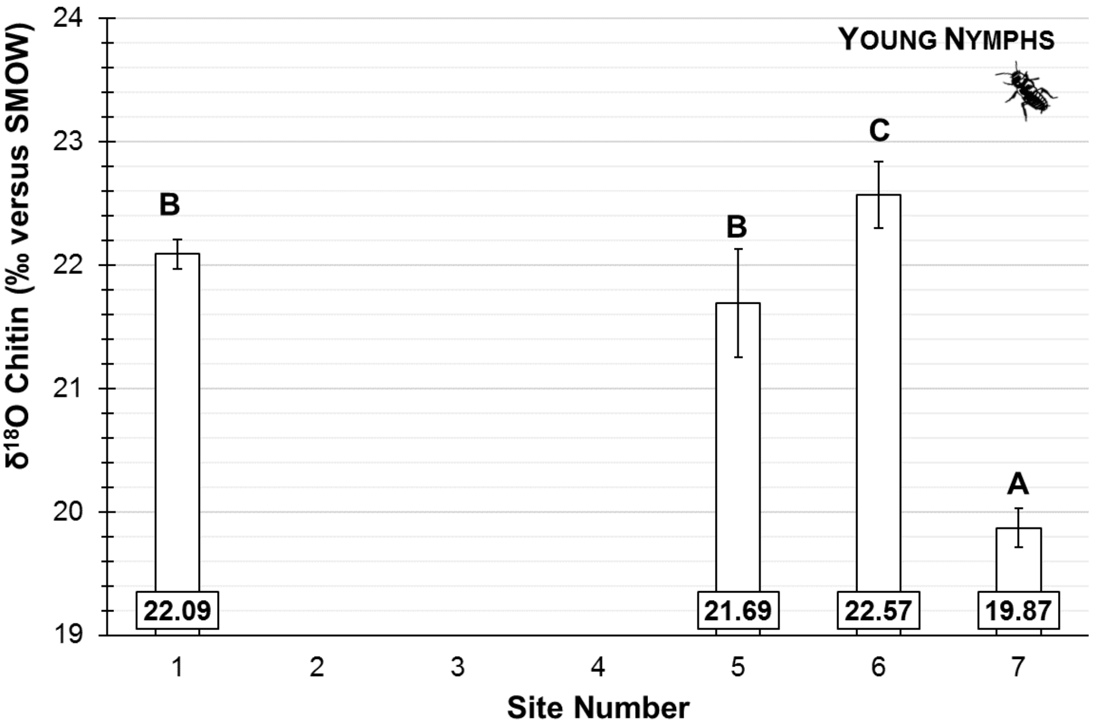


Figure 3.19 Mean δ^{18}O signature (with error bars) of young nymph cockroaches from each of the collection sites across the rainforest biome. No young nymph cockroaches were collected from Site 2, Site 3 or Site 4. Sites which share a letter are not significantly different (A p = 1.0, B p = 0.129, C p = 1.0).

Because the δ^{18}O signatures of adult *Periplaneta* cockroaches did not significantly differ across the sites where they were collected, they were excluded from the correlation analyses between δ^{18}O signature and site specific microclimatic conditions (Table 3-3). In contrast, the δ^{18}O signatures of cockroach nymphs showed a significant strong positive correlation with air temperatures over 24 hours (Spearman's $R_s = 0.841$, $p = 0.036$) and daytime air temperatures ($R_s = 0.886$, $p = 0.019$). The δ^{18}O signatures of nymph cockroaches also showed a significant strong negative correlation with diurnal relative humidity ($R_s = -0.943$, $p = 0.019$). However, the most highly significant correlation was between δ^{18}O and daytime relative humidity ($R_s = -0.886$, $p = 0.005$, Figure 3.20).

Table 3-3 Spearman's Rho correlations of the relationship between microclimate variable and $\delta^{18}O$ of cockroach chitin across the sites, as well as the correlation coefficient and significance level.

Variable mean correlated with $\delta^{18}O$	Correlation Coefficient (R_{s})	*p* value
24 hr air temperatures (AT)	0.841	**0.036**
24 hr relative humidity (RH %)	-0.886	**0.019**
Daytime AT	0.886	**0.019**
Daytime RH %	-0.943	**0.005**
Night time AT	0.493	0.321
Night time RH %	-0.714	0.111

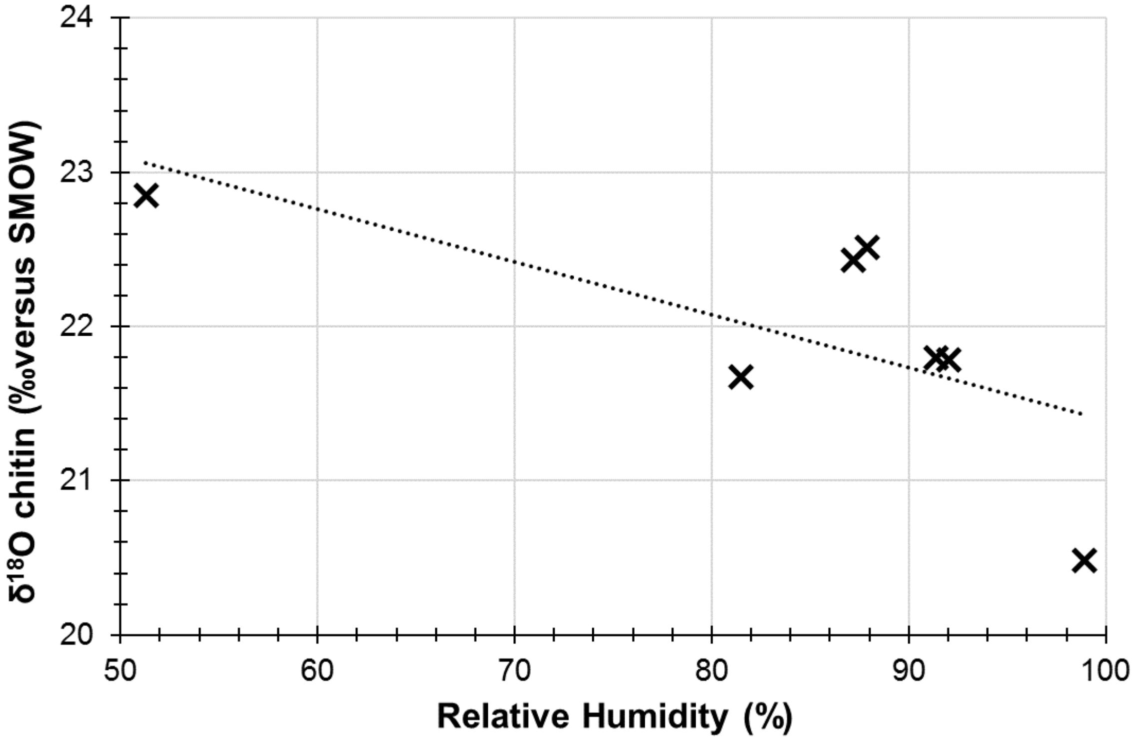


Figure 3.20 Spearman's Rho Correlation between mean relative humidity over 24 hours (RH %) and the $\delta^{18}O$ signature of cockroach chitin in the Eden Project rainforest biome ($R_s = -0.943$, $p = 0.005$).

3.3.3 FRACTIONATION IN COCKROACH CHITIN

There were significant differences between adult female cockroaches and the eggs they produced ($t = 6.99$, df = 4, $p = 0.002$), therefore the $\delta^{18}O$ signature of the adult did not appear to be transferred to the egg through egg production. The mean difference in $\delta^{18}O$ between adults and their oothecae was 4.88‰, with oothecae showing $\delta^{18}O$ depletion (17.15 ± 0.42‰) compared with the adults (22.03 ± 0.37‰). Table 3.4 provides the *t*-test results for the paired differences in $\delta^{18}O$ of cockroach hind right tibia (HRT) (standard sampling unit), and $\delta^{18}O$ of various other body parts revealing the extent of fractionation in $\delta^{18}O$ across the cockroaches body. To accompany Table 3-4, Figure 3.21 provides a visual aid detailing the extent of isotopic fractionation across the cockroach body compared to the HRT. Other than the oothecae, only the outer wings showed significant isotopic fractionation (t = 4.532, df = 4, p = 0.011), though this is perhaps unsurprising given that the wings are the final body part to harden during ecdysis, and must be dried in a warm exposed location.

Table 3-4 The extent of fractionation in body parts relative to hind right tibia (HRT) as a standard sampling unit. Results of paired *t*-test score and *p* value with significant fractionation values are shown in bold.

Body Part		Fractionation (‰)(± S.E) (relative to $\delta^{18}O$ of HRT)	*t* test score	*p* value
Legs	Front left	-0.14 (± 0.14)	0.856	0.455
	Front right	-0.21 (± 0.17)	1.26	0.274
	Middle left	0.22 (± 0.25)	0.903	0.418
	Middle right	0.13 (± 0.31)	0.426	0.692
	Hind left	0.52 (± 0.21)	2.424	0.072
Wings	Inner	-0.87 (± 0.42)	2.033	0.112
	Outer	-1.11 (± 0.24)	**4.532**	**0.011**
	Body	-0.48 (± 0.61)	0.785	0.476
	Egg	-4.88 (± 0.70)	**6.99**	**0.002**

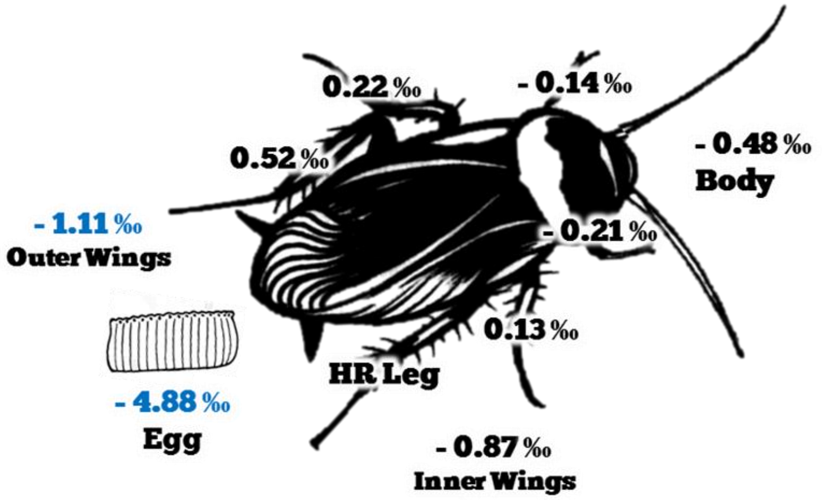


Figure 3.21 The extent of $\delta^{18}O$ fractionation across the cockroach body with significant fractionation values shown in blue.

The $\delta^{18}O$ signatures of chitin were successfully measured from all 10 of the *Pycnoscelus surinamensis* that were sent for analyses. There were significant differences in $\delta^{18}O$ signature between *Periplaneta australasiae* and *Pycnoscelus surinamensis* ($F = 8.222$, df = 1, $p = 0.01$, Figure 3.22). These specimens were all collected from the same site (Site 1, Oil Palm), however the $\delta^{18}O$ signatures of *Periplaneta* (22.68 ± 0.31‰) were on average 1.29‰ more isotopically enriched than *Pycnoscelu*s (21.39 ± 0.31‰). These two cockroach species are quite distinct in terms of their taxonomy and the way that they use their habitats.

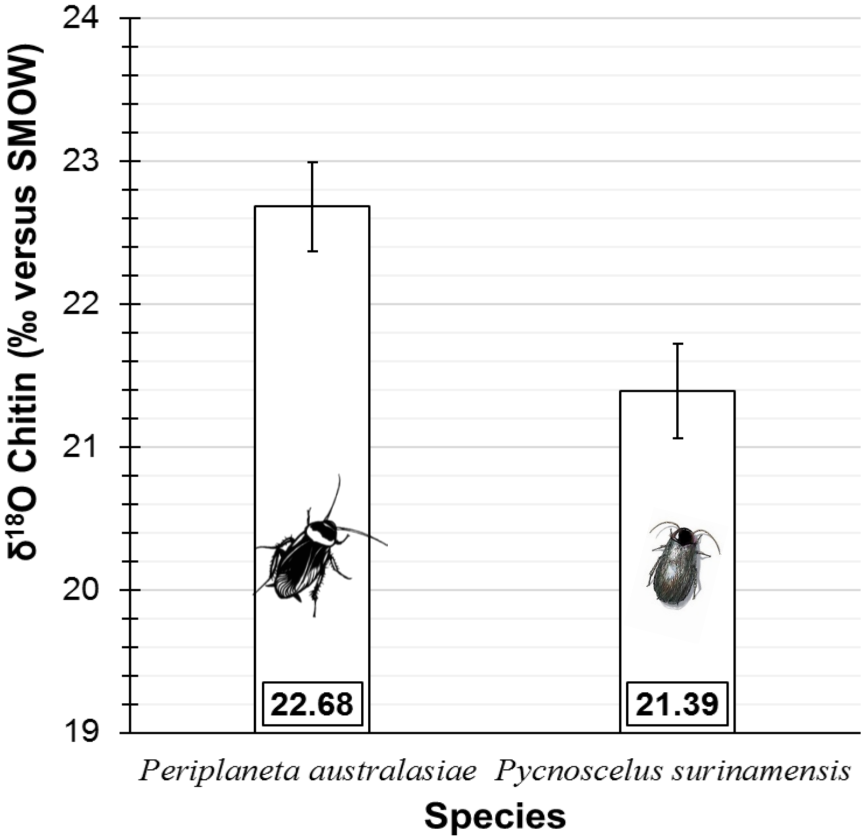


Figure 3.22 Mean $\delta^{18}O$ signatures of ten adult *Periplaneta australasiae* (Australian cockroach) ($n = 10$) and ten *Pycnoscelus surinamensis* (Suriname cockroach) ($n = 10$) collected from Site 1 (Oil Palm) in the Eden Project's rainforest biome ($F = 8.22$, $p = 0.01$).

3.3.4 BORNEAN COCKROACHES

Isotopic signatures were obtained from 95 of the 99 cockroaches collected from five large bird's nest ferns in Danum Valley. Table 3-5 details the number of cockroaches that were analysed from each fern. An overall range in $\delta^{18}O$ of 9.78‰ was recorded between the cockroaches, with 7.11‰ as the lowest value and 16.89‰ as the greatest $\delta^{18}O$ signature. Although the mean $\delta^{18}O$ signature of cockroaches did not differ significantly between the ferns (One Way ANOVA $F = 2.245$, df = 4, $p = 0.073$, Figure 3.23), there was a mean difference of 1.87‰ between the lowest and highest cockroach $\delta^{18}O$ signature in each of the ferns. Similarly, although there was an overall mean difference of 0.96‰ between adult and nymph cockroaches, the difference in $\delta^{18}O$ signature was not significant ($F = 3.041$, df = 1, $p = 0.081$, Figure 3.24). There was no significant interaction between cockroach life stage, and the fern from which it originated (General Linear Model, GLM $F = 0.16$, df = 4, $p = 0.956$). This was likely because the range in $\delta^{18}O$ signatures of cockroaches recorded from each fern showed a degree of overlapped between life stages. This meant that there was no significant separation of $\delta^{18}O$ according to life stage, or between the ferns.

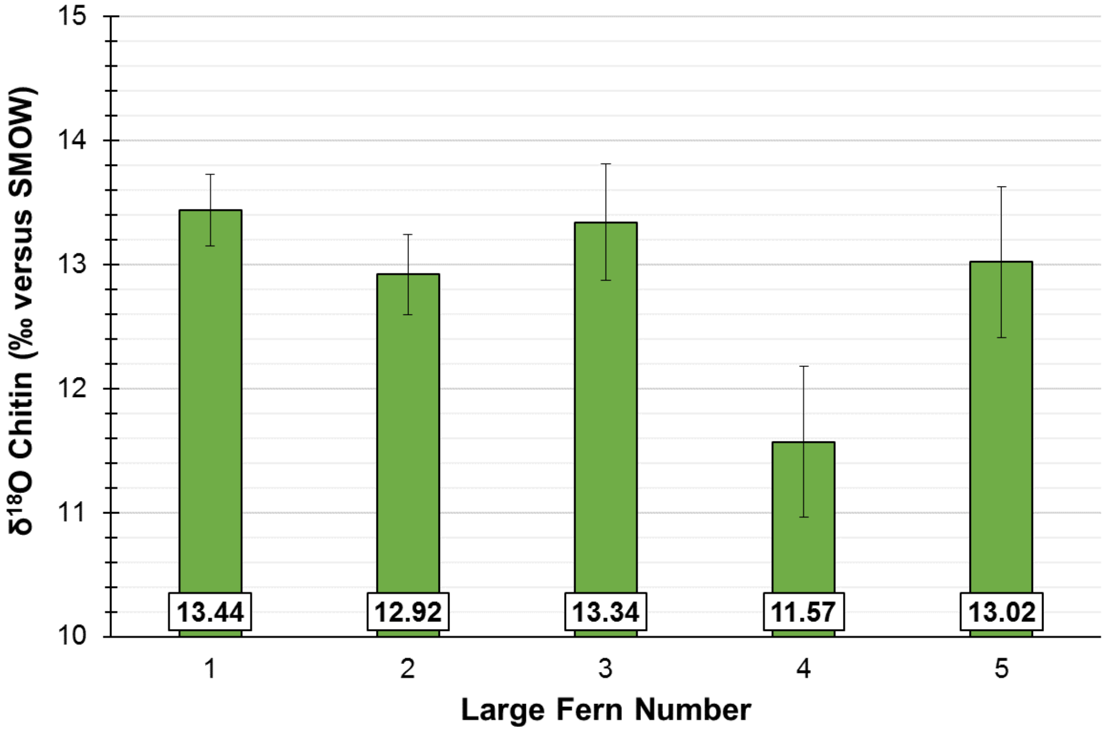


Figure 3.23 The mean $\delta^{18}O$ signatures of cockroaches collected from five large bird's nest ferns in Danum Valley (F = 2.245, $p = 0.073$). The number (n) of cockroaches analysed from each fern is presented in Table 3-5.

Table 3-5 Fern number (*n*), number of cockroaches analysed from each fern, their mean $\delta^{18}O$ signature (with standard error) as well as the range in $\delta^{18}O$ signatures recorded from each fern.

Fern *n*	***n* of cockroaches**	**Mean $\delta^{18}O$ (± S.E ‰)**	**Range in $\delta^{18}O$ (‰)**
1	26	13.44 (± 0.29)	11.37 – 15.49
2	25	12.92 (± 0.32)	8.95 – 15.58
3	18	13.34 (± 0.47)	10.7 – 16.89
4	10	11.57 (± 0.81)	8.41 – 14.77
5	16	13.02 (± 0.61)	7.11 – 14.63

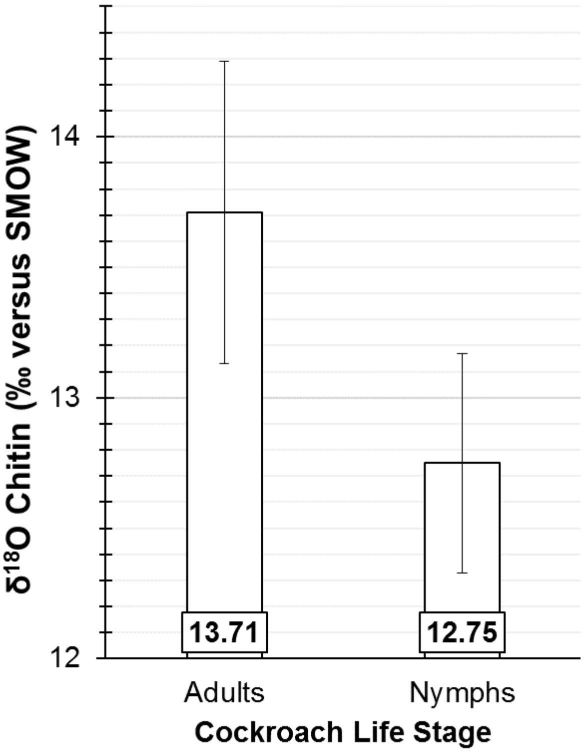


Figure 3.24 Mean $\delta^{18}O$ signature of adult ($n = 34$) and nymph ($n = 61$) cockroaches collected from bird's nest ferns in Danum Valley ($F = 3.041$, $p = 0.081$).

No significant differences were detected in the $\delta^{18}O$ signatures of cockroach chitin between the seven species of cockroach ($F = 1.908$, df = 6, $p = 0.088$, Figure 3.25). Each species of cockroach which was analysed is described with taxonomic detail in Table 3-6. It was likely that no significant differences were detected between cockroach species because there was such a high degree of overlap in the range of $\delta^{18}O$ values recorded for each species (Figure 3.26). Similarly, there were no significant interactions between cockroach species and life stage ($F = 0.72$, df = 6, $p = 0.545$).

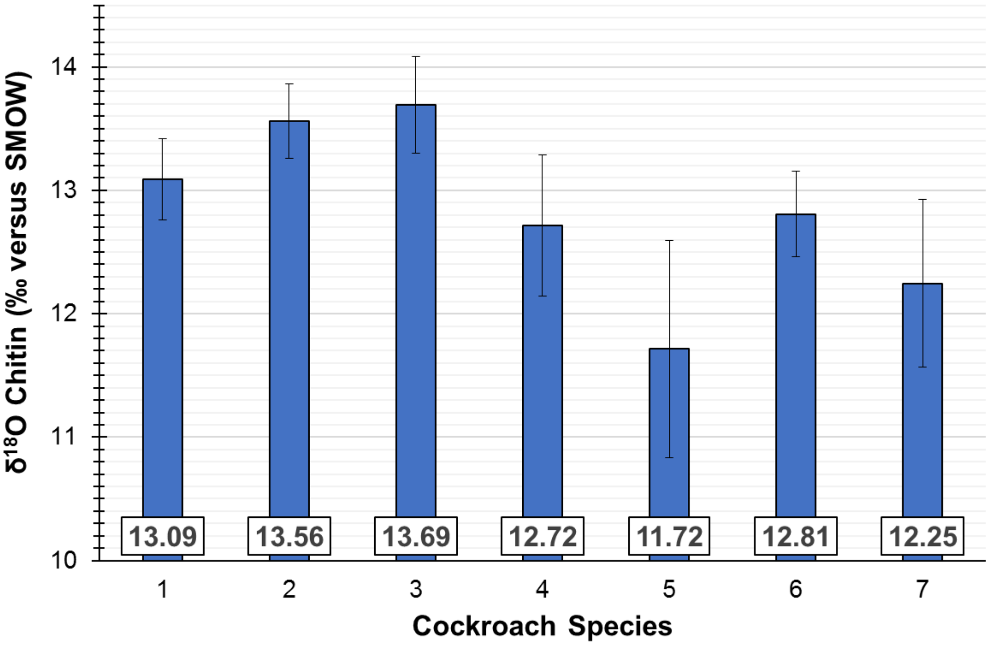


Figure 3.25 Mean δ^{18}O signature of each of the seven species of cockroach collected from five bird's nest ferns in Danum Valley (F = 1.908, p = 0.088).

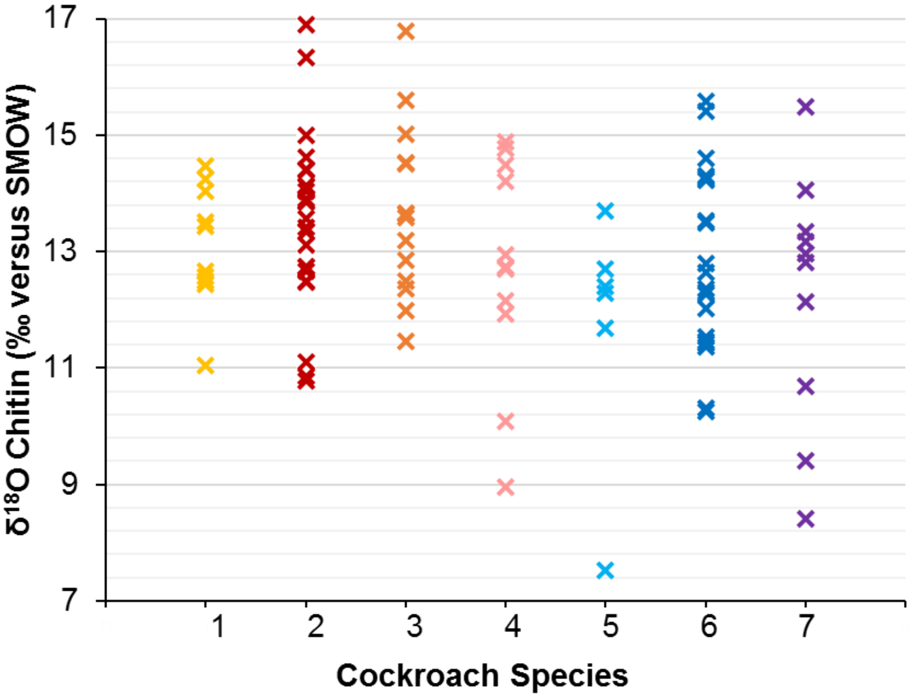


Figure 3.26 Range of δ^{18}O signatures recorded for each of the seven cockroach species. Each marker denotes the δ^{18}O signature of an individual cockroach.

There was no evidence to suggest that cockroach phylogeny influenced the δ^{18}O signature of chitin in the cockroaches collected from bird's nest ferns. As no significant differences were observed between cockroach families (F = 0.355, df = 2, p = 0.702, Figure 3.27). The family of cockroaches that each species belongs to is provided in Table 3-6. It is likely that no significant differences were detected between families because there was high degree of overlap in the range of δ^{18}O signatures recorded within and between cockroach families.

Table 3-6 Recognisable taxonomic unit (RTU), taxonomic information, number of specimens analysed, range of signatures across species, and mean δ^{18}O of species (with standard error).

RTU	**Full name**	**Family**	***n***	**Mean δ^{18}O‰ (± S.E)**	**Range δ^{18}O‰**
1	*Rhabdoblatta dysticoides* Kirby, 1903	Blaberidae	10	13.09 (± 0.33)	11.05 – 14.47
2	*Margattea* sp. Shelfford, 1911	Ectobiidae	24	13.56 (± 0.30)	10.79 – 16.89
3	*Panesthia* sp. Serville, 1831	Blaberidae	14	13.56 (± 0.30)	11.45 – 16.79
4	Undet. Corydiidae Saussure, 1864	Corydiidae	11	12.72 (± 0.57)	8.95 – 14.88
5	Undet. Ectobiidae sp. 1 Brunner von wattenwyl, 1865	Ectobiidae	6	11.72 (± 0.88)	7.11 – 13.70
6	*Haanina adusta* Hebard, 1929	Blaberidae	20	12.81 (± 0.35)	10.26 – 15.58
7	Undet. Ectobiidae sp. 2 Brunner von wattenwyl, 1865	Ectobiidae	10	12.25 (± 0.68)	8.41 –15.49
		Total	95	13.01 (± 0.17)	7.11 – 16.89

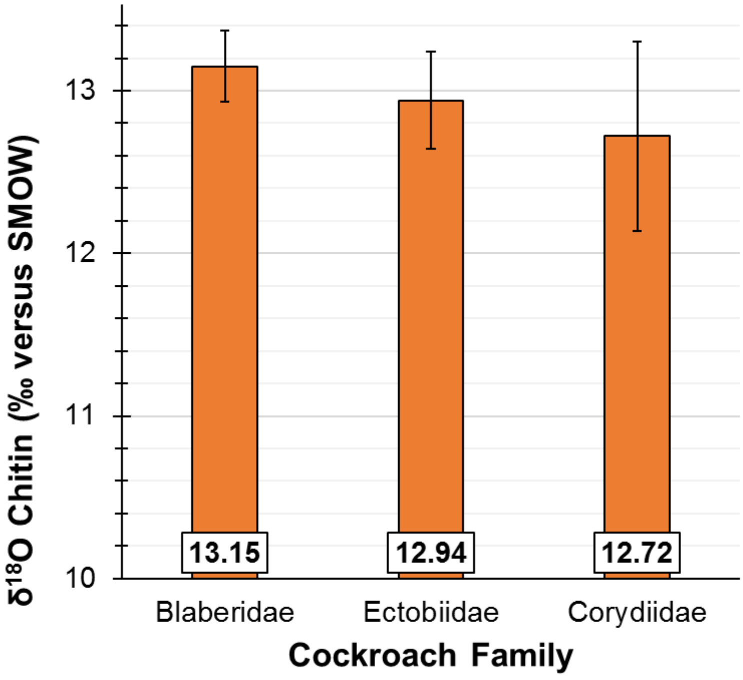


Figure 3.27 Mean δ^{18}O signature of each cockroach family (Blaberidae $n = 44$, Ectobiidae $n = 40$, Corydiidae $n = 11$) recorded from ferns in Danum Valley ($F = 0.355$, $p = 0.702$).

3.4 DISCUSSION

Global invertebrate populations are suffering in the face of anthropogenic disturbance and climate change (Lister and Garcia, 2018, Stork, 2018). This is especially prevalent in biodiversity hotspots such as Bornean tropical rainforest, where so much of the invertebrate biodiversity remains undocumented (Mori et al., 2017). Invertebrates that respire through spiracles are sensitive to moisture (Dial et al., 2006), and will be particularly vulnerable to extinction under climate change (Moritz and Agudo, 2013). This study sought to build the evidence base for using stable isotopes of oxygen from the chitinous exoskeletons of insects and other tracheated arthropods, to outline their vulnerability or resilience to habitat disturbance and climate change. Using pest cockroaches from an anthropogenically established but functional rainforest (Donald et al., 2018), and tropical cockroaches collected from bird's nest ferns in Danum Valley (Ellwood et al., 2002), the isotopic composition of insect chitin was indeed revealed to be a quantitative marker of the microclimatic conditions under which the animals were living.

The first question this study sought to answer was to what extent does microclimate influence the oxygen isotopic ($\delta^{18}O$) signature of chitin? Just two previous studies have shown that $\delta^{18}O$ in chitin is related to the atmospheric conditions provided by an insect's habitat, rather than the environmental water source (Ellwood et al., 2011, van Bergen et al., 2016). My study has revealed that, just as the microclimatic conditions across the Eden Project's Rainforest Biome (RFB) differed significantly, so too did the $\delta^{18}O$ signatures of the cockroaches collected from across the biome. The answer to my first question is therefore yes, microclimate predictably and significantly influences the $\delta^{18}O$ of insect chitin. The $\delta^{18}O$ signature of *Periplaneta australasiae* differed significantly between the collection sites across the RFB ($F = 15.12$, $p < 0.001$, Figure 3.15), with the greatest differences between cockroaches occurring between the two most microclimatically distinct sites. Over 24 hours, Site 6 provided the hottest (29.6°C) and driest conditions (51.3%) whereas Site 7 provided cool (25.0°C) and humid conditions (98.8%). In a rainforest, air temperatures typically increase with distance from the ground because leaf area index (canopy coverage) is reduced and convection currents dissipate heat energy upwards (Chapter 2). This was reflected in the rainforest biome because Site 6 which, on the 'cliff top', represented the highest vertical sampling point in the biome, approximately 30m higher than any of the other sites. By comparison, Site 7 was at the bottom of the Amazon thematic area's 25m high waterfall. This would have kept the air consistently humid and thermally buffered.

It was hardly surprising that Site 6 and 7 showed some of the greatest differences in climatic conditions. Although Site 2, which was situated in the Tropical Islands thematic area, provided the lowest AAT's (22.1°C) over 24 hours, Site 7 provided the most consistently high humidity

(98.8%). Had temperature been the most significant microclimatic variable to influence $\delta^{18}O$ of chitin, $\delta^{18}O$ signatures in cockroaches should have been lowest at Site 2. Although daytime and 24 hour cycle temperatures were significantly related to $\delta^{18}O$, daytime RH % showed the most highly significantly correlation with $\delta^{18}O$ of chitin ($p = 0.005$, Table 3-3). Consequently, the difference in daytime relative humidity between Site 6 and Site 7 of 47.5%, equated to a clear and significant difference of 2.37‰ in the $\delta^{18}O$ of chitin

In the Eden Project's RFB, the $\delta^{18}O$ of chitin was also shown to differ significantly with cockroach life stage. On average, the $\delta^{18}O$ signatures of adult *Periplaneta* (22.29‰) were 0.42‰ and 0.83‰ higher than both the late (21.87‰) and young nymphs (21.45‰). While the difference between adult cockroaches and late nymphs were not significant, the $\delta^{18}O$ of adult cockroaches was significantly higher than those of the young nymphs ($p = 0.005$). However, the difference between the greatest values of $\delta^{18}O$ recorded for adult and young nymphs *Periplaneta* was just 0.94‰, indicating that there is substantial overlap in the microclimate conditions tolerated by nymphs and adults. This is perhaps unsurprising given that they are the same, widespread invasive species, and likely one of the most climatically tolerant species of cockroach in the world.

The $\delta^{18}O$ signatures of adult *Periplaneta* cockroaches did not differ significantly across the RFB ($F = 0.51$, $p = 0.679$). However, this was not the case for young ($F = 26.73$, $p < 0.001$) and late ($F = 10.47$, $p < 0.001$) *Periplaneta* nymphs, which both showed significant differences between sites, with the greatest statistical differences between Sites 6 and 7. However, there is potentially a degree of bias as no adult cockroaches were collected from Sites 6 and 7, and therefore no isotopic signature exists for adults at these sites. The sites from which adult cockroaches were collected (Sites 1, 2, 3 and 4) were also the least significantly different in terms of their microclimate. Therefore the homogeneity of $\delta^{18}O$ signatures in adult *Periplaneta* across the RFB may actually be a reflection of the homogeneity of the microclimatic conditions of these sites. Conversely, for the four sites where adult cockroaches were collected, the mean range in $\delta^{18}O$ signatures was much greater (4.16‰) than those recorded from young (1.71‰) and late nymphs (2.57‰). This divergence of $\delta^{18}O$ signatures in adult *Periplaneta,* relative to the convergence shown by cockroach nymphs, likely indicates that the adults, which are able flyers (Schal et al., 1984) moved around the biome to a much greater extent than the nymphs. As such, the $\delta^{18}O$ signatures of adult *Periplaneta* would not necessarily reflect the environmental conditions of the site where they were collected, but rather capture the total variation in climatic conditions across the biome.

Cockroach nymphs do not have wings, therefore they will be more restricted in their dispersal abilities than adult cockroaches. Dispersal limitation would certainly explain why late instar nymphs showed slight δ^{18}O enrichment relative to young nymphs at Eden. Nymphs of earlier development stages would be unlikely to move far from their hatching site. The extent of δ^{18}O variation within a species was another key question posed by this study, and it seems that for *Periplaneta* cockroaches at least, a significant degree of variation occurs, but this variation was a reflection of variation in microclimatic conditions.

Another aim of this study was to determine whether oxygen isotopic fractionation of chitin occurred across individual insect exoskeletons. To overcome any potential differences in δ^{18}O as a result of site-specific differences in microclimate, rather than differences in δ^{18}O caused by fractionation, values of δ^{18}O were analysed as differentials from the δ^{18}O signature of a standard sampling unit, which was the hind right tibia (HRT). Differentials were calculated as the δ^{18}O recorded from a given body part minus the δ^{18}O recorded from the HRT. Doing so enabled a direct and reliable comparison of the extent of fractionation across the body. If significant fractionation had been detected across the exoskeleton, it would mean that future studies would need to be very concise and consistent with their collection of chitin samples. With the exception of the outer wings (Figure 3.21), no significant δ^{18}O fractionation occurred across the cockroach exoskeleton (Table 3-4). On average, the δ^{18}O of the other parts of the cockroach exoskeleton differed by just ± 0.27‰ compared with the standard sampling unit. While standardised sampling units in ecological studies ensure consistency and comparability (Srivastava et al., 2004), the discovery that the effect of fractionation is negligible across the exoskeleton provides reassurance that chitin can be obtained from any part of the exoskeleton and still provide a representative δ^{18}O for a given specimen.

Many invertebrates abandon limbs when threatened in order to avoid predation (Lewis, 1981, Schal et al., 1984), and indeed cockroaches often drop legs and antennae when handled or disturbed. By showing that fractionation across the body is not of significant concern, the progress of isotopic studies of chitin need not hinge on the availability of consistent chitin samples – almost any part of the exoskeleton will do. It also means that obtaining chitin samples need not be detrimental to the target species, because any lost limb can be used in isotopic analysis, and most arthropods will replace lost limbs upon their next moult (Lewis, 1981, Bell et al., 2007). Brooding cockroaches also drop eggs as an evasion technique (Willis et al., 1958) with new eggs laid every 16 days or so (Bell et al., 2007). In this study cockroach eggs were opportunistically collected, with egg laying females becoming the specimens whose exoskeletons were sampled in their entirety. The δ^{18}O of cockroach eggs were significantly depleted (-4.88*‰)* relative to the adults that produced them. While this is interesting, it is perhaps unsurprising given that cockroaches tend to lay their eggs in the coolest, dampest places available to them (Willis et al., 1958). This is likely because, as we have seen here, the youngest nymphs show the greatest response to climatic conditions. While a myriad of studies have considered isotopic fractionation in vertebrate egg production, revealing it to be a proxy for habitat use and physiology (Montanari, 2018), there is nothing in the literature with regard to invertebrate egg production (Schimmelmann, 2011).

This study showed that the significant differences in $\delta^{18}O$ of *Periplaneta* across the RFB were a reflection of site specific microclimatic differences. However, significant differences in $\delta^{18}O$ were also detected between *Periplaneta australasiae* and *Pycnoscelus surinamensis* ($p = 0.01$) collected from the same site (Site 1). These species specific differences in $\delta^{18}O$ may have arisen through physiological or behavioural differences. *P. surinamensis* are members of the family Blaberidae (giant cockroaches), which are typically burrowing cockroaches (Zangl et al., 2018) and almost exclusively parthenogenetic (Roth and Willis, 1956). This means that *P. surinamensis* reproduces asexually, and that the entire population are almost exclusively female. In fact, the widespread success of *P. surinamensis* as an invasive species has been attributed to its ability to reproduce asexually (Pellens and Grandcolas, 2002). Because *P. surinamensis* shows relatively high rates of cutaneous water loss compared with other cockroaches (Parker Jr and Niklasson, 1995), it favours a subterranean existence to conserve water. As *P. surinamensis* spends most of its time burrowing in moist soil and other damp material, it would logically show lower $\delta^{18}O$ signatures than *P. australasiae*, which spends a lot of time scurrying around in leaf litter (Kramer and Brenner, 2009). Certainly, the sensitivity of *P. surinamensis* to desiccation would explain why no specimens were recorded from the hottest and driest parts of the biome. However, *P. surinamensis* also does well in oil palm plantations (Pellens and Grandcolas, 2002), despite the characteristic extremes in oil palm climate (Chapter 2), plantations provide *P. surinamensis* with an abundance of rotting palm, an ideal burrowing substrate.

This study has shown that, not only is it possible to detect differences in $\delta^{18}O$ signatures between species, but that these differences most likely reflect the way that species use their habitats, rather than their phylogenetic position. Habitat use is largely a reflection of microclimatic conditions (Scheffers et al., 2014a, Wardhaugh et al., 2014) and many cockroaches, such as members of the family Blaberidae, burrow because they are at high risk of desiccation. These cockroaches are characterised by flattened bodies and reduced antennae, making them well adapted for burrowing and wedging into crevices. However, this body shape also provides a large surface area to volume ratio relative to other cockroaches, such as *Periplaneta australasiae* which are foraging cockroaches of the family Ectobiidae. Animals with large surface area to volume ratios provide a greater surface area for water loss. These cockroaches likely show lower $\delta^{18}O$ signatures, as well as smaller ranges in recorded $\delta^{18}O$, because they spend more time in subterranean spaces and moist habitats to minimise water loss. Here I have shown that $\delta^{18}O$ signatures can be used to infer species behavioural strategies, and in turn their habitat requirements.

No significant differences in $\delta^{18}O$ were detected from the Bornean cockroaches, which originated from five large bird's nest ferns in Danum Valley (Ellwood et al., 2002, Ellwood and Foster, 2004). Where significant differences were recorded between sites at the Eden Project, no significant differences in $\delta^{18}O$ signature occurred between ferns (F = 2.245, p = 0.073). While significant differences were recorded between adult and nymph *Periplaneta australasiae* in the RFB, no significant differences were recorded between life stages in the Bornean cockroaches (F = 3.041, p = 0.081). Although in both instances, the results approached significance, with adult cockroaches showing higher $\delta^{18}O$ signature relative to nymph cockroaches. On average, the difference between adult and nymph cockroaches in Borneo was 0.96‰, which was greater than the average difference between adults and nymphs at the Eden Project (0.63‰).

Although a significant difference occurred between *Periplaneta australasiae* and *Pycnoscelus surinamensis* in the RFB, no significant differences were detected between the seven Bornean cockroach species (Table 3-6). However, the point of this study was to confirm that the $\delta^{18}O$ signature of insect chitin reflects microclimatic conditions. Chapter 2 revealed that microclimatic conditions in the ferns were consistent regardless of location in the canopy, and indeed across habitats. Therefore a degree of homogeneity in the $\delta^{18}O$ of cockroaches collected from the ferns in Borneo was to be expected. The lack of significant differences in the $\delta^{18}O$ signatures of Bornean cockroaches likely reflected the habitat homogeneity and buffered climatic conditions that the ferns provided. This indicated that $\delta^{18}O$ in chitin responds to climatic conditions, but also provides quantitative evidence, in the form of a physiological marker, that bird's nest ferns are important thermal refuges.

The overall range of $\delta^{18}O$ signatures recorded from across the collection of Bornean cockroaches (9.78‰) was nearly double that of the *Periplaneta* cockroaches collected at the Eden Project (5.72‰). However, the also ferns contained a random assortment of species. Therefore we did not detect species specific differences in $\delta^{18}O$ at the fern level. However, the overlap in $\delta^{18}O$ signatures between species, suggests complementary resource use of the ferns by cockroaches. While the Bornean cockroaches represented an ecological community, the Eden cockroaches were largely represented by a single species, allowing us to explore the intricacies of $\delta^{18}O$ separation within a species. The divergence in $\delta^{18}O$ signatures of adult cockroaches at the Eden Project reflected their greater degree of movement around the biome relative to the nymphs. Further to this, individuals using their habitats in different ways showed different signatures, whereas in Borneo the cockroaches were essentially scattered between the ferns. This would explain the broad range of overlapping δ^{18}O signatures, and resulting overall homogeneity observed in the Bornean cockroaches. Indeed this underlines the sensitivity of stable isotope studies.

The mean range of δ^{18}O signatures recorded for each species of Bornean cockroaches was 5.73‰, which was almost exactly the same as the range of signatures recorded for *Periplaneta* across the RFB (5.72‰). Cockroaches of the family Ectobiidae (leaf litter cockroaches) (Schal et al., 1984), are likely to spend more time foraging and interacting directly with the atmosphere than burrowing species. Therefore they should show a greater range in δ^{18}O signatures compared to those that spend a greater deal of time in microclimatically buffered soils or damp organic material. Although no significant differences were detected between the three families of cockroaches ($F = 0.355$, $p = 0.702$), Ectobiidae (typically a foraging group) showed a greater range in δ^{18}O signatures (9.37‰), compared with the Blaberidae (6.53‰) and the Corydiidae (5.93‰*)* which are both burrowing groups. Indeed this supports what we saw at the Eden Project, that differences in δ^{18}O may be attributed either to behavioural or phylogenetic differences that lead cockroaches to interact with their habitat in different ways.

This study focused on the δ^{18}O in chitin of cockroaches collected from fairly distinct habitats: a tropical botanical garden, and five large canopy epiphytes. Though these settings were distinct in microclimate and location, the cockroaches collected from them share a rainforest connection. The RFB, albeit anthropogenically established, is a functioning rainforest (Donald et al., 2018), and the bird's nest ferns were collected from the high canopy of Bornean primary tropical rainforest. I showed in Chapter 2 that rainforests are characterised by moderated temperatures and consistently high humidities. Cockroaches collected from RFB sites with similar microclimatic conditions did not exhibit significantly different δ^{18}O signatures. Similarly in Borneo, bird's nest ferns provided statistically homogeneous microclimates, and consequently there were no statistically significant differences in the mean δ^{18}O signatures of the cockroaches inhabiting them. This provides strong evidence that δ^{18}O signatures in insect chitin respond to climate rather than environmental source water, which would be constant in both the RFB and in Borneo.

Rainforests are structurally complex, providing a range of microhabitats, and subsequently a wide range of microclimatic conditions. However, habitat complexity is reduced as rainforest is disturbed and degraded (Figure 3.28). For invertebrates living in disturbed habitats, such as oil palm, we would not only expect convergence in δ^{18}O signatures, but these signatures should also on average be higher than those of animals in rainforest habitats. Figure 3.28 models the range of δ^{18}O signatures that may associated with a habitat, based on its complexity, and the range of microclimatic conditions it provides.

Chapter 2 revealed that rainforests, from the forest floor through the vertical dimension and into the canopy, provide a broad range of climatic conditions. Although the low canopy remains consistently cool and moist, the high canopy can become as hot and as dry as an oil palm plantation. Consequently, the range of $\delta^{18}O$ signatures that would be recorded from rainforest animals would reflect the broad range in climatic conditions that the rainforest habitat provides. However, as shown by the model (Figure 3.28), with increasing habitat disturbance, the range of $\delta^{18}O$ signatures that would be recorded are reduced, until eventually just a small range of high $\delta^{18}O$ signatures would be recorded from an oil palm plantation.

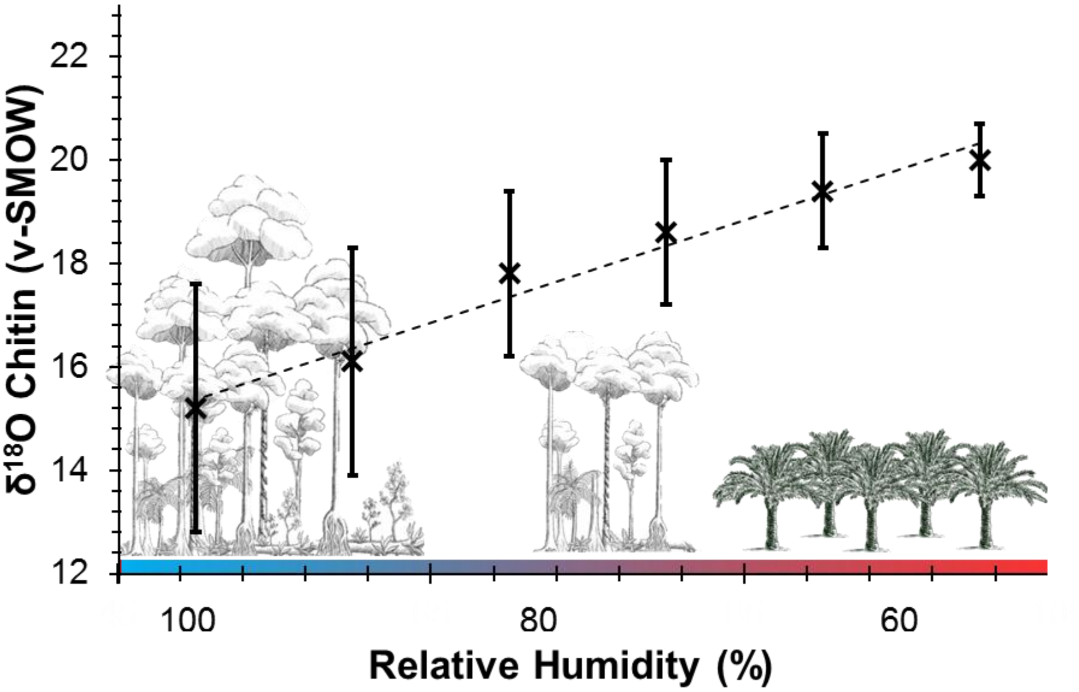


Figure 3.28 Model predicting the effect of declining relative humidity on the $\delta^{18}O$ signature of chitin in insect communities along a habitat gradient. The $\delta^{18}O$ signature will increase as conditions become hotter and drier, and the range of signatures recorded from the community would be reduced as vulnerable species are lost through the disturbance gradient.

If the recorded $\delta^{18}O$ signatures for a given species in the rainforest were consistently outside of the range of $\delta^{18}O$ signatures associated with the hot and dry oil palm landscape, this would indicate strongly that conditions in the oil palm would be beyond the tolerance of that particular species. Given that species tend to avoid climatic conditions beyond their tolerance (Suggitt et al., 2011), this would allow us to identify which species may risk extinction through the conversion of rainforest to oil palm, or under climate change. To truly understand the extent that the $\delta^{18}O$ of insect chitin can provide a marker of physiological tolerance and vulnerability under climatic change, we need to understand how $\delta^{18}O$ in chitin responds in different habitats (as predicted by the model in Figure 3.28). This chapter has provided evidence that: the $\delta^{18}O$ of chitin is related directly to relative humidity; that species with different behavioural and physiological traits can show isotopic distinction; and that these isotopic distinctions can be used to quantify habitat preferences and thermal tolerances. However, the $\delta^{18}O$ of chitin can only truly become a marker of climatic tolerance when we have shown precisely how the $\delta^{18}O$ signature of ecological communities respond to habitat gradients such as the transition from rainforest to oil palm plantation.

3.5 SUMMARY

- The oxygen isotopic composition ($\delta^{18}O$) of insect chitin is a reflection of the environmental conditions under which an insect has lived. When there are significant climatic differences between habitats, there will be significant differences in $\delta^{18}O$.
- Differences in $\delta^{18}O$ of chitin seem to be independent of genetics. Significant differences in climate are reflected as significant differences in the $\delta^{18}O$ of chitin, regardless of whether individuals are the same species i.e. *Periplaneta australasiae* at the Eden Project.
- The $\delta^{18}O$ of chitin is most closely associated with daytime relative humidity, although $\delta^{18}O$ of chitin also significantly correlates with temperature.
- With the exception of the outer wings, the effect of fractionation on the $\delta^{18}O$ of chitin was shown to be negligible across the cockroach exoskeleton. This means that future studies could use chitin from any part of the exoskeleton and this would still provide fairly accurate and comparable $\delta^{18}O$ signatures.
- The $\delta^{18}O$ signatures of nymph or young cockroaches is more closely associated with the microclimatic conditions of a given habitat. This is likely because adult cockroaches can fly, and therefore move around to a much greater extent than the wingless nymphs.
- At the Eden Project, the significant differences in $\delta^{18}O$ between *Periplaneta australasiae* and *Pycnoscelus surinamensis* were likely because of their different habitat preferences rather than discreet differences between species. In Borneo all of the cockroaches collected came from climatically buffered bird's nest ferns, and consequently no discreet differences between species were detected.
- Species will have significantly different $\delta^{18}O$ signatures if their behavioural or physiological traits lead to different interactions between the cockroach and its habitat. Where individuals experiences different climatic conditions, this will be reflected in their $\delta^{18}O$ signatures.
- Knowledge of the relationship between $\delta^{18}O$ and microclimatic conditions can indeed be used to predict which species will be lost through climatic change.

4 HOW IMPORTANT ARE PREDATORS IN BIRD'S NEST FERNS?

CONTEXT

Bird's nest ferns are ideal model systems because every trophic level is represented in their ecological communities, from primary producers to herbivores, detritivores and predators. While a substantial body of research has considered the ecological interactions and forces governing the lower trophic levels, there is a distinct knowledge gap concerning predators in bird's nest fern. Centipedes are apex predators in invertebrate food chains and exist in large numbers in bird's nest ferns. Centipedes, and other invertebrate predators, drive ecosystem function by regulating decomposer populations. Yet we know nothing of the ecology or functional significance of these top predators in forest canopies and focused studies on this group under natural conditions are rare in the literature. In fact, centipedes have never been collected from Sabah and the only time centipedes were collected from Borneo was during the Oxford University Expedition to Sarawak in 1932. Given the current pressures on Borneo's natural landscape, it seems timely to take stock of this grossly understudied group. This chapter provides the first detailed observations of the diversity and community composition of centipedes in the rainforest canopy using the bird's nest fern model system. It describes the role of the ferns in the life history of centipedes, revealing the ferns to be important nesting sites in the canopy. Competition and predation are pillars of traditional ecological theory. However, the rules that typically govern ecological communities on the forest floor are frequently broken in the upper reaches of the forest canopy. This chapter reveals that a functionally significant community of centipedes reside in the forest canopy, and offers new insight into the ecological interactions between those at the top of the food chain. The results also suggest that predation may be much more important in governing canopy communities than previously thought.

4.1 INTRODUCTION

4.1.1 KEYSTONE PREDATORS

Centipedes (Myriapoda: Chilopoda) are a group of ferocious predatory invertebrates. They are one of the oldest, most widely distributed, extant terrestrial arthropod groups, finding their greatest diversity in the tropics of Southeast Asia (Bonato et al., 2016). Although some 3150 species have been recorded, it is likely that many remain undescribed (Lewis, 1981, Edgecombe and Giribet, 2007). This is especially true for Sabah, where centipedes have never been collected. Centipedes have probably received relatively little attention compared with other arthropod groups because of their venomous bite and the difficulties associated with studying such animals in the field. Centipede bites are excruciatingly painful, and in the case of larger centipedes such as the *Scolopendra* species, require urgent medical attention

(Remington, 1950, Mohri et al., 1991, Fung et al., 2011, Fenderson, 2014). There are a number of recorded instances where envenomation has resulted in death (Lewis, 1981). The defining characteristic of this group of formidable arthropods is their venom tipped forcipules which are enlarged front legs that are modified into fangs (Lewis, 1981) (Figure 4.1).

Figure 4.1 First pair of walking legs in centipedes are modified into venom injecting fangs also known as forcipules.

Centipedes predate a wide range of invertebrates, from springtails and earthworms (Gao et al., 2017), to many kinds of larval and adult insects, including cockroaches (Molinari et al., 2005), beetles (Juen and Traugott, 2007) and flies (Formanowicz Jr and Bradley, 1987). Some of the larger centipedes belonging to the family Scolopendridae also predate on vertebrates such as geckos and skinks (Donald et al., 2017b), snakes (Chiacchio et al., 2017), and small mammals, including bats (Lindley et al., 2017) and mice (Clark, 1979). In turn centipedes are prey items to a wide range of vertebrates (Catling, 1988, Shiel et al., 1991), however there are documented instances where even consumption of centipedes by larger animals such as snakes, have been insufficient to subdue them (Arsovski et al., 2014).

As centipedes predate such a wide range of invertebrates, they play a significant role in soil trophic interactions, yet their importance as top predators in canopy food webs has received little attention. The regulation of prey populations by predators exerting top down control, is a well-known phenomenon in trophic ecology (Lawrence and Wise, 2000, Schneider and Brose, 2013). Lower trophic levels i.e. detritivores and fungivores, can be directly controlled through predator prey interactions (Zhao et al., 2013, Gao et al., 2017). Centipedes are opportunistic in nature (Guizze et al., 2016, Chiacchio et al., 2017), and their ability to switch prey items makes them highly successful across a range of habitats (Formanowicz Jr and Bradley, 1987, Klarner et al., 2017). As centipedes are prevalent in many terrestrial ecosystems (Klarner et al., 2017), they influence the structure of soil fauna communities worldwide.

Despite the fact that centipedes are keystone predators, and represent a functionally significant component of ground soil fauna (Kalisz and Powell, 2000, Nordberg et al., 2018), they have received less attention than more conventional soil organisms. Ground soil food webs have been studied in detail (de Ruiter et al., 1995, Wardle, 2002, Ettema and Wardle, 2002, Wurst et al., 2018), however far less attention has been directed upwards to the trophic structure of suspended soils, such as those associated with canopy epiphytes like the bird's nest fern (Donald, 2018). Centipede communities from ground soil are still poorly understood, however the ecology and behaviour of centipedes in the rainforest canopy is virtually unknown.

4.1.2 A MULTIDIMENSIONAL LANDSCAPE

Typically, trophic interactions between soil invertebrates have been studied for animals collected from the 'ground zone', which represents 0 – 6 inches above the ground (Elton, 1973). This two-dimensional view of the world is reflected by the way in which arthropod abundance, even within tropical forest canopies, is expressed (as per m^2) (Basset, 2001). However, entomological perspectives are changing, as the number of studies focussing on the spatial and vertical distribution of arthropods within forest canopies has risen (Basset et al., 1992, Ellwood et al., 2002, Basset et al., 2003, Ellwood et al., 2009, Basset et al., 2015). More recently, in the face of habitat disturbance and species extinctions (Lister and Garcia, 2018, Stork, 2018), studies have focused on the spillover of organisms, and their associated functions, from natural into degraded habitats such as logged forests and oil palm plantations (Foster et al., 2011, Blitzer et al., 2012, Lucey and Hill, 2012, Edwards et al., 2014). However, little consideration has been given to the functional cascade as species turnover between the forest floor and canopy. This is perhaps surprising, not least because species that are adapted to cope with harsh physical conditions in the forest canopy (Chapter 2) should be resilient to climate change and habitat degradation (Williams et al., 2008, Huey et al., 2012). Concern for forest animals under climate change is largely focused on those that live on the forest floor, which is the most stable forest strata (Williams et al., 2008, Scheffers et al., 2014a). However, many of these animals can also be found in the suspended soils of canopy microhabitats, and indeed the wider canopy environment (Ellwood and Foster, 2004). The habitat requirements and climatic tolerances of these animals may not be as narrowly defined as previously thought.

4.1.3 INTO THE CANOPY

Accessing the canopy is no easy feat for non-flying invertebrates, but perhaps centipedes are adapted for an arboreal lifestyle. Studies have recorded centipedes from within forest canopies, including the trunks (Frund, 1987) and tree crowns in temperate forest (Gruppe et al., 2008). Gruppe *et al* (2008) showed a complete separation of centipede species between the ground, tree trunks and canopy. Interestingly, previous studies showed that centipedes can rotate their body when falling (Anderson et al., 1995), in the same angular momentum that ensures that cats always land on their feet (Kane and Scher, 1969). This previously unaccounted for locomotory trait in centipedes could be an adaptation to arboreal life. Centipedes also have retroverted claws at the end of each leg (Bonato et al., 2010) which makes them strong and able climbers; indeed *Scolopendra* centipedes suspend part of their bodies from cave ceilings in order to predate bats (Molinari et al., 2005, Lindley et al., 2017).

The canopies of Southeast Asia's lowland tropical rainforests are among the tallest on Earth, frequently exceeding heights of 50m (Ellwood and Foster, 2001). For a centipede, travelling from the forest floor to the high canopy would be the equivalent of a human climbing to the top of Dubai's Burj Khalifa (823m). Despite the tremendous scaling necessary, Ellwood *et al* (2002) recorded high abundances of centipedes (a mean of 126 ± 60) in large mature ferns (~200kg). These centipedes, which were not taxonomically placed, contributed 12% of the total invertebrate biomass of the ferns, and 5% of the total biomass of the wider tree crown (Ellwood and Foster, 2004). This was comparable to the 8% that centipedes contributed to the total biomass of ground soil communities (Kalisz and Powell, 2000).

In terms of their species richness, abundance and biomass, centipedes will be fundamental to ecosystem function, but to date nothing has been done to elucidate the community structure, or the role that centipedes play in the canopy environment. This chapter investigates the biology of rainforest centipedes using the bird's nest fern as a model system, pinpointing the precise three-dimensional distribution of species throughout the canopy. I answer the following questions: (1) How abundant are centipedes in bird's nest ferns? (2) How much biomass do these centipedes contribute to the rainforest canopy? (3) How similar is the species diversity of centipedes in the high and low canopy? (4) How are these species assembled into communities? And finally, (5) why do centipedes use bird's nest ferns?

4.2 METHODS

4.2.1 STUDY SITE

The fieldwork for this study took place in the Danum Valley Conservation Area in Sabah, Borneo in April 2018 (4.55º N, 117.40º E; *ca* 100 m elev.). The conservation area covers approximately 43,000 hectares and is classified as lowland evergreen dipterocarp forest

(Marsh and Greer, 1992). The high canopy was accessed by inserting climbing lines into the highest branches (Ellwood and Foster, 2001), and using Double Rope Access Technique (DRT) (Maher, 2006). The low canopy (Moffett, 1993, Moffett, 2000) was accessed by ladder, or DRT. The annual average rainfall at the Danum Valley Field Centre is 2822 mm, with a mean annual temperature of 26.7 ºC and a mean annual relative humidity of 94.5 % at 08 00 h and 73% at 14 00 h (Walsh and Newbery, 1999).

4.2.2 FERN SAMPLING AND CENTIPEDE IDENTIFICATION

With the aid of several research assistants, 44 bird's nest ferns were collected from the forest canopy. The ferns were all of a similar size with a rosette diameter of 30 – 60cm (as per Ellwood *et al*, 2002) and fresh weights of ~5 kg. Of these ferns, 22 were collected from the high canopy (~50m) and 22 from the low canopy (~4m). All of the ferns were collected from *Parashorea tomentella* trees (Sym.) Meijer (Dipterocarpaceae). The ferns were plucked from their attachment sites and placed in heavy duty, transparent plastic bags. Clear bags were necessary to allow us to see large and aggressive centipedes emerging from the ferns. The bags were sealed and lowered from the tree using a pulley system. At the field centre, ferns were removed from their bags and divided into smaller sections. These components included the soil, leaves and leaf litter. All fern material was further sorted by hand, and any animals encountered were placed into 75% ethanol solution. In instances where large centipedes emerged, these animals were collected in plastic boxes and placed in the freezer. We counted centipede nests and the number of eggs or young centipedes during the sorting process. Adult centipedes curled protectively around a clutch of eggs or young juveniles confirmed brood nests. The remains of the soil core (Ellwood et al., 2002, Turner and Foster, 2009) were placed into Winkler bags (Besuchet et al., 1987) for four days.

Upon removal of the Winkler bags, we checked the fern material again using a magnifying lens and collected any remaining animals. All specimens were transferred to clean ethanol solution and stored in a freezer at – 20 ºC for preservation. We exported all animals to the UK in Whirlpac™ bags at the end of the field season. In the UK, specimens were sorted to working taxonomic groups e.g. beetles (Coleoptera), ants (Formicidae) and springtails (Collembola), and counted. Centipedes were identified to recognisable taxonomic unit (RTU) using taxonomic keys (Lewis, 2010a, Lewis, 2010b) as well as primary taxonomic literature, and stored in 70 % ethanol solution. All centipede species identifications are provided in Appendix I.

4.2.3 ESTIMATIONS OF BIOMASS

In order to preserve the specimens (Wardhaugh, 2013), estimations of centipede biomass were derived from power law equations (Rogers et al., 1976, Ellwood and Foster, 2004). Body length was measured from the tip of the head to the end of the last trunk segment, excluding the posterior legs. For specimens that were contorted, string was used to record the body length. All measurements were taken to the nearest 0.1mm using callipers or a calibrated graticule under the microscope. Power law models were used to establish body size – weight relationships of the form $y = a (x)^{b}$, with y the dry weight (mg) of the specimen, x the body length and b the regression coefficient.

4.2.4 STATISTICAL ANALYSIS

Patterns of species co-occurrence were compared with statistical randomizations of the original centipede species occurrence data. Using the null model software EcoSim (Gotelli and Entsminger, 2004), it was possible to simulate 10,000 random matrices for each analysis and test the differences between these and the observed communities. *C*–score (Stone and Roberts, 1990) analyses were performed to measure the average number of checkerboard pairs for species that co-occurred from a matrix of all of the species that were present across the ferns. For communities structured by competition, as would be expected for solitary and aggressive predators such as centipedes, the *C*–score should be greater than expected by chance (Gotelli, 2000). By using EcoSim's default randomization algorithm, and maintaining the total number of occurrences for each row and column, each generated matrix had the same number of samples as the original matrix (Connor and Simberloff, 1979). This algorithm had a low chance of falsely rejecting the null hypothesis (Type I errors), but provided good computing power for the detection of non-random patterns (Gotelli, 2000). *C*–score analysis detects whether interspecific competition structures the communities. To determine whether centipede abundance, size, individual biomass or total biomass were equal across the forest strata, Mann Whitney *U* Tests were performed. Multivariate ordinations (nMDS) and analysis of similarity percentage (SIMPER) were conducted using PRIMER 7 (PRIMER-e, 2017). Abundance and biomass data were log10 transformed to meet assumptions of normality. One Way ANOVA's were conducted on species richness (S), Shannon's Diversity Index (H), Simpson's Diversity Index (D), and Pielou's Evenness (J') for each of the ferns across the forest strata. Finally, One Way ANOVA's were performed on daytime temperatures in the ferns and the canopy.

4.3 RESULTS

4.3.1 CENTIPEDE ABUNDANCE AND DISTRIBUTION

A total of total of 305 centipedes were collected in this study. In the high canopy, all but one of the ferns contained centipedes, giving a total of 185 centipedes from 21 bird's nest ferns. In the low canopy, 120 centipedes were recorded from 16 bird's nest ferns (Figure 4.2). Six ferns in the low canopy did not contain centipedes. The mean number of centipedes per fern was 8.4 ± 2.9 in the high canopy and 5.5 ± 1.6 in the low canopy. This gave an overall mean of 6.9 ± 1.6 centipedes per fern across ferns from both heights. Across all of the ferns collected, some 84% (37/44) contained centipedes, as well as an abundance of other arthropods (refer to Section 4.3.8). Although there were more centipedes in the high canopy than in the low canopy, the distribution of centipedes per fern was not significantly different between the two heights (Mann Whitney *U* = 191. 5, *p* = 0.232, Figure 4.3).

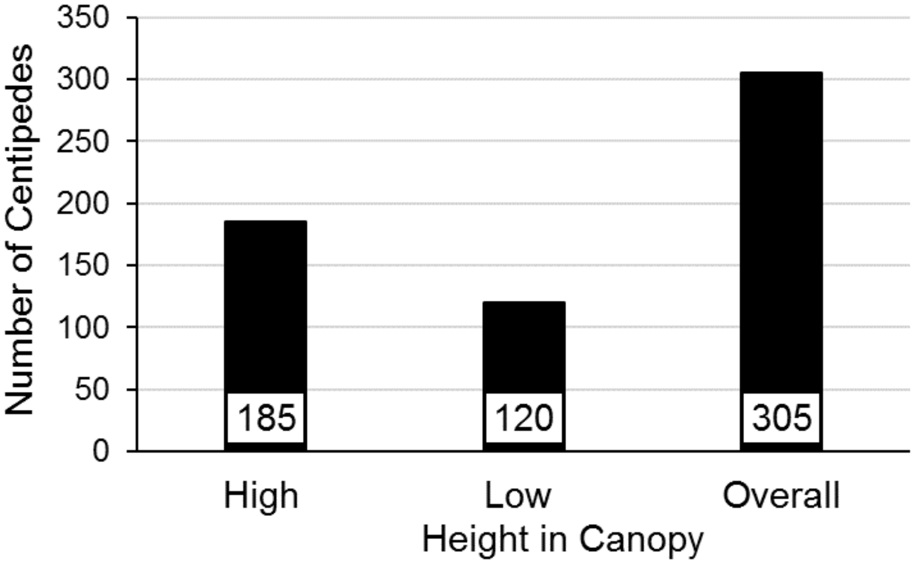


Figure 4.2 Total number (*n*) of centipedes recorded from ferns in the forest canopy.

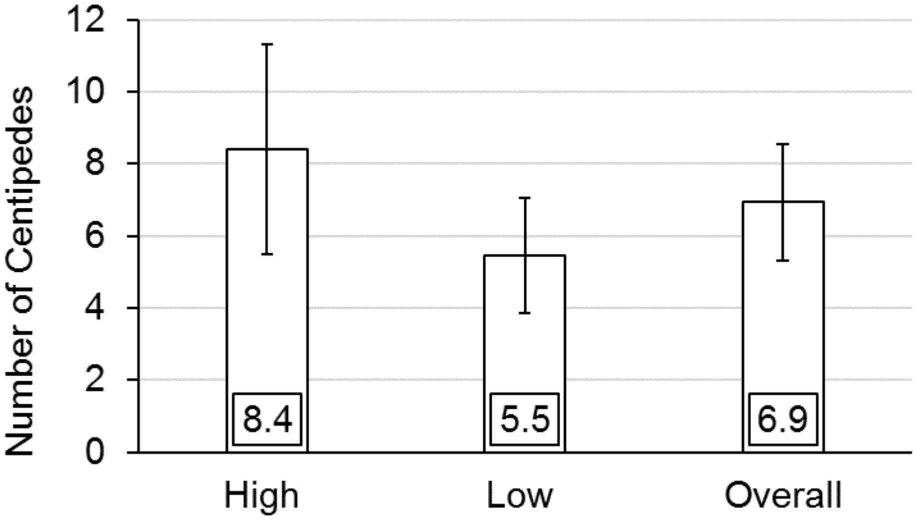


Figure 4.3 Mean number of centipedes per fern from the forest canopy.

4.3.2 BIOMASS

A total centipede biomass of 11,298 mg was recorded across the ferns, equating to 256.8 ± 51.3 mg per fern. Given that there are around 50 bird's nest ferns in a hectare of rainforest canopy in Danum Valley (Ellwood et al., 2002), this study essentially captured the biomass of one hectare of canopy's worth of centipede biomass (256.8 mg x 50 bird's nest ferns per hectare = 12,838 mg per hectare).

Of the total biomass recorded from this study (11,297 mg), the bulk was concentrated in the high canopy (70.4 % High = 7952 mg, 29.6% Low = 3346 mg, Figure 4.4). Even though the number of centipedes did not differ significantly between the high and low canopy, the centipedes were typically larger (Section 4.3.4), and so the biomass contributed by individual centipedes was greater in the high canopy (High = 49 ± 10.8 mg, Low = 22.5 ± 1.7 mg, One Way ANOVA $F = 14.87$, $p < 0.001$, Figure 4.5). Consequently, the mean biomass of centipedes per fern in the high canopy was more than double that of ferns in the low canopy (High = 362 ± 88 mg, Low = 148 ± 43.3 mg, Mann Whitney $U = 131.0$, $p = 0.009$, Figure 4.6).

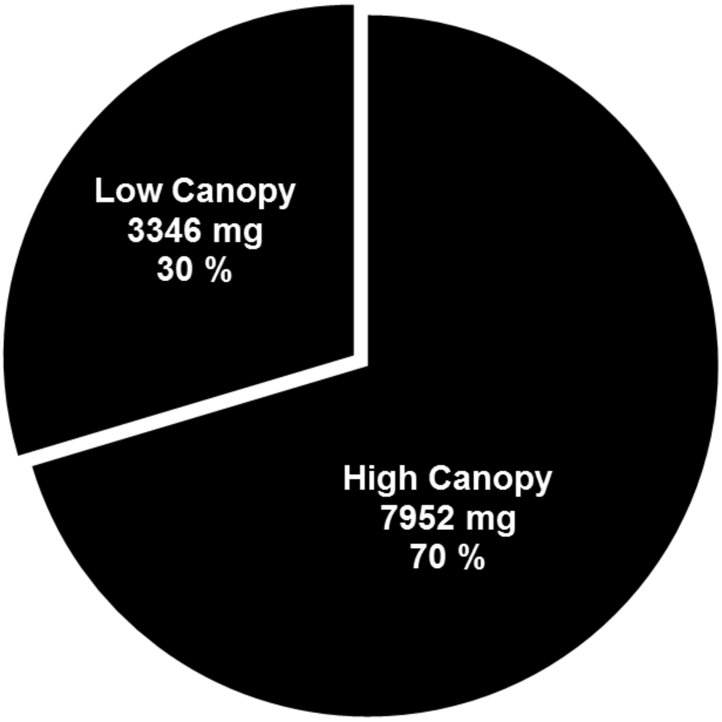


Figure 4.4 Proportions of the total centipede biomass collected in this study (11,298 mg) in the high and low canopy.

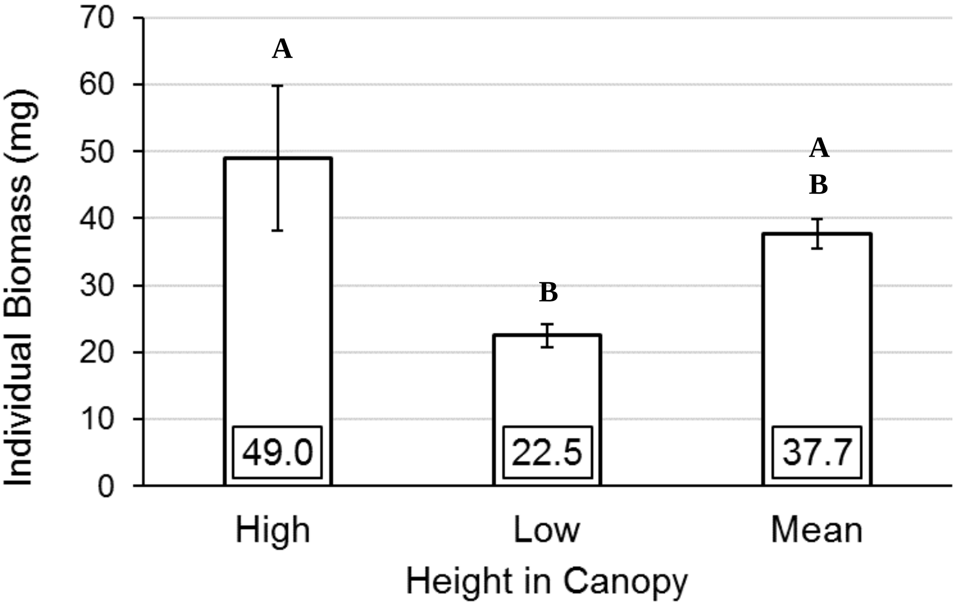


Figure 4.5 Mean individual biomass of centipedes from the high canopy, low canopy and overall. Bars with different letters denote significant differences ($p < 0.001$).

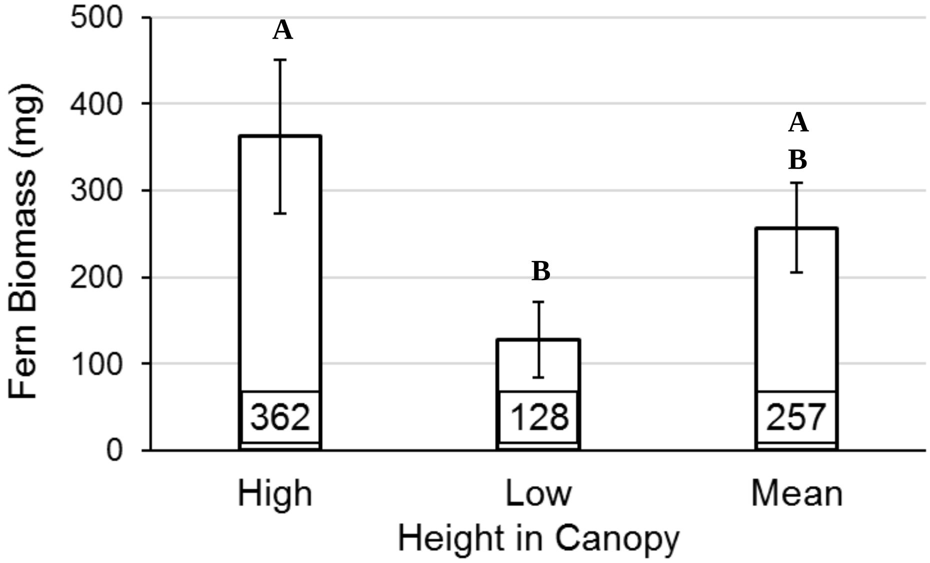
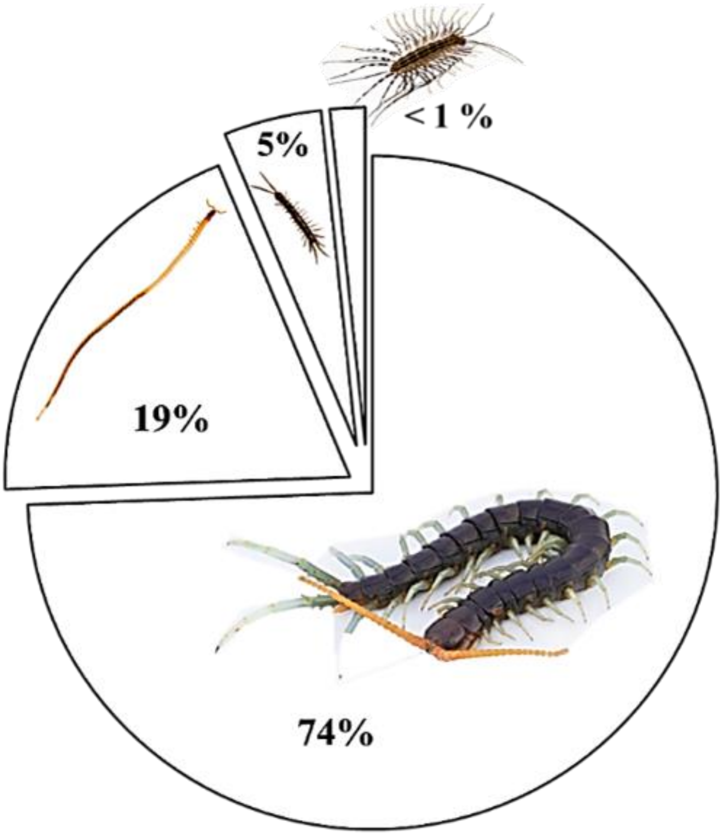


Figure 4.6 Mean total biomass of centipedes from the high canopy, low canopy and overall. Bars with different letters denote significant differences ($p = 0.009$).

4.3.3 TAXONOMY

The centipedes recorded in this study belonged to four Orders (Scolopendromorpha n = 227, Geophilomorpha n = 59, Lithobiomorpha n = 14 and Scutigeromorpha n = 5) (Figure 4.7) across 8 families and 13 recognisable taxonomic units (RTU's) (Table 4-1). At the level of Order, the community composition of centipedes was consistent at both heights (Figure 4.8) with Scolopendromorpha dominating with contributions of 71% (Low) and 75% (High) to the total centipede biomass. Similarly, the Geophilomorpha contributed 22% (High) and 25%

(Low) of the total biomass. However, at the level of family, the structure showed a marked difference with the greatest contribution to total biomass coming from centipedes of the family Scolopendridae, making up 75% (5936mg) of the biomass in the high canopy, but just 31% (1050mg) of the total biomass in the low canopy (Figure 4.9). The remaining contribution of Scolopendromorph centipedes in the low canopy came from Cryptopidae (1317mg), which accounted for 39% and the greatest contribution to biomass in the low canopy. Cryptopidae and Scolopendridae are both families in the order Scolopendromorpha. The Mecistocephalidae (Geophilomorpha) contributed 18% (1444mg) of the total biomass in the high canopy, and a comparable 22% biomass in the low canopy (749mg). Other families belonging to the Order Geophilomorpha included the Ballophilidae and Schendylidae, although both families were represented by a single specimen.



SCOLOPENDROMORPHA

n = 227, 74%

GEOPHILOMORPHA

n = 59, 19%

LITHOBIOMORPHA

n = 14, 5%

SCUTIGEROMORPHA

n = 5, <1%

Figure 4.7 Number of centipedes of each order, with illustration of the characteristic body form of each group.

Table 4-1 List of centipede species including full taxonomic name and authority, family affiliation, number of animals collected from low and high canopy, mean individual biomass (± standard error).

Morphospecies	Family	*n* collected		Mean individual biomass (mg) (± SE)
		Low	High	
Ballophilus sp. Cook, 1896	Ballophilidae	1	0	81.8
Cryptops sp. or spp. Leach, 1815	Cryptopidae	68	2	19.1 (± 0.95)
Lamyctes sp. Meinert, 1868	Henicopidae	4	7	13.6 (± 3.8)
undetermined Lithobiidae	Lithobiidae	2	1	25.2 (± 3.2)
Mecistocephalus cf. *punctifrons* Newport, 1843	Mecistocephalidae	14	34	35.0 (± 1.6)
Mecistocephalus sp Newport, 1843	Mecistocephalidae	2	6	52.0 (± 3.5)
Otostigmus angusticeps Pocock, 1898	Scolopendridae	1	121	37.2 (± 2.5)
Otostigmus sp. 1	Scolopendridae	0	2	94.2 (± 8.0)
Otostigmus sp. 2	Scolopendridae	18	0	33.0 (± 5.3)
undetermined Schendylidae	Schendylidae	0	2	81.6 (± 23.8)
Scolopendra subspinipes Leach, 1815	Scolopendridae	10	5	111.2 (± 28.9)
undetermined Scutigeridae	Scutigeridae	0	2	41.7 (± 23.7)
undetermined Thereuoneminae	Scutigeridae	0	3	22.0 (± 9.8)
	Total	120	185	

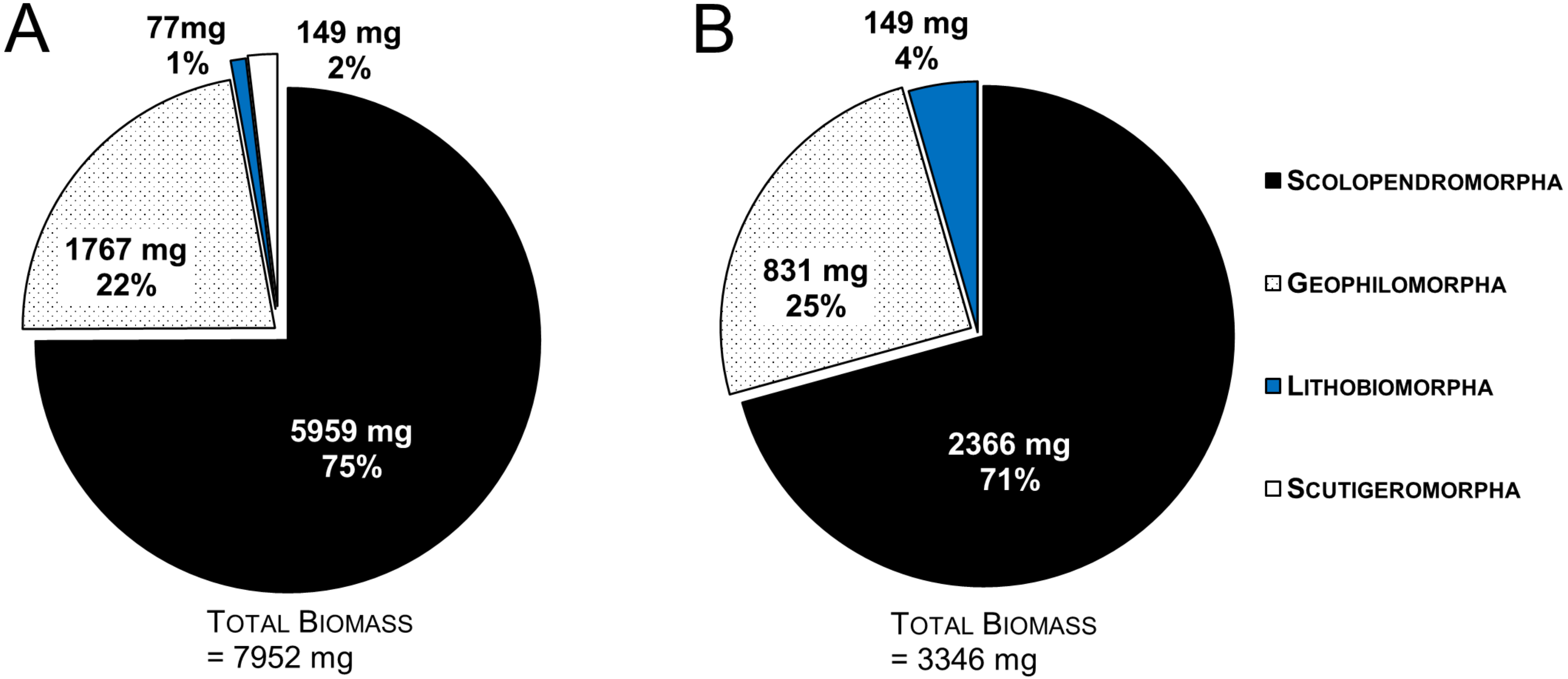


Figure 4.8 The distribution of biomass contributed by centipedes of each of the four Orders of Chilopoda in (A) the high canopy, and (B) the low canopy.

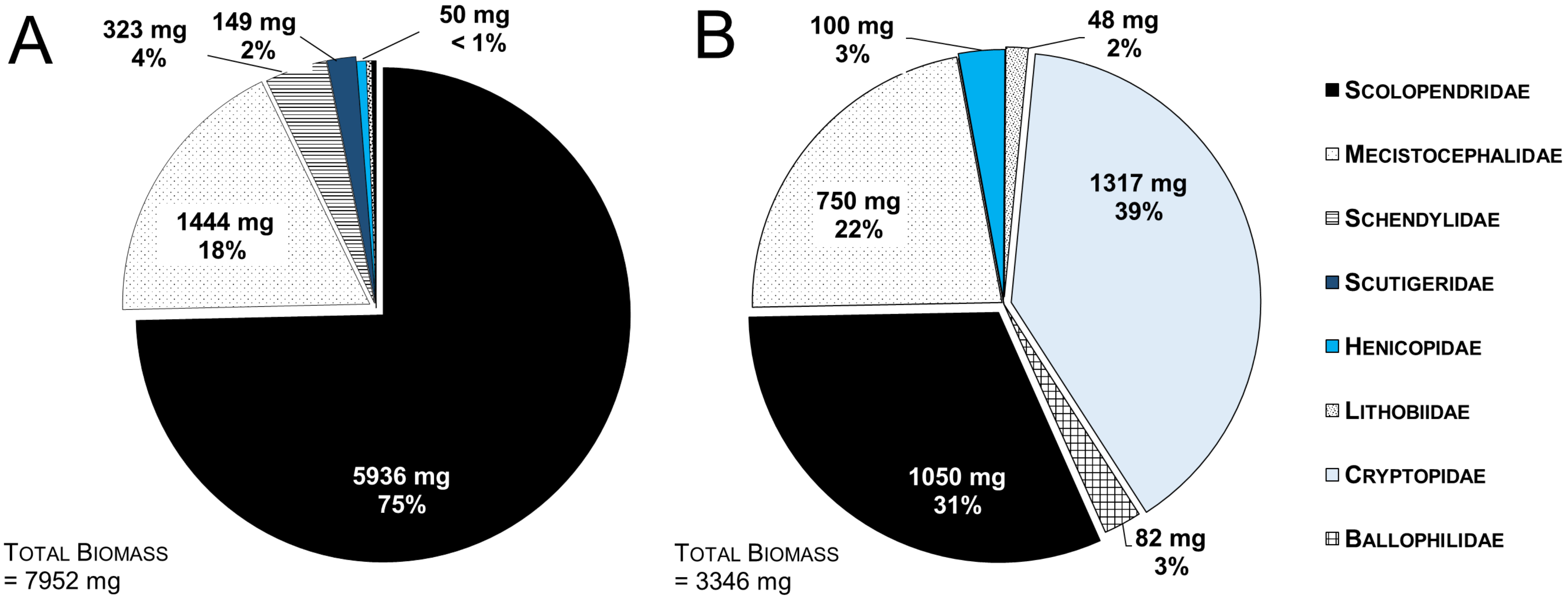


Figure 4.9 The distribution of biomass contributed by centipedes of different Families in (A) the high canopy, and (B) the low canopy.

4.3.4 BODY SIZE

Centipedes in this study ranged in body length between 2.6mm and 119.9mm (mean 15.1 ± 0.8mm), with a range of individual biomasses between 4.1mg and 311 mg (mean 37.7 ± 2.2mg). *Scolopendra subspinipes* (Leach, 1815) were the largest individual centipedes to be recorded in this study, with body lengths up to 119.9 mm. *Lamyctes* sp. (Meinert, 1868) were the smallest, one adult *Lamyctes* sp. specimen recorded from the high canopy was just 2.6mm in length. In the high canopy, individual centipedes were significantly larger (17.5 ± 1.3mm) than those in the low canopy (11.4 ± 0.6 mm) (Mann Whitney *U* = 9067.5, *p* = 0.007, Figure 4.10), and this significant increase in body size was responsible for the increased biomass of centipedes in the high canopy.

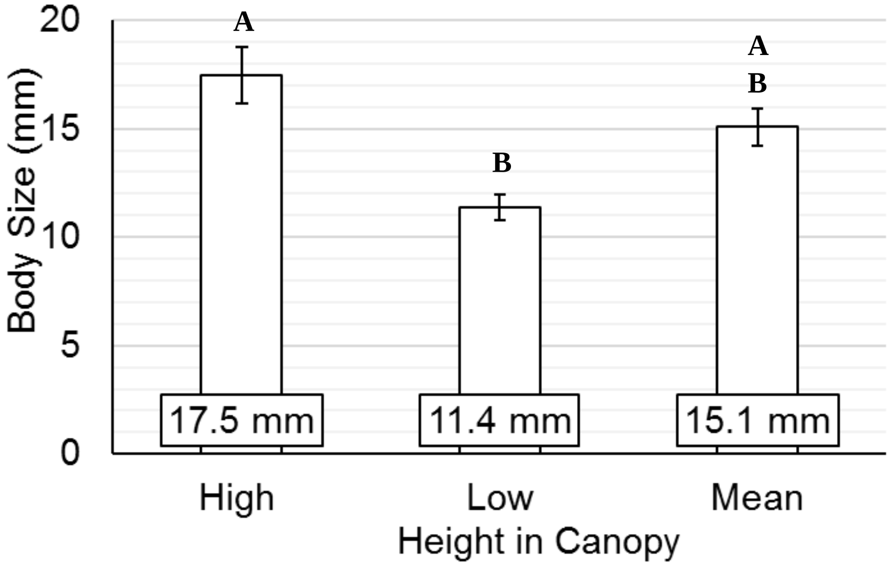


Figure 4.10 Mean body size (mm) of centipedes in the high and low canopy, as well as the overall mean. Bars with different letters denote significant differences (*p* = 0.007).

4.3.5 COMMUNITY ASSEMBLY

Overall, the community structure was remarkably similar within, and between the high and low canopy, with Scolopendromorph centipedes constituting about two thirds of the overall community at both heights. One Way ANOVA's showed no significant differences in Species Richness (S) (*F* = 2.49, *p* = 0.13), Shannon's diversity index (H) (*F* = 2.39, *p* = 0.13), Simpson's Diversity Index (D) (*F* = 1.88, *p* = 0.18), or Pielou's Evenness Index (J') (*F* = 1.70, *p* = 0.20) between the high and low canopy. At the higher taxonomic level of order, the community composition was consistent, but at the species level, there was a near complete separation between the forest strata. Bray Curtis similarity analysis and non-metric multidimensional scaling (nMDS) of the community assemblage data confirmed the distinct separation in species between the high and the low canopy (Figure 4.11). While a small degree of overlap was observed, SIMPER analysis revealed an average dissimilarity of 86% between the forest strata. Proportional contributions to partitioning the communities was greatest in the

Scolopendromorphs *Cryptops* spp. 29% (which dominated in the low canopy), followed by *Otostigmus angusticeps* 18%, *Scolopendra subspinipes* 8% and the geophilomorph, *Mecistocephalus* spp. 19% (which were abundant in the high canopy).

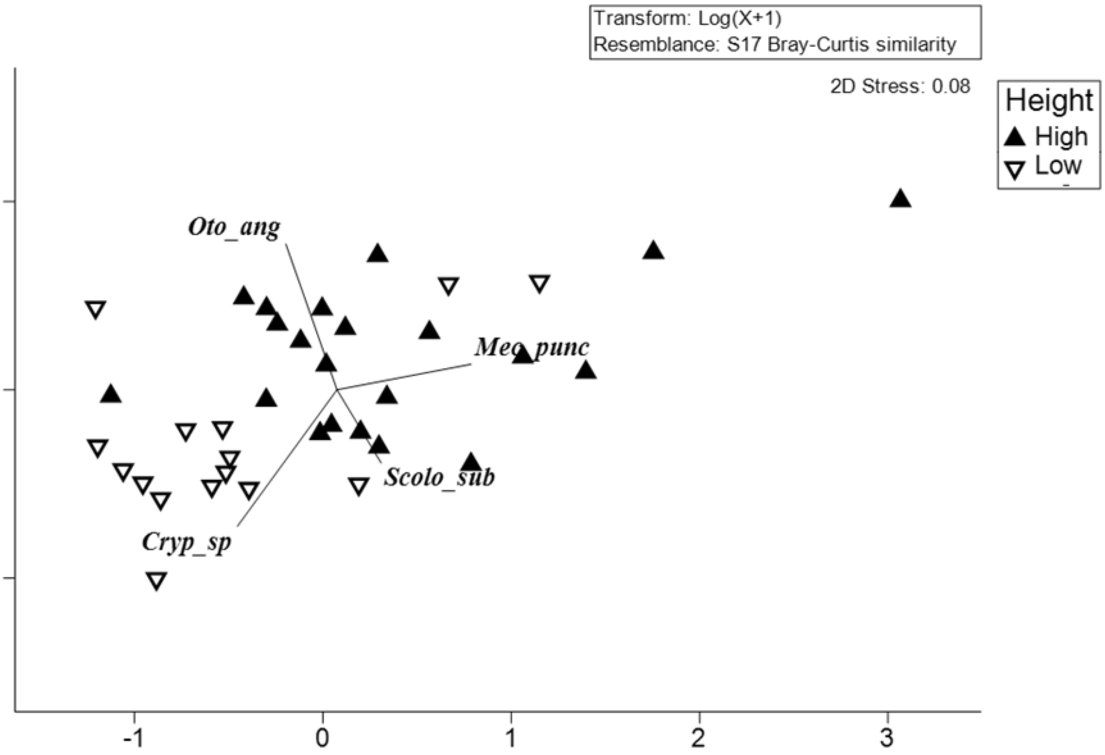


Figure 4.11 Non metric multidimensional scaling (nMDS) of the community structure of centipedes in bird's nest ferns collected from the high and low canopy. Vectors are overlaid illustrating which centipede species were responsible for pulling the distribution in a given direction.

4.3.6 COMPETITION

In competitively structured communities, *C*–scores should be greater than expected by chance, that is, the C_{obs} should significantly greater than the C_{sim}. Despite an almost complete vertical stratification in the centipede community, which could have been indicative of a highly competitive community, *C*–score analysis did not reveal any significant checker boarding ($C_{obs} = 16.62$, $C_{sim} = 16.59$, $p = 0.44$). Separating the centipedes into their respective high and low canopy communities also returned non-significance in terms of species co-occurrence, although in the low canopy the observed *C*–score was lower than that of the simulated random communities ($C_{obs} = 3.97$, $C_{sim} = 7.91$, $p = 0.38$) suggesting species aggregation rather than segregation. In contrast, the observed *C*–score in the high canopy was higher than that of the random simulations, suggesting species segregation ($C_{obs} = 8.05$, $C_{sim} = 7.81$, $p = 0.085$) although this was not significant.

4.3.7 NESTING BEHAVIOUR

In this study, 10 active centipede nests were recorded across seven bird's nest ferns (Table 4.2). Each nest consisted of an adult female curled protectively around a clutch of eggs or a cluster of young juveniles. Centipedes nesting with eggs had between 18 and 32 eggs, while the nests with juveniles consisted of between 9 and 24 hatchlings. Four additional suspected nests were noted, due to the presence of similarly sized young juveniles (between 5 and 12 centipedes). However in the absence of an adult these groups were not recorded as nests. Three bird's nest ferns supported more than one active nest. Each of these shared nest sites was recorded from high canopy ferns. Just two centipede nests were recorded from bird's nest ferns in the low canopy. All of the recorded centipede nests belonged to centipedes of the family Scolopendridae (Table 4-2). On three instances, during the fern sampling processes, we observed filial cannibalism (Siriwut et al., 2014) whereby the adult centipede began to consume the eggs after the nest was disturbed.

Table 4-2 Morphospecies, location in canopy, number of nests, nest size and development stage of nests.

Morphospecies	**Height in canopy**	***n* of nests**	**Nest size**	**Development stage of nests**
Otostigmus angusticeps Pocock, 1898	High	6	18 and 27 18, 22, 23, 24	Eggs Hatchlings
Otostigmus sp. 2	Low	1	17	Hatchlings
Scolopendra subspinipes Leach, 1815	High Low	2 1	26 and 32 9	Eggs Hatchlings

4.3.8 PREY ABUNDANCE

Other than the centipedes (Chilopoda), invertebrates from a further 30 taxa were recorded from the ferns. A full list of the taxa recorded are provided in Appendix II. The major taxa, of which more than 50 individuals were collected across the ferns, are shown in Figure 4.12. Including centipedes, the mean number of individuals per fern was 427 (± 107). This meant that there were a substantial number of potential prey items in the ferns (Figure 4.13). In both Figure 4.12 and Figure 4.13, centipedes are shown in red, providing a direct comparison of their abundance, relative to that of potential prey items in each fern. Spiders (Araneae) are highlighted in both Figure 4.12 and Figure 4.13. While spiders may fall prey to centipedes, spiders are also top invertebrate predators. Interestingly the mean abundance of spiders per fern was not significantly different to that of the centipedes (Mann Whitney U = 644.5, p = 0.345).

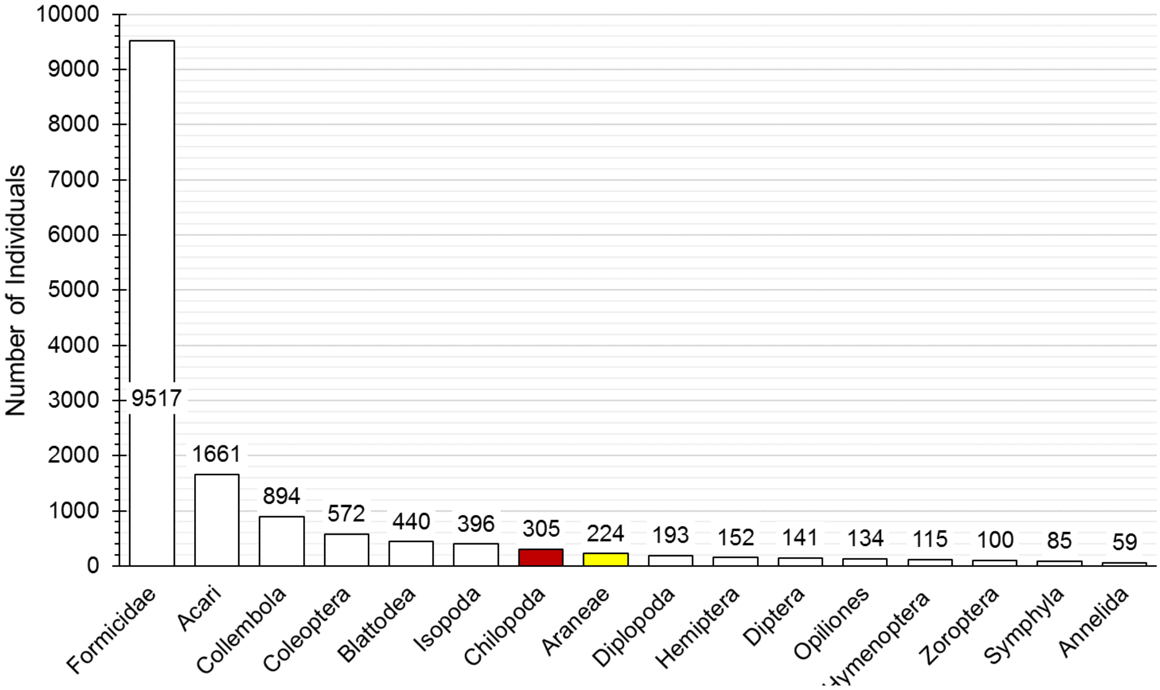


Figure 4.12 Total abundance of the 16 taxonomic groups represented by more than 50 individuals across the bird's nest ferns collected for this study. Centipedes (Chilopoda) in red. Spiders (Araneae) in yellow.

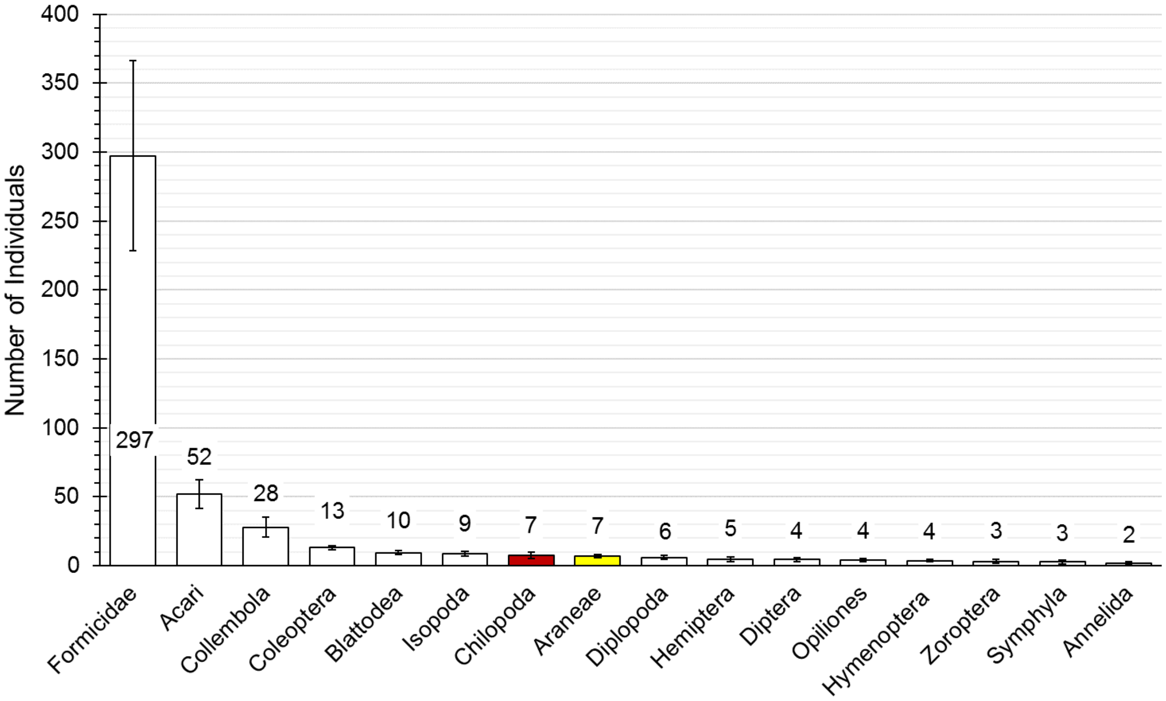


Figure 4.13 Mean abundance per fern (with standard error) of the 16 most abundant groups recorded across the bird's nest ferns (n = 44). Centipedes (Chilopoda) in red. Spiders (Araneae) in yellow.

4.3.9 MICROCLIMATE IN BIRD'S NEST FERNS

Although the microclimatic conditions inside bird's nest ferns were explored in detail in Chapter 2 of this thesis, additional data were collected to compliment this study of centipedes in the canopy. Mean daytime temperatures inside the ferns at both heights were lower than those in the surrounding canopy (One Way ANOVA, F = 15.39, $p < 0.001$, Figure 4.14). In the high canopy, mean daytime temperatures inside the ferns (26.3 ºC ± 0.2) were 3°C cooler than ambient air temperatures in the canopy (29.3ºC ± 0.4). Remarkably, the difference between ambient air and fern internal temperatures was three times greater than the difference between the high and low canopy (29.3 ± 0.4ºC versus 28.4 ± 0.5 ºC). At 15:00, the difference between fern temperatures and ambient air temperature in the high canopy was 6 ºC (Figure 4.14). Even in the low canopy, the fern was up to 1.6 °C cooler than ambient air temperature. Generally, as ambient air temperatures increased, the ferns became cooler, leaving a difference of just 0.5 °C in mean temperature between the high and low canopy ferns. The difference was not significant (Tukey HSD p = 0.756). These results were consistent with those of Chapter 2.

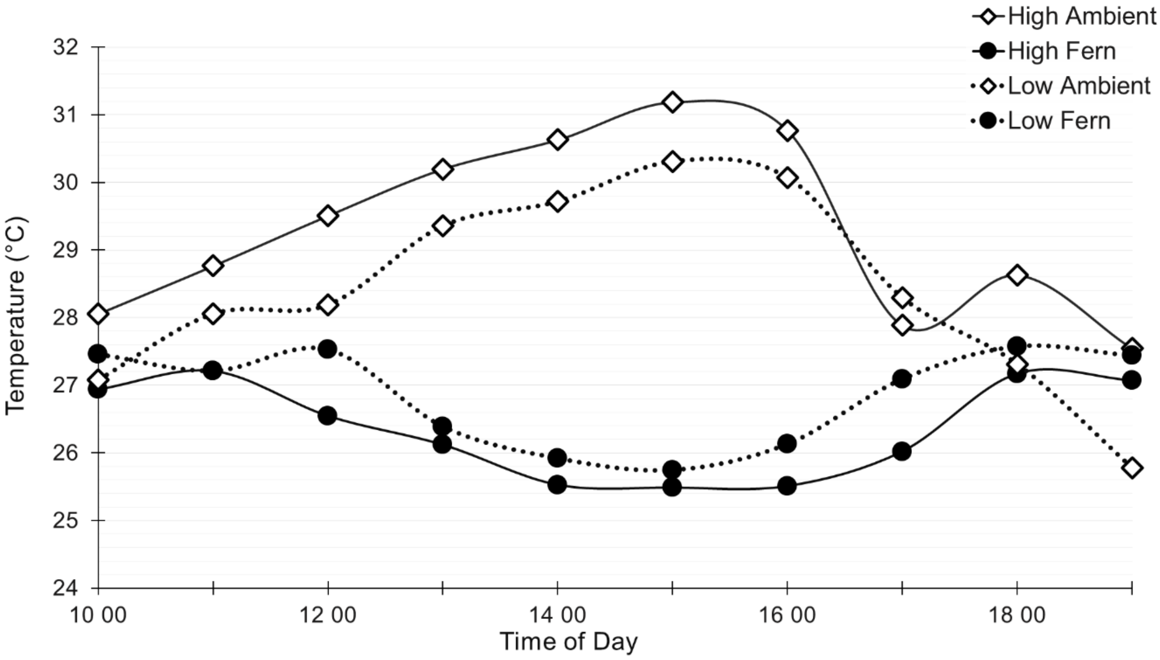


Figure 4.14 Daytime temperature variation of bird's nest ferns and the canopy environment between 10:00 and 19:00.

4.4 DISCUSSION

This chapter has revealed widespread complementary usage i.e. coexistence and resource sharing, of bird's nest ferns by centipedes. A somewhat unexpected outcome given that, from what is known of centipedes, one would expect them to be territorial and aggressive towards one another. Bird's nest ferns are, however, abundant throughout the world's tropical rainforests, supporting a wide range of animals, from arthropods (Ellwood et al., 2002, Ellwood and Foster, 2004) to vertebrates such as geckos and skinks (Donald et al 2017), frogs (Scheffers et al., 2014c) and bats (Tan et al., 1999). This chapter provides the first detailed account of predators, and the highest trophic level in the ferns. And even though predation is critical to the functioning of ecosystems, no other study has considered the effect of predation on the ecological community in the bird's nest fern model system. The ferns themselves are keystone species, and have a disproportionately large effect on the functioning of the canopy ecosystem. However, the importance of the ferns, not just to ecosystem function, but to the preservation of species at all trophic levels, makes them an umbrella species for conservation. Prioritising bird's nest ferns in conservation decisions will safeguard the diverse communities of both vertebrate and invertebrate species that the ferns support as well as the unique resources that the ferns provide.

This chapter has revealed that bird's nest ferns are a cornucopia brimming with an abundance of potential prey items for predators. So it is perhaps unsurprising that centipedes and other predators including spiders, which showed similar abundances (Figure 4.13), would seek out the ferns when foraging. Although foraging is less efficient in complex environments (Menge and Sutherland, 1976), centipedes can switch between foraging strategies according to prey abundance (Scharf et al., 2011). When prey abundance is high, centipedes adopt a sit and wait strategy (Guizze et al., 2016). When abundance is low, they actively forage and ambush prey (Formanowicz Jr and Bradley, 1987). Bird's nest ferns are an abundant source of herbivorous, saprophagous, xylophagous and frugivorous invertebrates, all of which make easy prey for centipedes. As top predators of an opportunistic nature (Edgecombe and Giribet, 2007, Chiacchio et al., 2017), centipedes likely seek out bird's nest ferns when roaming the rainforest canopy. Indeed the bird's nest fern cornucopia may be the reason why these 'terrestrial' predators venture into the canopy.

A previous study of centipedes on the rainforest floor which used 1 m x 1m quadrats, found a mean biomass of 31.62 mg / m^2 (Klarner et al., 2017). Because the study by Klarner *et al* (2017) sampled centipedes from the top 5cm of soil, their values for abundance and biomass represent $0.05m^3$ of habitat ($1m \times 1m \times 0.05m = 0.05m^3$). In this study, each bird's nest had a soil core diameter of ~30cm, and subsequently a radius of 15cm. The radius can be used to calculate an approximate volume of soil contained in the spherical fern soil core. As such, each bird's nest fern in this study contained approximately 0.014m^3 of soil. Therefore our sampling units represented three and a half times less soil by volume (0.014 m^3 versus 0.05 m^3) than Klarner *et al* (2017), yet the biomass of centipedes contained in fern soils was an order of magnitude greater (256.7 mg versus 31.6 mg). This shows clearly that centipede biomass, and therefore predatory functional biomass, is more highly concentrated in canopy suspended soils. This is perhaps not surprising given the relative frequency with which we discovered centipedes nesting in bird's nest ferns. However, it also suggests that predation pressures, and the stress on other invertebrates to avoid predation, will be much higher in suspended soils.

Biomass is a traditional measure of the functional significance (Schneider and Brose, 2013) of individual animals, but this chapter also focussed on species diversity and community composition. Whilst competition was not detected to be the driver of species assembly among centipedes, a clear and distinct vertical stratification in the community composition was observed between the high and low canopy. Even though at the highest taxonomic level of Order, the community structure appeared consistent (Figure 4.8), at the family level the community structure showed a marked shift (Figure 4.9). Families of the Order Scolopendromorpha, Scolopendridae and Cryptopidae, accounted for 74% of all centipedes recorded, and were responsible for partitioning the high and low canopy. SIMPER analysis revealed that *Cryptops* spp. [Family: Cryptopidae], *Otostigmus angusticeps* and *Scolopendra subspinipes* [Family: Scolopendridae] accounted for 29%, 18% and 8% respectively of the total variation observed between the high and the low canopy. *Cryptops* spp. were abundant, and contributed a significant amount of the biomass to ferns in the low canopy, yet they were almost absent from the high canopy. *Cryptops* spp. were one of the smaller species to be collected in this study (Table 4-1), and centipedes from the high canopy were significantly larger than those in the low canopy. Body size may be a limiting factor with regards to accessing the canopy. It would be more energetically expensive for small bodied non-flyers to access the canopy, but also the desiccation risks would be higher. There may also be greater risk of predation for smaller centipedes in the high canopy. *Cryptops* are also blind (lacking ocelli), and while the low canopy may be a worthwhile foraging extension of the forest floor, the high canopy may be a frontier too far removed from the subterranean existence to which these centipedes are adapted. By contrast, *Otostigmus* and *Scolopendra* are large and aggressive centipedes (Guizze et al., 2016). They are also accomplished climbers (Lindley et al., 2017, Molinari et al., 2005), it is also therefore logical that these centipedes would dominate the high canopy.

Studies have examined competitive interactions and species assemblages at lower trophic levels in the bird's nest fern (Ellwood et al., 2009, Snaddon et al., 2012, Fayle et al., 2015, Ellwood et al., 2016). However, no study has focused on assembly at the highest trophic levels.

Centipedes are not social but typically aggressive, and one would therefore expect them to show negative spatial associations with each other. Yet this chapter has revealed that centipedes coexist in the ferns, resulting in high overall abundances. Why do bird's nest ferns support such a high diversity and abundance of centipedes? Well, it is likely that the fern's thermal buffering capabilities (Chapter 2), as well as the abundance of a wide range of prey animals, make the ferns a resource worth sharing.

Competition and coexistence over such valuable resources leads to niche partitioning and species complementarity. Indeed, studies have found evidence of mutualisms and species aggregation in bird's nest ferns (Ellwood et al., 2016). According to classical ecology, e.g. Diamond (1975), communities are shaped by interspecific competition for shared resources, and while this may be the case in trophically complex systems such as the wider forest environment, in simple systems, predation is likely the dominant driver of species interactions (Menge and Sutherland, 1976). Niche partitioning and species complementarity could explain why the *C*-scores did not detect any significant competitive interactions between centipedes in any of the ferns. Complementary resource use leads to fewer antagonistic interactions (Ashton et al., 2010), and this would explain the consistently high invertebrate diversity found in bird's nest ferns (Ellwood et al., 2002, Ellwood and Foster, 2004). Negative spatial associations have been shown between centipedes and trophically similar groups such as geckos (Hickerson et al., 2004), possibly the product of interspecific competition or predation between different predator guilds (Hickerson et al., 2012, Hickerson et al., 2018). This chapter looked within the centipede community and did not detect competition, suggesting that centipedes share the bird's nest fern resource in a complementary way. However, this raises the intriguing question of precisely how centipedes and synaptic groups partition the ferns. Previous studies have found competition between arthropods to be less important in the harsh conditions of the high forest canopy (Ellwood et al., 2009, Ellwood et al., 2016), and in the absence of competition among the centipedes, we should look at other explanations for community structure such as complementarity. Niche partitioning, namely the sharing of resources, would explain the patterns of usage by centipedes in bird's nest ferns.

Centipedes are able climbers (Remington, 1950), but because they lack a discrete epicuticular layer (Cloudsley-Thompson and Crawford, 1970), they are highly vulnerable to desiccation. Similar to the moist, dark crevices that centipedes frequent, bird's nest ferns are a moist, dark refuge in the canopy. They provide a stark contrast to the characteristic extremes in temperature and humidity of the wider canopy environment (Chapter 2 and Figure 4.14). Indeed, air surrounding the ferns is cooler and more humid than ambient conditions in the forest canopy (Freiberg and Turton, 2007, Scheffers et al., 2014c) (Chapter 2). Many of the climatically sensitive animals known to use bird's nest ferns (Chapter 2 and Chapter 3), are also documented prey items of larger centipedes (Guizze et al., 2016, Chiacchio et al., 2017). Such an abundance of prey could in itself encourage centipedes to access the canopy and lie in wait (Molinari et al., 2005, Guizze et al., 2016). It is easy to imagine why ferns are attractive for predators. They are a climatically buffered base from which to ambush other shelter seeking animals, or to forage throughout the canopy. Because centipedes risk desiccation in the canopy, they are certain to benefit from the dampening capabilities of bird's nest ferns, and these buffering abilities underline the importance of the ferns as a resource at vulnerable times, the most vulnerable of which would be when nesting.

Centipedes provide parental care (Tallamy, 2001, Bonato and Minelli, 2002, Edgecombe and Giribet, 2007, Trumbo, 2012, Siriwut et al., 2014). Based on the fern's buffering abilities (Chapter 2), and abundance of prey items (Figure 4.13), they are ideal 'nurseries'. While there are numerous reports of the reproductive and brooding behaviours of centipedes of the family Scolopendridae (Brunhuber, 1970, Mitić et al., 2012, Cupul-Magaña et al., 2018), this is the first study to report on centipede nesting in the rainforest canopy. In addition, multiple nests were recorded from a single fern on three occasions. There are no other recorded instances of centipedes sharing nesting sites. Most likely this is because centipedes remain with their broods, and as such they are vulnerable during this life stage (Lewis, 1981, Machado, 2000).

Not only has this study provided the first focused account of predators in bird's nest ferns, but it has also provided the first detailed account of centipedes in the forest canopy. It revealed that the ferns are critically important microhabitats for centipedes, and that previous estimates of the abundance and biomass of this predatory group needs significant upwards revision for forest ecosystems. This study has provided evidence that predation pressures are higher in forest canopy soils, and therefore predation may be more important than competition in structuring canopy communities. This study adds centipedes to the growing list of animals that depend on the unique resources provided by bird's nest ferns, and highlights the importance of bird's nest ferns as a microhabitat and resource for so many species. Bird's nest fern should henceforth be considered an umbrella species, and prioritised in conservation strategies for the preservation of multi-trophic communities and their associated functions.

4.5 SUMMARY

- Bird's nest ferns support a high abundances of centipedes and are used as a canopy nesting site. On this basis, consideration for the significance of centipedes to ecosystem function needs to be revised upwards given the impressively large biomasses they contribute to the canopy environment.
- Centipedes of the family Henicopidae were not known from Borneo before this study, and the undetermined Thereuoneminae centipede of the family Scutigeridae is almost certainly an undescribed species endemic to Borneo.
- The community structure of centipedes is vertically stratified through the forest canopy, and this is not a result of competition but likely of species specific abilities with regards to accessing the rainforest high canopy.
- The lack of competition between centipede species was surprising, and suggests that centipedes share the bird's nest ferns' resource in a complementary way.
- Given the high abundance of large centipedes and other predators, predation may be the most important ecological force structuring rainforest canopy invertebrate communities.

5 CAN BIRD'S NEST FERNS BE USED AS CONSERVATION TOOLS?

CONTEXT

Rapid expansion of industrial agriculture is one of the greatest threats to natural ecosystems, and in recent decades tropical rainforests have suffered devastating losses. Oil palm plantations are frequently associated with deforested land, and now occupy an estimated 20 million hectares of land globally. This will almost certainly increase as production strives to meet the demands of an ever expanding human population. Agricultural expansion is closely linked with a range of environmental and social issues, including wildlife conflict and loss of ecosystem services. Yet plantations are not barren landscapes, and they should not be abandoned by conservationists. With effective management and conservation objectives, mature oil palm plantations can harbour substantial biodiversity. Indonesia and Malaysia have some of the oldest plantations, and indeed many are approaching the end of their productivity. These plantations could, and indeed should, be returned to a more natural state, because this will improve biodiversity and restore ecosystem function in these ubiquitous landscapes. An emerging area of interest relates to the actions or interventions that will ensure biological maintenance, and the restoration of biodiversity in decommissioned oil palm plantations. This chapter forms a comprehensive study of bird's nest ferns across a large RSPO certified plantation in Sabah, and reports on a novel experiment involving the translocation of bird's nest ferns and their inhabitants from rainforest into oil palm plantation. This chapter represents the culmination of my research, establishing the evidence base for using bird's nest ferns as conservation tools to maintain and improve biodiversity in the oil palm landscape.

5.1 INTRODUCTION

5.1.1 PALMS OF CONTROVERSY

In less than two centuries, oil palm (*Elaeis guineensis*) (Figure 5.1) was transformed from subsistence crop, to the world's most widely consumed cash crop. In 1848, four oil palm seedlings arrived at Bogor's Botanical Gardens in Java, Indonesia, the first to reach Southeast Asia. Fifty years later, Malaysia's first commercial oil palm plantation opened in Selangor to replace a failing coffee estate. By 2017, Indonesia and Malaysia were producing 57 million tonnes of palm oil per year, contributing 86% of total global oil palm production (Iskandar et al., 2017). Palm oil makes commercial sense, compared with other major oil crops, because production costs are low, yields are high and turnaround is fast (Hansen, 2007). This, combined with widespread cultivation and versatility in product use has firmly established palm oil as the world's most popular vegetable oil (Abdullah and Wahid, 2010). Oil palm is now cultivated widely throughout the tropics (Sheil et al., 2009), with expansion taking place in Thailand, Colombia, Nigeria and Papua New Guinea (Pirker et al., 2016).

Figure 5.1 Oil palm (*Elaeis guineensis*) fresh fruit bunch (FFB) on the ground in a plantation.

Although the palm oil industry creates prosperity, its frequent association with environmental degradation (Rival and Levang, 2014) has sparked much controversy. Although other industries such as livestock and soya production can be equally if not more destructive, palm oil seems to be the current 'hot topic'. As the feud between environmental groups and industrial representatives over the impact of oil palm goes on (Rist et al., 2010), it remains difficult to separate fact from fiction (Sheil et al., 2009). However, it is a fact that the industry is immensely valuable (Koh and Wilcove, 2007) and that demand for palm oil is still rising (Gilbert, 2012, Khatun et al., 2017), therefore the incentive to convert land to oil palm plantation is also increasing (Laurance et al., 2014).

5.1.2 LANDSCAPE TRANSFORMATION

The transformation from natural ecosystem to agricultural land (Figure 5.2) drives a loss in biodiversity (Turner and Foster, 2009, Kongsager and Reenberg 2012). The prolific, large-scale conversion of rainforest to oil palm in recent decades has therefore raised justifiable concerns, not only for biodiversity, but also for ecosystem function in the tropics (Phalan et al., 2013, Barnes et al., 2014, Dislich et al., 2017).

Concern over the loss of biodiversity through forest conversion relates directly to the specific transformation of the habitat. Although forest clearance by fire has been illegal since 2015, plantations were historically, and are often still, established following forest clearance with fire (Gaveau et al., 2016) . The loss of vegetation, combined with the use of heavy machinery, leads to soil destruction, and this disturbs natural water catchment and nutrient cycling (Butler, 2011). The removal of above-ground vegetation also decreases structural diversity, and destroys particular niches associated with the structurally complex forest (Foster et al., 2011). In both primary and secondary forests, the canopy can be reduced from 50m (Okuda et al., 2003) to bare ground, or a few meters in young plantations. This drives wild fluctuations in microclimatic conditions (Luskin and Potts, 2011), and in the absence of a buffering canopy (Chapter 2), oil palm plantations become much harsher environments (Turner and Foster, 2006, Hardwick et al., 2015). Although young plantations are exposed to high levels of solar radiation and dramatic temperature fluctuations, mature plantations can be quite hospitable (Luskin and Potts, 2011, Corley and Tinker, 2015).

Figure 5.2 Forest of High Conservation Value (HCV) bordering a mature oil palm plantation.

Mature oil palm plantations can support a substantial level of biodiversity (Peh et al., 2006, Turner et al., 2008, Gray et al., 2016) because of their climatic stability (Luskin and Potts, 2011). Native species are therefore likely to persist when conservation and management strategies are integrated (Perfecto et al., 2009, Tscharntke et al., 2012). Action to mitigate the effect of habitat transformation (Maddox, 2007) not only provides a platform for diversity maintenance and ecosystem function (Foster et al., 2011), but also the longevity of crop production (Zhang et al., 2007, Gray et al., 2017).

In recent years the drive for sustainable production has grown substantially (Tan et al., 2009, Khatun et al., 2017). With evidence mounting for the relationship between biodiversity and ecosystem function, there has been a concerted effort to improve sustainability within the palm oil industry (Begum et al., 2018, Courtney et al., 2018) and the establishment of the

Roundtable on Sustainable Palm Oil (RSPO) in 2004 was a major landmark. Under the RSPO certification scheme various 'best practices' have been developed and incorporated, not only to reduce the industry's environmental impact, but to encourage cooperation and transparency within the industry itself (Sheil et al., 2009). While there have been few independent assessments of their application and effectiveness in practice (Turner et al., 2008, Rupani et al., 2010, Ghazali et al., 2016, Khatun et al., 2017, Courtney et al., 2018), the industry's willingness to adapt as new developments come to light provides real hope for the future.

5.1.3 BIRD'S NEST FERNS IN OIL PALM PLANTATIONS

The importance of bird's nest ferns as microclimatically buffered safe houses for biodiversity is known, and has been explored throughout this thesis. The ferns not only provide a resource for foraging and nesting (Chapter 4), but because they are climatically buffered (Chapter 2), they permit animals to survive in environments that may otherwise be beyond their climatic tolerances. According to previous work by Turner (2005), bird's nest ferns are naturally more abundant in oil palm plantations than in tropical forest. It is therefore possible that the relative importance of bird's nest ferns to ecosystem function is heightened in oil palm plantations, given the reduction in complexity of the wider habitat and its associated losses in biodiversity (Fayle et al., 2008), though this remains unexplored.

It is likely that the ferns' ability to buffer microclimate is of great importance to animals inhabiting plantations, where conditions can be much harsher than in tropical rainforest (Chapter 2). Bird's nest ferns are an ideal refuge for sensitive fauna (Scheffers et al., 2014a), but the limited availability of alternative microhabitats in oil palm likely makes them even more significant for the maintenance of biodiversity. If bird's nest ferns ameliorate the transition from forest to oil palm (Foster et al., 2011), they would certainly provide a unique opportunity to conserve, or even improve, biodiversity in the oil palm landscape.

5.1.4 BIRD'S NEST FERNS AS CONSERVATION TOOLS

As habitat degradation and climatic change threaten global biodiversity, translocation of individuals or groups of species across landscapes, is becoming an increasingly popular conservation tool (Weeks et al., 2011). While translocation programmes share a common goal of population persistence and resilience, success rates have been fairly low (Griffith et al., 1989, Fischer and Lindenmayer, 2000, Hunter Jr, 2007). However, given the widespread conversion of forest to agricultural land, and current rates of environmental change, it may be very timely to evaluate the potential of species translocation into oil palm.

Translocation refers to the movement and release of an individual, group or other ecological material from one location to another. Typically it has been used to create and maintain viable populations of single, focal species (Weeks et al., 2011). Ultimately, ecological restoration aims to increase species diversity, structure and functionality, by improving the resilience of communities to environmental stressors at the regional landscape scale (Ruiz-Jaen and Aide, 2005, Armstrong and Seddon, 2008, Seddon et al., 2014). Whether a translocation programme achieves its aims depends on a suite of factors, including species physiology, ecology, phylogeny, plasticity, adaptation and population and community dynamics (Armstrong and Seddon, 2008, Iacona et al., 2017, Malone et al., 2018), and prior knowledge of these confounding factors would increase the likelihood of successful translocations (Malone et al., 2018). However, given the current situation, it seems that a strategic mixing of populations would offer a practical and cost-effective method of establishing viable populations capable of persisting under environmental change (Heller and Zavaleta, 2009, Weeks et al., 2011).

By following procedures analogous to organ transplants, it was hypothesised that bird's nest ferns, along with their associated multi-trophic functional community, could be transplanted from rainforest into oil palm plantations. We were not only confident that the ferns would survive translocation, but that the transplanted associated invertebrate inhabitants would establish metacommunities of rainforest animals in oil palm plantations. These species, native to the geographic location and adapted to live within the ferns, should be able to use the bird's nest fern mosaic to disperse across the landscape, recolonising the environment and restoring ecosystem function. While there are risks associated with translocations (IUCN, 2013), the potential benefits to the ecosystem, of species recolonising the oil palm landscape justifies such work. The hypothesis for this final chapter was built on a foundation of knowledge including the following observations: (1) bird's nest ferns buffer against climatic extremes (Chapter 2); (2) the ferns provide important refuges for animals in the forest canopy, even being used as nurseries (Chapters 3 and 4); (3) the ferns occur naturally in oil palm plantations (Turner, 2005); (4) the animals supported by the ferns are native to this geographical location, and adapted to live within bird's nest ferns (Ellwood and Foster, 2004); and (5) the ferns can be manipulated and easily moved around the forest canopy with minimal disturbance to their animal inhabitants (Ellwood et al., 2002, Ellwood et al., 2009).

The fern fauna were highly unlikely to become pests in plantations because the plantation was established within the native range of these animals. Indeed, many of these animals may already occur in oil palm plantations. A successful transplant could increase biodiversity within the oil palm landscape, leading to automatic regeneration of the fern communities as the ferns would produce spores leading to the propagation of new ferns. These new, self-generating fern communities would underpin ecosystem functions such as decomposition and nutrient cycling (Donald et al., 2017a, Donald, 2018). The conceived experiment was designed to provide the evidence base for bird's nest ferns as conservation tools in oil palm plantations. Underpinning this were four main questions: (1) What are the natural faunal communities living in bird’s nest ferns in oil palm plantations? (2) What fauna will colonise vacant ferns introduced into the landscape? (3) Can ferns, and their animal inhabitants, be successfully transplanted from rainforest into the oil palm landscape? And (4) Can these animals disperse across the landscape and lead to the successful establishment of metacommunities?

5.2 METHODS

5.2.1 OIL PALM AND FERN SURVEYS

The Sabahmas Oil Palm Estate (5.18º N, 118.41 º E) (Figure 5.3) (henceforth referred to as Sabahmas) is an RSPO certified plantation owned by WILMAR International Limited. The estate covers 10,000 hectares of land, 9,300 ha of which is planted with oil palm under the widely adopted regime of 144 palms per hectare (Annammala et al., 2012). Consequently, there are over 1 million oil palms on the estate. Sabahmas has two on-site production mills and an oil palm nursery, the estate is responsible for every stage of its own oil production. In October 2017, a reconnaissance visit was made to the estate in order to confirm that bird’s nest ferns occurred naturally on site. Surveys were conducted based on a random stratified sampling design whereby a random site number was selected and five transects of 20m x 100m (equalling one hectare), were used to confirm fern abundance. We surveyed a total of 40 hectares of plantation across a range of age categories, including immature (2 years or less), young (3-5 years), mature (6-19 years), and old growth plantations (20+ years) for bird’s nest ferns. Each fern encountered during the surveys was assigned to a size category according to maximum frond diameter: (1) small (<30 cm); (2) medium (30-60 cm); and (3) large (>60 cm) as per Ellwood et al. (2002). We also measured height of fern on the palm (m), number of leaves and reproductive status (determined by presence of spores). From this, the mean population density (ferns ha^{-1}) was determined, as well as an approximate total abundance of ferns on the estate

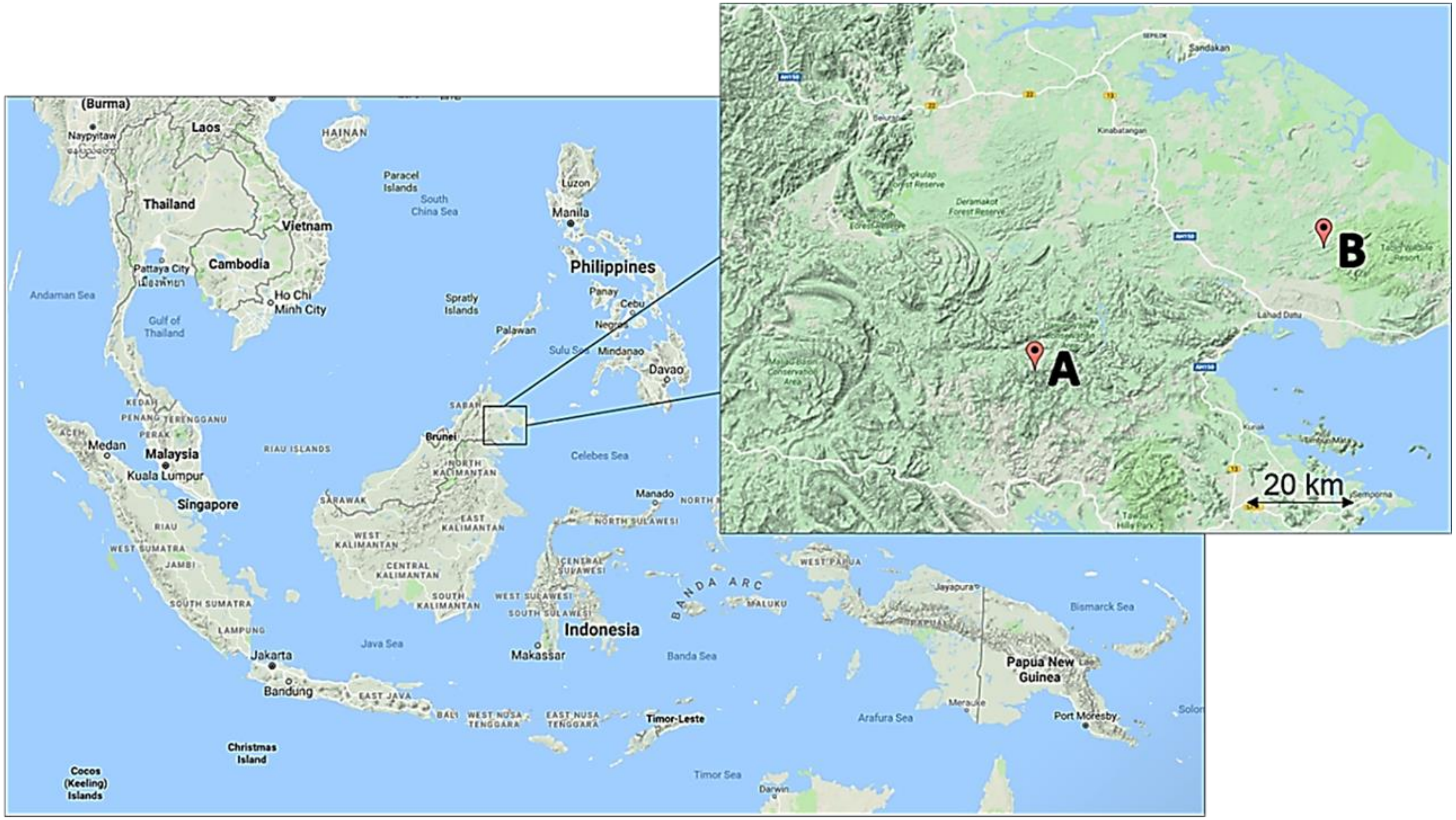


Figure 5.3 Location of study site in (A) Danum Valley and (B) Sabahmas Oil Palm Estate in Sabah (modified from Google Maps, 2018).

5.2.2 TRANSPLANT EXPERIMENT SITE SELECTION

Following a strict selection criteria several sites across Sabahmas in which the transplanting experiment plots could be established were identified. Sites were suitable if they: (1) avoided flood prone areas; (2) were not situated on steep slopes; and (3) had no stream or drainage system running through. Sites were avoided when they did not support naturally occurring ferns, as this may have indicated unfavourable growing conditions. The sites selected were located in Plantations 149 and 151 of Sabahmas 2 (Figure 5.4). All selected sites were large enough to ensure that no experimental plot came within 100m of the roadside, or within 250m of another plot in any direction. It was assumed that a separation distance of 250m would minimise the transfer of animals between plots while ensuring that climate and habitat conditions remained fairly constant.

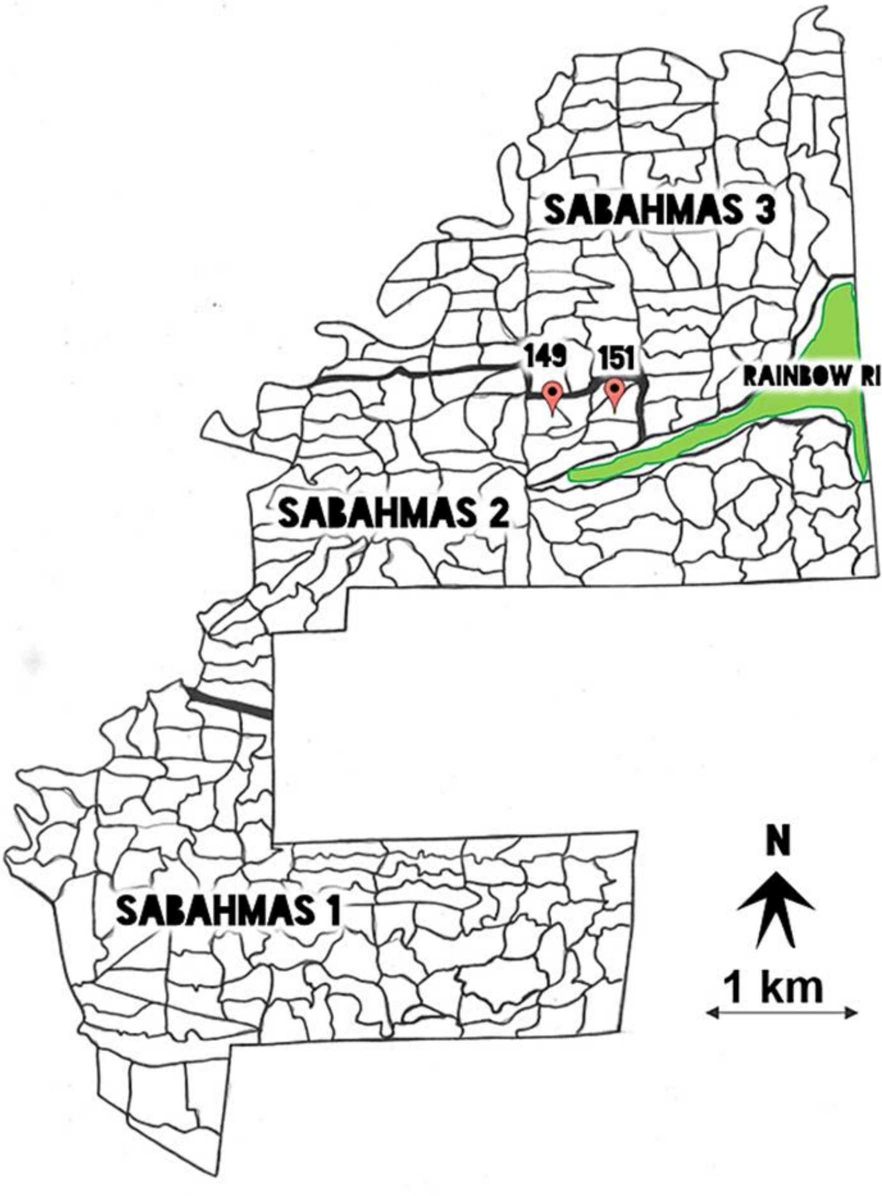


Figure 5.4 Sabahmas Estate map with location of experiment plots in sites 149 and 151.

5.2.3 PREPARATION OF STANDARDISED VACANT FERNS

The standardised ferns used in the recolonisation experiments were named 'vacant' ferns, as they contained no animals at the start of the experiment. To prepare vacant ferns, 34 bird's nest ferns (~5 kg fresh weight, rosette diameter ~50 cm) were collected from primary rainforest in Danum Valley. All ferns were collected from the trunks of small trees between 4m and 8m above the forest floor using a ladder. At the field centre, the ferns were flushed with water and detergent to remove their original inhabitants (Ellwood et al., 2009). The ferns were then repacked to a standard size using sterilised fern material harvested from various large ferns located around the field centre. The fern's soil core is its most important sub-habitat (Ellwood et al 2002), so it was important to ensure the ferns were of equal size. Plant pots (30 cm in diameter x 25 cm in height) were used, not only to ensure equal size, but to ensure that each fern soil core was made up of equal volumes of soil. The repacked soil core was held in place by handmade baskets of fishing net. All ferns were assigned a unique identity tag and attached to trees using nylon cord. Prior to their introduction to the plantation, all vacant ferns were stored indoors and watered daily. For transport to the oil palm estate, the ferns were loaded into the cargo bed of a 4x4 vehicle and covered with protective shade netting.

5.2.4 LOCATION AND COLLECTION OF TRANSPLANT FERNS

The forest around Danum Valley Field Centre was surveyed on foot to identify large ferns which would be suitable for transplanting into the oil palm plantation. Ferns were considered suitable when they satisfied three conditions: (1) they were the only fern occupant of the host tree crown; (2) they provided good climbing access (Ellwood and Foster, 2001); and (3) there were no indications of a wasp or bee nest in the tree crown or surrounding canopy. Suitable ferns were marked using a Global Positioning System (GPS) device (Garmin GPSMAP 64s). Five large bird's nest ferns (fresh mass >50kg) were extracted from the rainforest canopy in Danum Valley. All ferns were collected from ~40m in the canopy using modified rope access techniques (Anderson et al., 2015) and a pulley system to bring them safely to the forest floor. To secure the ferns with minimal loss of invertebrate inhabitants, they were cloaked in a fine mosquito net and gently coaxed from their attachment sites. The weight of the fern coming free of the branch activated a counter balance system which lowered the fern to the ground. The ferns were then carried back to the field centre, where they were loaded into the cargo bed of a 4x4 vehicle. Two 4x4's were required to transport the five large ferns, all of which were covered with protective shade netting for transport to the plantation.

5.2.5 EXPERIMENTAL DESIGN AND FERN INSTALLATION

This experiment was designed to establish the evidence base for using bird's nest ferns as conservation tools to restore native biodiversity in oil palm plantations. In total, 52 bird's nest ferns were installed across four plots in Sabahmas 2. Each plot consisted of 13 ferns attached to an oil palm (Figure 5.5). All ferns were attached at breast height (~1.2 m) using nylon rope. Large transplant ferns were secured using net hammocks around the tree trunk. Large transplant ferns served as biodiversity 'sources' whilst vacant ferns provided biodiversity 'sinks' to absorb animals as they emigrated from large transplant ferns. Figure 5.5 illustrates the layout of each experimental plot. Plot 1 provided a control of oil palm ferns, plucked from the trunks of other oil palms around the estate and arranged into the matrix. These ferns provided a baseline for the natural faunal community of bird's nest ferns in oil palm plantations. Plot 2 consisted of 13 vacant ferns, detailing those animal communities able to utilise new microhabitats in oil palm plantations. Plot 3 consisted of a vacant fern at the centre of the plot, surrounded by four large transplanted ferns, which in turn were surrounded by eight vacant ferns. Plot 4 consisted of a single transplanted fern surrounded by 12 vacant ferns. Essentially, Plot 3 was designed to answer the major question of this chapter, that is, whether transplanting bird's nest ferns could restore biodiversity in oil palm plantations. Assuming both ferns and animals survived transplanting, Plot 4 was designed to test whether animals could disperse from fern to fern across the landscape. Hence, Plot 3 consisted of one degree of separation between transplanted and vacant ferns, whereas Plot 4 allowed for two degrees of separation between transplanted and vacant ferns. The transplanting experiment would be considered a success if: (1) the ferns survived being transplanted from rainforest to oil palm; and (2) the transplanted ferns still contained large numbers of animals and high levels of biomass. If vacant ferns in proximity to transplanted ferns (Figure 5.5) contained more animals and more biomass than those that were simply colonised by animals from the plantation, this would be further evidence of a successful transplant. As shown in Figure 5.5, each plot in this study covered an area of approximately 560m^2. We observed 11 bird's nest ferns growing around the edges of the plots, and we relocated these ferns to minimise interference with the experiment. The experiment ran for six months between November 2017 and May 2018, during which time six return visits were made to Sabahmas to ensure that all ferns remained attached to their respective tree trunks. On each occasion several ferns needed reattachment. Each instance of reattachment was recorded and these details are provided in the results section. The harvesting of fresh fruit bunches (FFB) continued as usual throughout the duration of the experiment.

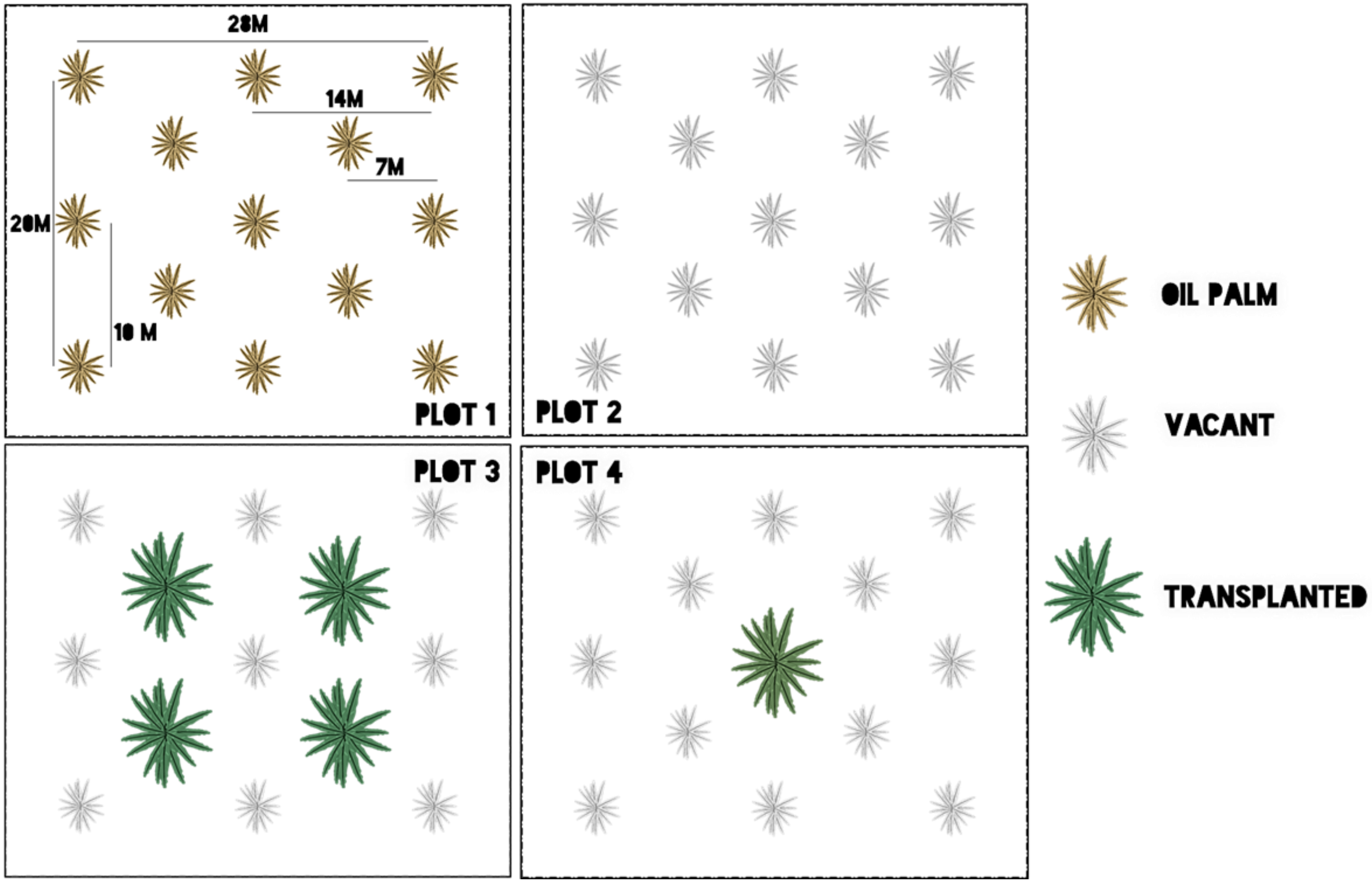


Figure 5.5 Layout for each experimental plot, and the type(s) of fern established in each. Plot 1 was a control, containing 13 oil palm ferns, undisturbed apart from being moved into the matrix. Plot 2 contained 13 vacant ferns to be colonised by oil palm animals only. Plot 3 consisted of four large transplanted ferns among nine vacant ferns. Plot 4 consisted of a single large transplanted fern among 12 vacant ferns. Each fern was attached to an oil palm and as illustrated, each plot covers an area of 560 m^2 (20m x 28m).

5.2.6 FERN COLLECTION AND INVERTEBRATE SAMPLING

Upon completion of the experiment, the ferns were collected and exhaustively sampled over a four week period in May 2018. Ferns were removed from the trees, sealed in large transparent plastic bags, and returned to Danum Valley Field Centre for processing. Sampling did not take place on the Sabahmas Estate as no suitable facilities were available. At the field centre, ferns were removed from the plastic bags, which were checked for escapees. Large animals such as spiders and centipedes, were collected in plastic containers and placed in a freezer at -20 ºC, which was more humane than placing them directly into ethanol solution. Ferns were removed from nylon netting, leaves cut away and checked for animals. The soil core was then sorted by hand by a team of up to six people. All animals were caught using entomological tweezers and placed in a jar of 75% ethanol solution. This jar containing the smaller escapees in ethanol was then sealed and stored in the freezer to preserve the specimens until further sorting could be done. After the soil was separated, the material was placed in a Winkler apparatus (Besuchet et al., 1987) for four days. A jar of 75% ethanol solution was suspended below each Winkler bag to collect animals as they emerged from the material inside. After four days the soil samples were observed under a microscope or magnifying lens to ensure that all animals had been removed. Specimens in the dirtiest solutions were processed first and placed in labelled vials containing clean solution. Large animals were placed in clean solution and sealed in Whirlpac^{TM} transport bags. Upon return to the UK, all specimens were sorted to the level of Order. The total number of individuals per Order were recorded from each fern across each of the plots. Cockroaches [Order: Blattodea] and Centipedes [Class: Chilopoda] were sorted to recognisable taxonomic unit (RTU) or morphospecies, and the number of individuals per species, as well as the total number of species per fern, was recorded across each of the plots. The full list of cockroach and centipede RTU's are provided in Appendix III. All specimens were stored in fresh alcohol solution and remain in frozen storage for preservation.

5.2.7 MEASURING INVERTEBRATE BIOMASS

Body length – mass regression equations were selected to determine biomass from body length for taxonomic groups represented by more than 10 individuals (see Table 5-1). For all animals, body length was measured from the tip of the head to the end of the abdomen (excluding cerci, ovipositors, wings and posterior legs). Measurements were taken to the nearest 0.1mm using callipers or a calibrated graticule under the microscope. Body width was also measured, across the widest part of the body (excluding the head and the appendages). Measurements were taken from up to 100 individuals of 23 taxonomic groups, with the exception of centipedes (Chilopoda) and cockroaches (Blattodea), of which all individuals were measured, as shown in Table 5.1. Power law regression equations are reliable (Wardhaugh, 2013), and were favoured over destructive sampling, in order to preserve specimens for future work. For four taxonomic groups, a generic invertebrate length-weight regression equation, $W = 0.0305 \times length^{2.62}$ (Rogers et al., 1976) was used to derive biomass in the absence of group specific allometric equations. For all other taxonomic groups, specific equations were used to derive biomass providing a greater degree of accuracy. The length – mass regression equations selected for each group are provided in Table 5-1. The biomass values derived using these equations were used in all subsequent analyses and comparisons. While the taxonomic groups detailed in Table 5-1 are of several levels including Order, Class and Family, they are distinct and recognisable groups. Henceforth they will simply be referred to under the umbrella terms of taxonomic group or order. The mean biomass of animals per oil palm fern was used to estimate the total biomass of animals contained within bird's nest ferns on the Sabahmas Estate.

Table 5-1 Taxonomic group, source of biomass regression equations, citations and the number of animals measured across each group.

Taxonomic group	**Original source** [1]	**Cited in** [2]	***n* measured**
Insecta			
Blattodea	[c]	1,	784
Coleoptera	[b]	1, 2	100
Collembola	[a]	1	100
Dermaptera	[a]	1	100
Diptera	[b]	1, 2, 3	87
Formicidae	[b]	1	100
Hemiptera	[b]	1, 2	86
Hymenoptera	[c]	1, 3	83
Lepidoptera	[b]	1, 2	51
Orthoptera	[b]	1	23
Psocoptera	[b]	1	33
Zoroptera	[b]	1	70
Non-insect Invertebrates			
Acari	[a]	1	100
Araneae	[c]	1, 3	100
Chilopoda	[c]	1, 3	258
Diplopoda	[c]	1	89
Gastropoda	[c]	1	22
Isopoda	[c]	1	100
Oligochaeta	[a]	1	89
Opiliones	[c]	1	57
Pseudoscorpiones	[c]	1	26
Symphyla	[b]	1	100
Uropygi	[b]	n / a	12

1. Biomass regression equation from [a] Rogers et al. 1975 [b] Schoener, 1980 [c] Richardson et al. 2000

2. Literature citing biomass equations: 1. Ellwood and Foster, 2004 2. Sample et al. 1993 3. Lang et al. 1999

5.2.8 STATISTICAL ANALYSES

A One–Way ANOVA was used to determine whether fern abundance was related to plantation age. Kruskal Wallis *H* tests were used to determine whether the distribution of (1) fern size and height in tree, and (2) fern height and reproductive status, were related. The strength of any association between height and leaf number were tested using Spearman’s Rho correlation. A one way ANOVA was used to determine whether leaf number differed between ferns of different sizes, and Pearson’s Chi Square test was used to determine whether fern size was related to reproductive status.

A Spearman’s Rho Correlation was used to determine whether the number of ferns that needed reattachment was significantly lower over time. A Chi Square contingency table was used to determine whether the proportional contribution of the major taxonomic groups varied between the experiment plots. One Way ANOVA’s were used to determine whether (1) the mean abundance of individuals per fern and (2) the mean biomass per fern differed significantly between ferns across the plots. These tests were repeated on datasets from Plots 3 and 4 after separating transplanted and vacant ferns, to determine whether transplanted ferns retained more individuals and more biomass. All data analyses were carried out using IBM SPSS Statistics Version 25.0.

Species Richness (R), Shannon’s Diversity Index (H), Simpson’s Diversity Index (D) and Pielou’s Evenness Index (J’) were calculated for the cockroaches and centipedes from each and every single fern using PRIMER 7 (PRIMER-e, 2017). One Way ANOVA’s were used to determine whether any of these indices differed significantly between the plots. As with the abundance and biodiversity data, these tests were used on datasets from Plots 3 and 4 after separating the vacant ferns and the transplanted ferns, to determine whether transplanted ferns retained significantly higher levels of species diversity. In each instance, non-metric multidimensional scaling’s (nMDS) were used to illustrate the distribution of species across the ferns according to (1) plot number and (2) fern type.

C-Score analysis (Gottelli, 2000) were used to determine whether competitive interactions governed cockroach and centipede species assemblages across the ferns. Cockroaches are exclusively decomposers (Chapter 3), while centipedes are top invertebrate predators (Chapter 4). While neither the species assemblages, nor the ecology of either of these groups is known from oil palm plantations, *C*-Score analysis provided a snapshot of the interactions between species of these two trophically distinct groups. As in Chapter 4, *C*–Scores based on the mean of 10,000 randomly generated matrices were determined, and tested against the observed *C*–Score using EcoSim © Intelligence Inc. Version 7.71.

5.3 RESULTS

5.3.1 FERN SURVEYS

5.3.1.1 ABUNDANCE

Not a single bird's nest fern was recorded during the surveys of immature (2 years or less) or young (3-5 years) oil palm plantations (20 hectares). Given that these plantations did not contain any ferns, these sites were excluded from subsequent analyses. A total of 705 bird's nest ferns were recorded in mature and old growth plantations. Of the 20 hectares of mature (6–19 years) and old growth (20+ years) plantation surveyed, a mean abundance of 35 ferns per hectare was recorded (705 ferns / 20 hectares = 35 ferns). Fern abundance did not differ between mature (n = 32 ± 7 ferns) and old growth sites (n = 40 ± 7 ferns) (One-Way ANOVA $F = 0.375$, df = 1, $p = 0.55$). Approximately 70% of growing land at Sabahmas was mature or old growth plantation (9,300 / 100 x 70 = 6510 hectares) (Sabahmas Estate pers. comm.). Using the mean number of ferns per hectare (35 ha^{-1}) and the approximate number of hectares that are either mature or old growth plantation (6510 ha), the total number of bird's nest ferns on the Sabahmas Oil Palm Estate is approximately 227,850 (35 ferns per hectare x 6510 hectares = 227,850 ferns). This is exclusive of ferns in riparian reserves, High Conservation Value (HCV) areas and the Tabin Wildlife Reserve.

5.3.1.2 PLANTATION AGE, FERN SIZE AND HEIGHT

Ferns recorded in this study were assigned to one of three size categories depending on the approximate distance between leaf frond tips. Large ferns had a leaf span of more than 60cm, that of medium ferns was between 30 and 60cm and small ferns had a leaf span of less than 30cm. In this study, 180 small ferns (<30cm), 263 medium ferns (30–60cm) and 263 large ferns (>60cm) were recorded. There was no statistical association between plantation age and fern size ($\chi^2 = 0.240$, df = 2, $p = 0.887$). That is, the number of ferns of each of the size categories did not differ between mature and old growth plantations. On average, large ferns grew lowest on the palm (2.4 ± 0.5 m), followed by medium (2.5 ± 0.6 m) and small ferns, which grew highest (2.8 ± 0.1 m). Large ferns generally occurred lower, while small ferns were generally higher up the trunk, although no significant relationship was found between fern size and height (Kruskal Wallis $H = 3.89$, df = 2, $p = 0.143$). In this study, not a single fern was recorded below 1m, nor was any fern recorded over 7m on oil palms.

5.3.1.3 LEAF NUMBER

Large ferns had significantly more leaves (19 ± 0.5 leaves), than medium (11 ± 0.2 leaves), or small ferns (7 ± 0.2 leaves) (One Way ANOVA $F = 416.4$, df = 2, $p < 0.001$). Although we have just seen that there was no significant relationship between fern size and the heights at which ferns were growing, there was a significant negative correlation between height and leaf number ($R^2 = -0.075$, $p = 0.045$, Figure 5.6). Ferns growing lower on the palms tended to have more leaves than those growing higher up. Figure 5.6 shows that ferns of different sizes grew at all heights, and this is why there was no relationship between fern size and the height of its attachment on the oil palm.

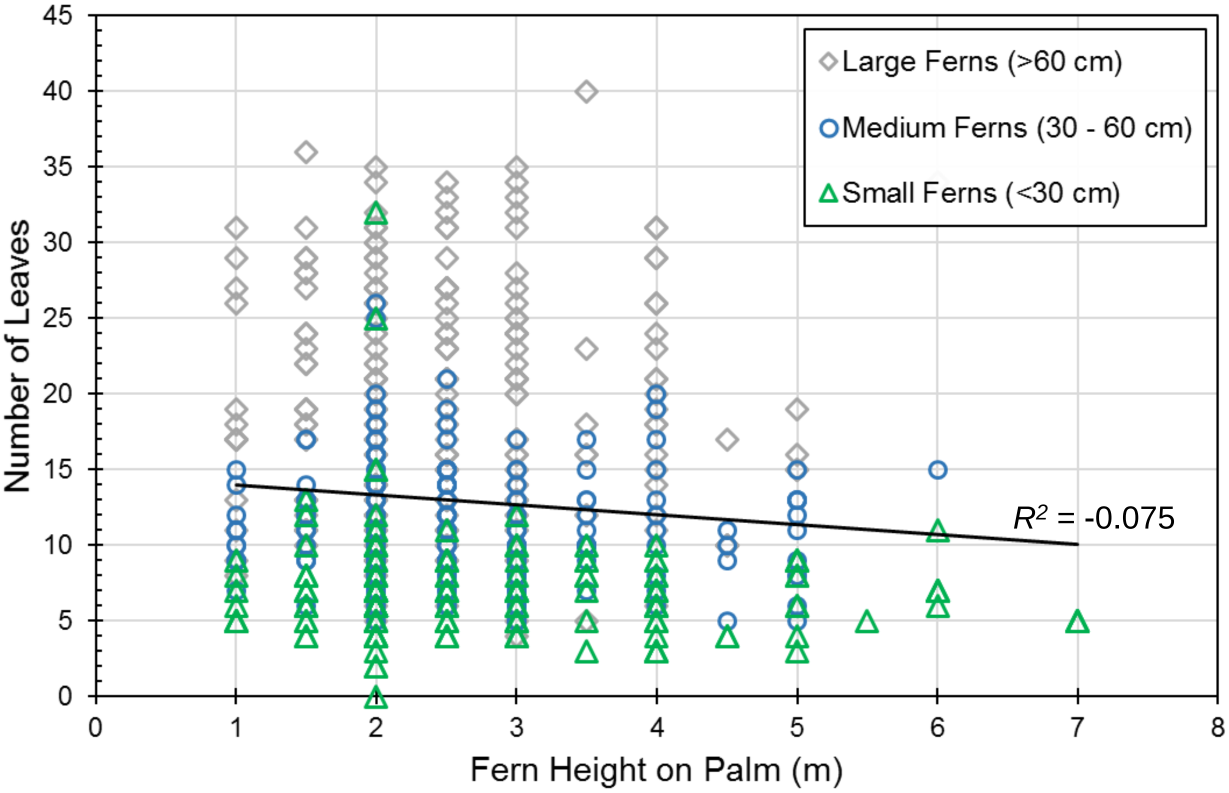


Figure 5.6 Significant negative correlation between fern leaf number and height on palm trunk (p = 0.045). Large ferns (>60cm leaf frond diameter) are represented by grey diamonds, medium ferns (30-60cm) are represented by blue circles and small ferns (<30cm) are represented by green triangles.

5.3.1.4 REPRODUCTIVE STATUS

Upon reproductive maturity bird's nest ferns begin to produce fertile leaves with spores on the underside (Khan and Kayani, 2008). Less than a third of all ferns in this study had spores (*n* = 221 / 705, = 31%), while the rest had no spores, and were therefore not sexually mature (*n* = 484 / 705, = 69%). The majority of reproductive mature ferns were large (*n* = 170), although some medium (*n* = 48) and a few small (*n* = 7) sexually mature ferns were recorded. The difference in the proportion of ferns that were reproductively active was highly significant across the size categories (χ^2 = 208.93, p < 0.001, Figure 5.7). Ferns growing lower on the palm trunks (2.4 ±0.6 m) were more likely to be sexually mature than those growing higher up (2.7 ±0.5 m) (H = 9.751, df = 1, p = 0.002). Sexually mature ferns were not recorded over 5m in trees but ferns without spores were recorded up to heights of 7m.

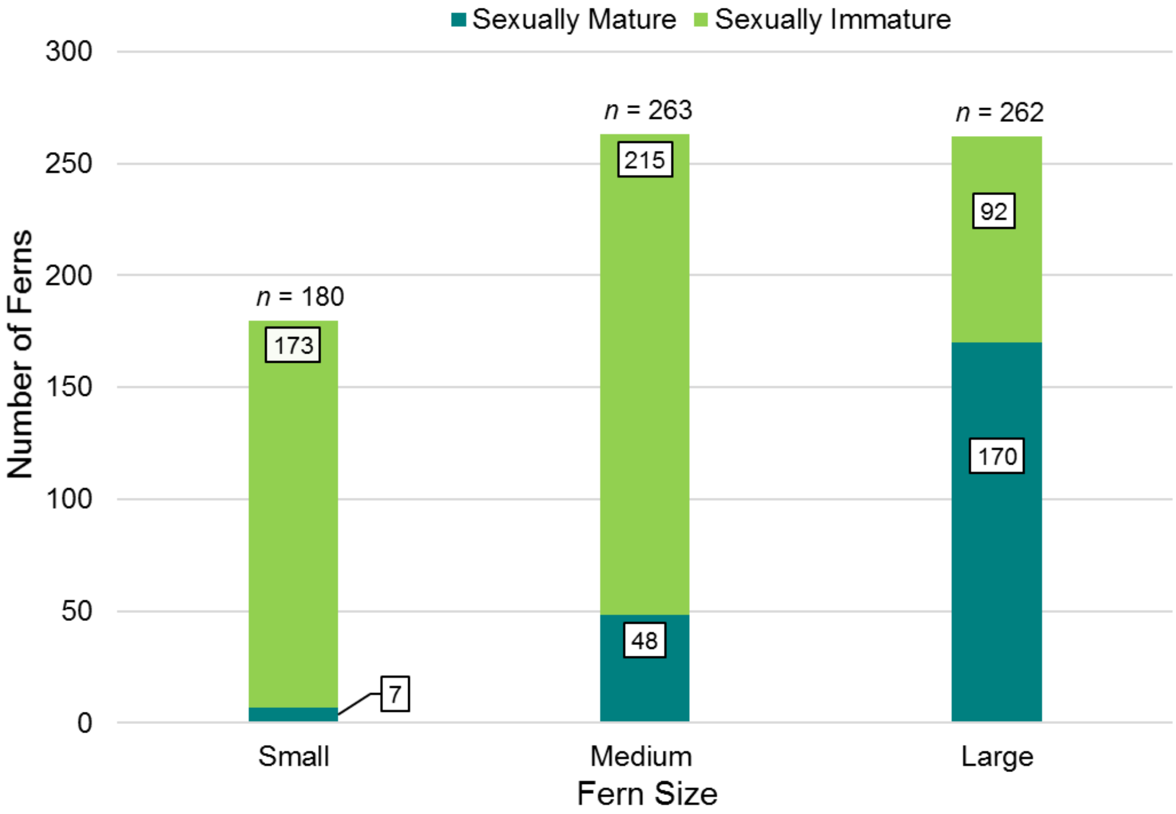


Figure 5.7 Stacked columns of the number of sexually mature versus immature ferns across the three size categories. Sections corresponding to sexually mature ferns are teal, and sections corresponding to sexually immature ferns are green.

5.3.2 FERN REATTACHMENT

Overall, 38 falls were recorded across 20 ferns (Table 5-2). The rate at which ferns needed reattachment decreased significantly with time (R_s = - 0.943, p = 0.005, Figure 5.8). On the first visit to the plantation, 11 ferns (21%) had fallen from their attachment sites on the palms, and needed reattachment, but by the final visit, just 3 ferns (6%) needed reattachment (Table

5.2). Five ferns fell twice (01:01, 03:07, 03:12, 03:13 and 04:06), four fell on three occasions (03:13, 04:02, 04:04, and 04:09) and two fell on four occasions (03:03 and 03:04). In each instance that fallen ferns were recorded, evidence of recent fresh fruit bunch (FFB) harvesting was noted in the plantation.

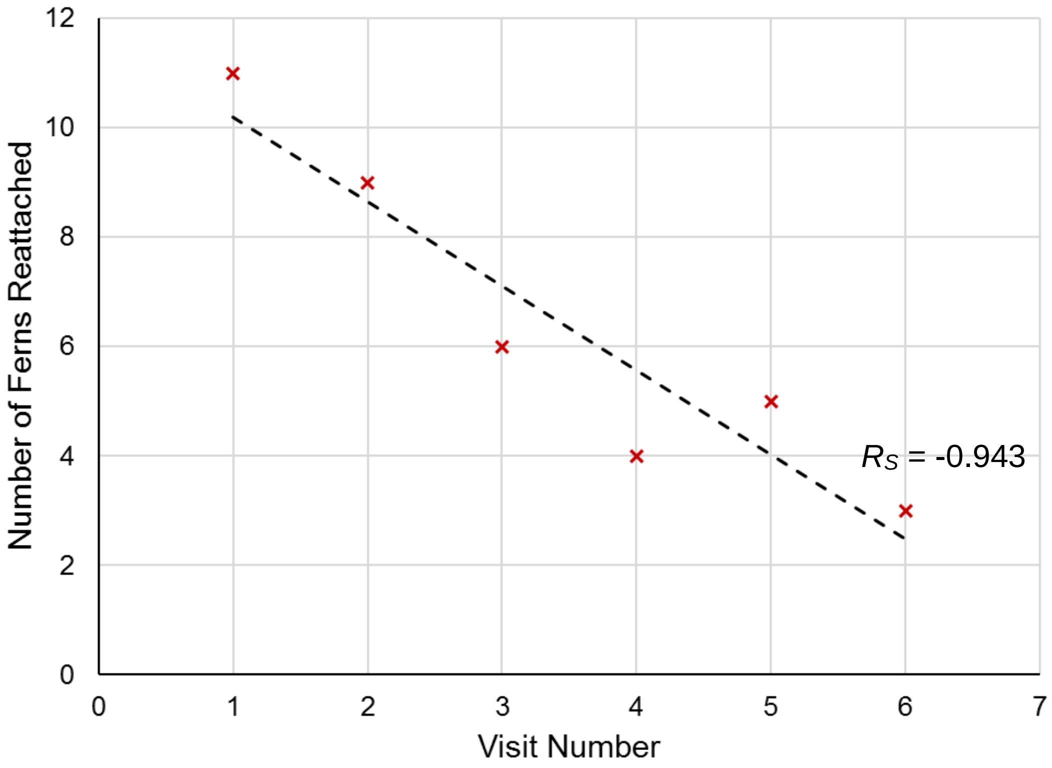


Figure 5.8 Number of ferns needing reattachment upon return visits to the oil palm plantation.

Table 5-2 Visit number and date (n), plot number, identity code of each fallen fern, the number of times a fern fell, and the number of ferns reattached on return visits to the plantation

Visit *n* (date)	Plot number and identity code of fallen ferns (plot *n*: fern *n*)				*n* reattached
	1	2	3	4	
1 (20/12/17)	01:03, 01:09	02:10	03:01, 03:03, 03:04, 03:12	04:02, 04:03, 04:06, 04:10	11
2 (15/01/17)	01:01	02:12	03:03*, 03:04*, 03:07, 03:13	04:02*, 04:04, 04:09	9
3 (07/02/18)	01:01*	n/a	03:04**, 03:12*,03:13*	04:04*,04:06*	6
4 (10/03/18)	n/a	n/a	03:03**, 03:11, 03:13**	04:09*	4
5 (01/04/18)	01:02	n/a	03:03***, 03:07*	04:04**, 04:09**	5
6 (25/04/18)	n/a	n/a	03:04***, 03:09	04:02**	3
7 (05/05/18)	[experiment end]				

* indicates that fern had already fallen once (*), twice (**) or three times (***) before.

5.3.3 BIODIVERSITY TRANSPLANTING

5.3.3.1 INVERTEBRATE ABUNDANCE

A total of 29,955 invertebrates from 29 taxonomic groups were collected from the 52 bird's nest ferns across the four experiment plots. Figure 5.9 shows the number of individuals of each of the 23 taxonomic groups that were represented by more than 10 individuals. Six groups were represented by more than 1000 individuals across all of the ferns, nine groups were represented by fewer than 1000 individuals but more than 100 individuals, and eight groups were represented by less than 100 individuals (Figure 5.9). Six taxonomic groups were were represented by ten or fewer individuals across the entire experiment, and are not represented in Figure 5.9 The Thysanoptera (8), Strepsiptera (5), Trichoptera (5), Pthiraptera (2), Mantids (2) and Archaeognatha (3) were excluded from further analyses.

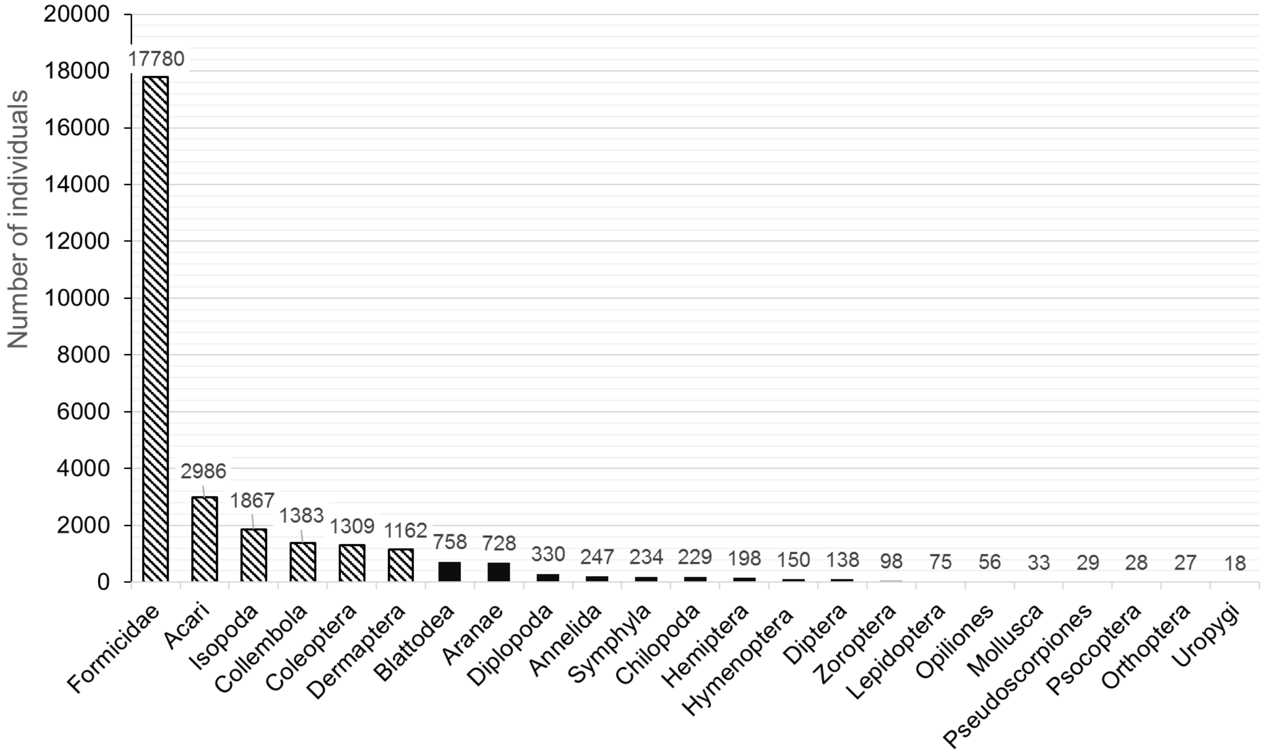


Figure 5.9 Invertebrate abundance across taxonomic groups represented by >10 individuals. Groups represented by >1000 individuals are striped, groups represented by >100 but <1000 individuals are black, and groups represented by <100 individuals are grey.

Plot 3, consisting of the four large transplanted ferns surrounded by vacant ferns (Figure 5.5) contained the most animals (9847 individuals; Figure 5.10), followed by Plot 4, consisting of one large transplanted fern surrounded by vacant ferns (8304). Plot 1, my control, consisting of the original oil palm ferns only, contained 6918 individuals, and Plot 2, which consisted of vacant ferns only, contained the least animals (4886). Although the total number of animals varied across the plots, the twelve most abundant groups were consistent (Figure 5.11).

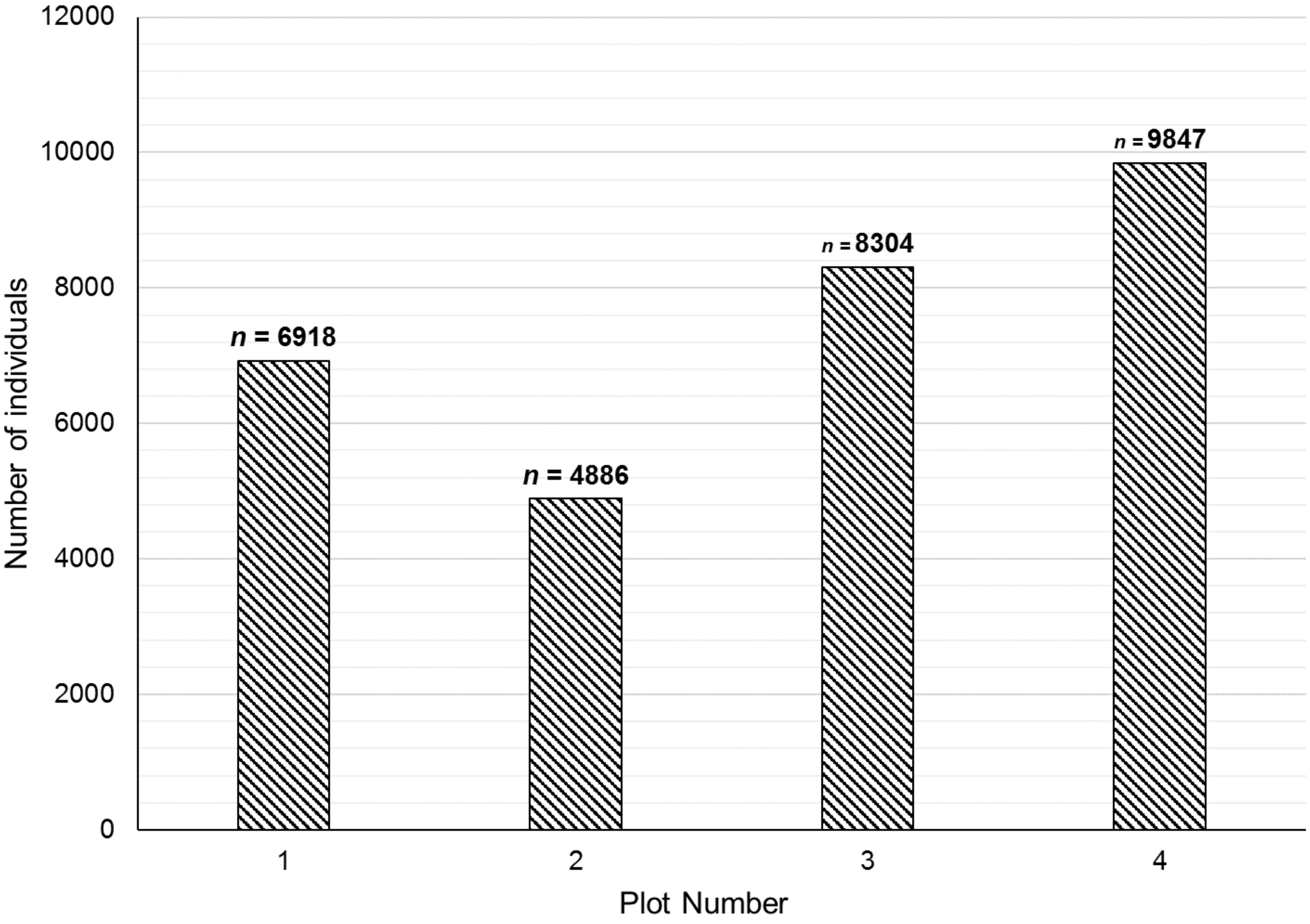


Figure 5.10 Total number of individuals recorded across each of the four experimental plots

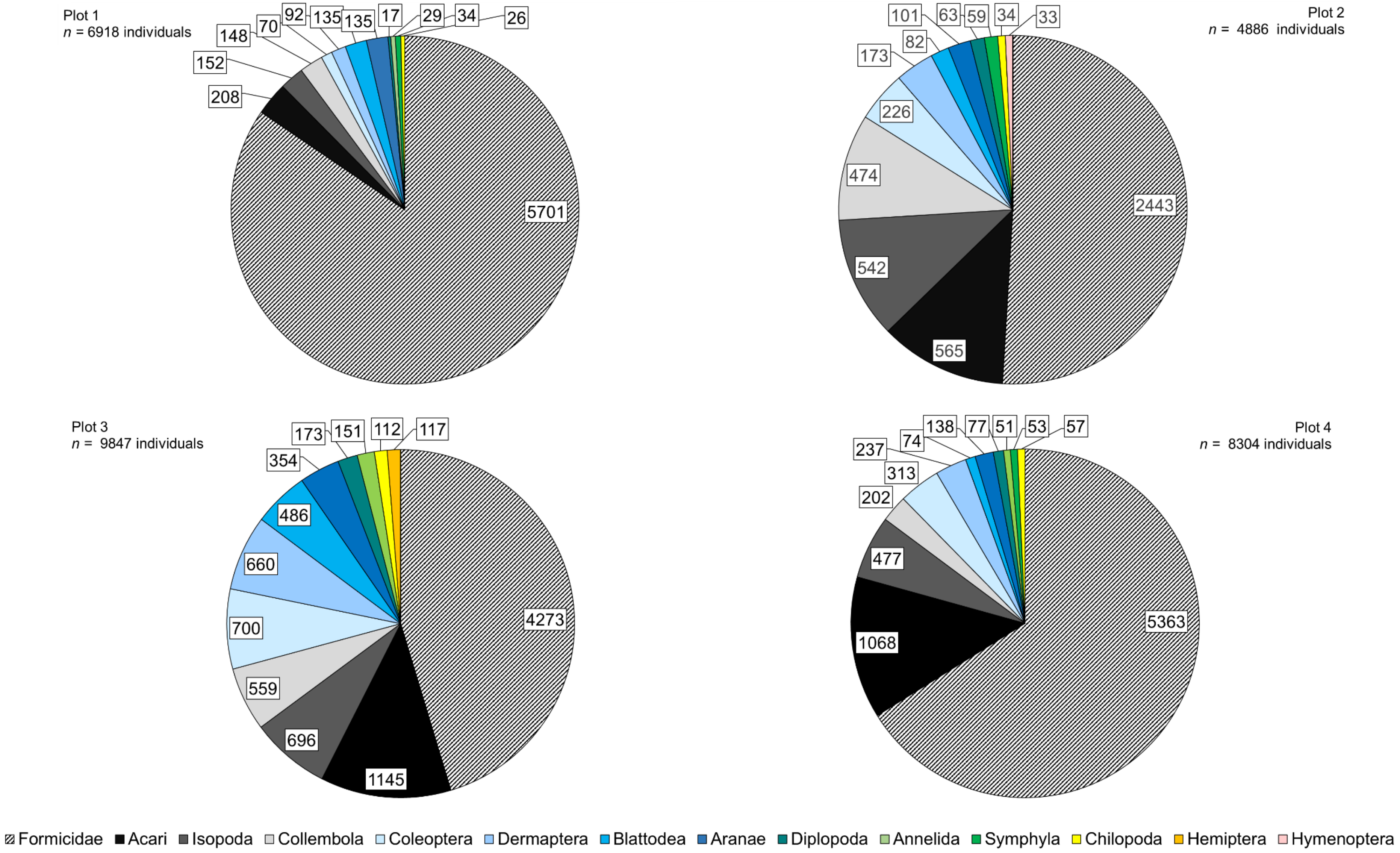


Figure 5.11 Number of individuals of the twelve most abundant taxonomic groups for each of the plots

Despite substantial differences in the total number of animals in each plot, the mean number of individuals per fern, including the transplanted ferns, did not differ significantly across the plots (Figure 5.12, Plot 1 = 532 ± 214, Plot 2 = 376 ± 155, Plot 3 =758 ± 300, and Plot 4 = 639 ± 300, One-Way ANOVA $F = 1.97$, df = 3, $p = 0.580$). The ants (Formicidae) were by far the most dominant group in Plot 1 (naturally occurring oil palm ferns) appeared to become less dominant in plots that contained solely vacant ferns (Plot 2) and both vacant and transplanted ferns (Plot 3 and Plot 4). Some 17,780 individuals (59% of all animals) in this study were ants, and so to ensure that the high abundance of ants had not distorted any underlying patterns in the number of animals per fern, the data were reanalysed excluding ants. Still there was no significant difference in the total number of animals per fern across the plots ($F = 1.645$, df = 3, $p = 0.191$).

Naturally occurring oil palm ferns (Plot 1, control) supported 532 individuals on average. Using this value multiplied by the population density of 35 ferns ha^{-1}, it was calculated that approximately 18,620 individual animals could be supported by bird's nest ferns in a hectare of oil palm plantation (532 per fern x 35 ferns ha^{-1} = 18,620). Also using our estimation of the total number of ferns on the Sabahmas estate (227,850 ferns), it was calculated that as many as 1.21×10^8 animals could live in naturally occurring bird's nest ferns on the Sabahmas estate.

On average, the number of animals per fern, including the transplanted ferns, did not differ between the plots. However, this did not elucidate as to whether transplanted ferns contained more animals than the other ferns they shared a plot with. Until now, all ferns, including the large transplanted ferns, were included in the analysis by plot. Plots 3 and 4 contained large transplanted ferns, as well as vacant ferns, whereas Plot 1 contained only oil palm ferns, and Plot 2 contained only vacant ferns. The data was re-analysed to compare the abundance of animals in the transplanted ferns of Plots 3 and 4 with the vacant ferns in Plots 3 and 4. The five transplanted ferns contained, on average, four times more individuals per fern (1841 ± 569), than the vacant ferns in Plots 3 and 4 (426.0 ± 145) (Figure 5.13, One-way ANOVA $F = 5.52$, df = 3, $p = 0.002$). While the number of animals in transplanted ferns were significantly higher than any of the other types of ferns, there were no differences in the number of animals per fern between the oil palm ferns in Plot 1, vacant ferns in Plot 2, or vacant ferns in Plots 3 and 4 (Tukey $p = 0.670$).

Transplanted ferns contained some 31% (9,206 individuals) of all of the animals recorded in this study, despite accounting for just 9.6% (5 ferns) of the total number of fern. They retained significantly high abundances of invertebrates following translocation from rainforest to oil palm. There was also evidence that transplanted invertebrates were able to disperse from the transplanted ferns across the plantation. In addition to species from the two indicator groups i.e. the cockroaches (Section 5.3.3.3) and centipedes (Section 5.3.3.4), *Pheretima* spp. (giant earthworms of the taxa Annelida) were recorded in both vacant and transplanted ferns in Plot 3 and Plot 4, but were absent from Plot 1 and Plot 2. *Pheretima* spp. are not known to occur in oil palm plantations (Sabahmas Estate pers. comm.), but have been recorded in bird's nest ferns in primary rainforest (Ellwood et al. 2002).

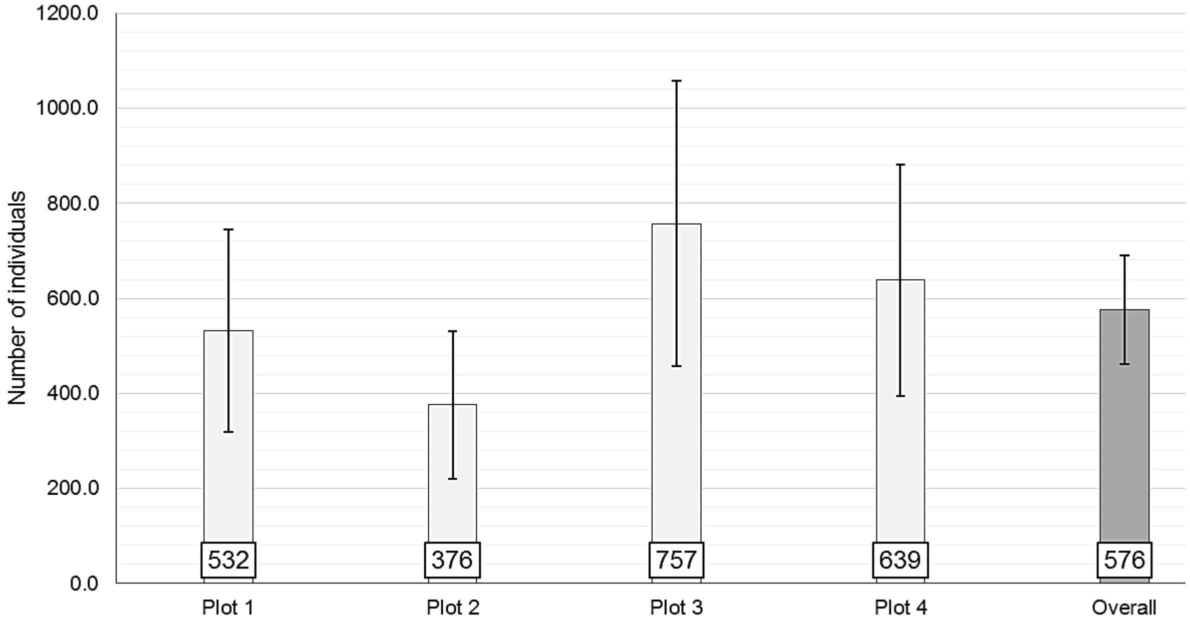


Figure 5.12 Mean number of individuals per fern (including transplant ferns) across each plot (F = 1.97, df = 3, p = 0.580) and overall experiment mean.

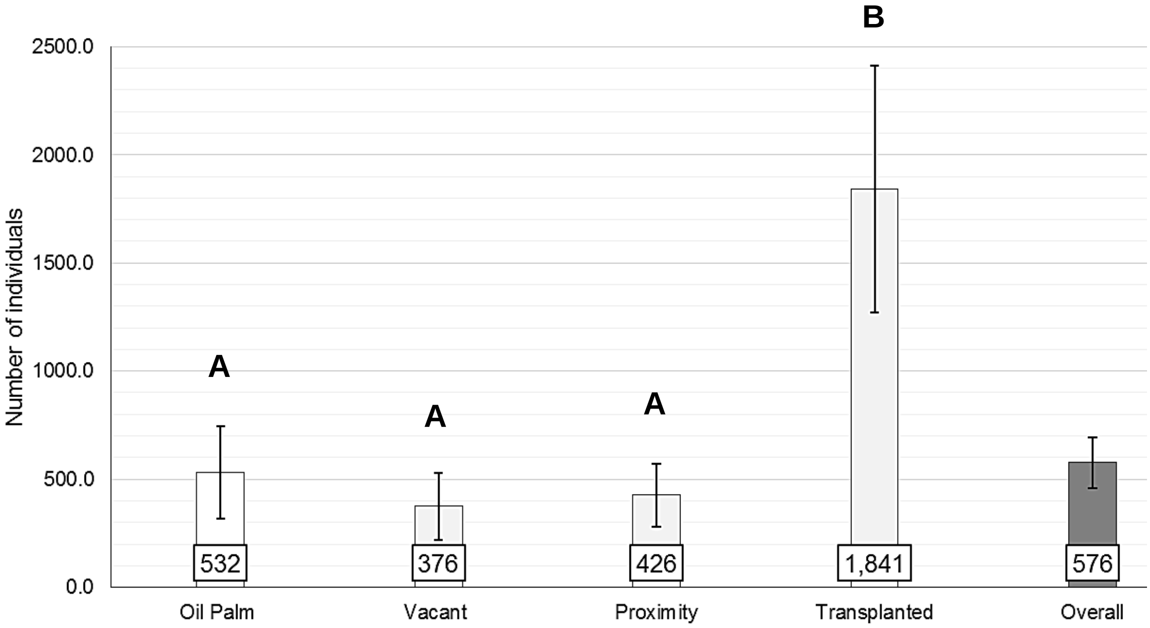


Figure 5.13 Mean number of individuals per fern across the different types of fern and overall mean. Bars with different letters denote significant differences (F = 5.52, df = 3, p = 0.002)

5.3.3.2 INVERTEBRATE BIOMASS

Approximately 71,100 mg of biomass was recorded from invertebrates across the ferns (Figure 5.14). The largest contributions to overall biomass were made by the cockroaches (Blattodea = 11,508mg, 16%), woodlice (Isopoda = 11,500mg, 16%), ants (Formicidae = 10,437mg, 15%), spiders (Araneae = 8851mg, 12%), worms (Oligochaeta = 7744mg, 11%), centipedes (Chilopoda = 7486mg, 11%), earwigs (Dermaptera = 6322mg, 9%), millipedes (Diplopoda = 3692mg, 5%) and beetles (Coleoptera = 1931mg, 3%) (Figure 5.14). Other taxonomic groups, which contributed less than 1% of the biomass, included whip scorpions (Urogypi = 441mg, 0.6%), harvestmen (Opiliones = 405mg, 0.6%), true bugs (Hemiptera = 211mg, 0.3%), snails (Gastropoda = 140mg, 0.2%), mites (Acari = 64mg, 0.1%), symphylan (Symphyla = 57mg, 0.1%), caterpillars (Lepidoptera = 51mg, 0.1%) wasps (Hymenoptera = 51mg, 0.1%) and springtails (Collembola = 39mg, 0.1%). Angel insects (Zoroptera = 21mg, <0.1%) pseudoscorpiones (Pseudoscorpiones = 14mg, <0.1%), flies (Diptera = 14mg, <0.1%) and booklice (Psocoptera = 0.7 mg, <0.1%) contributed less than 0.1% to overall biomass. Some groups made a disproportionate contribution to biomass relative to their abundance (Figure 5.15) and the groups which made the most important contribution to abundance were not necessarily the most important contributors to biomass. For example, mites (Acari) and Springtails (Collembola) were two of the most important contributors to total abundance, yet because of their diminutive sizes; their contribution to biomass was near negligible. In contrast to the high abundance yet low biomass contribution of the mites and springtails, the worms (Annelida, 247 individuals) and millipedes (Diplopoda, 330 individuals) which were comparatively low in abundance made substantial contributions to biomass.

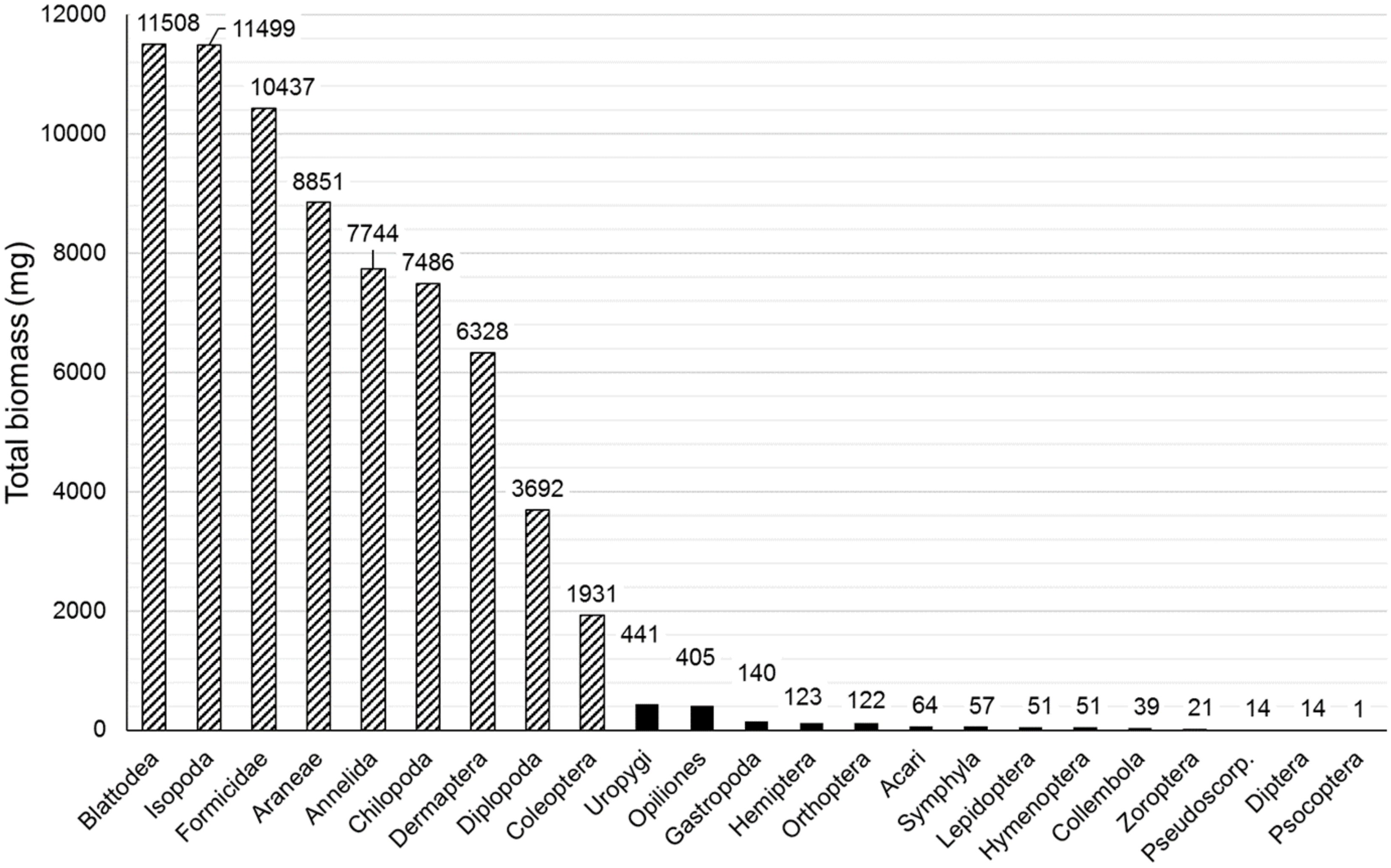


Figure 5.14 Total biomass (mg) recorded from different taxonomic groups. Groups which contribute in excess of 1000 mg of biomass are filled with striped pattern, groups which have a total biomass of less than 1000 mg are filled in black.

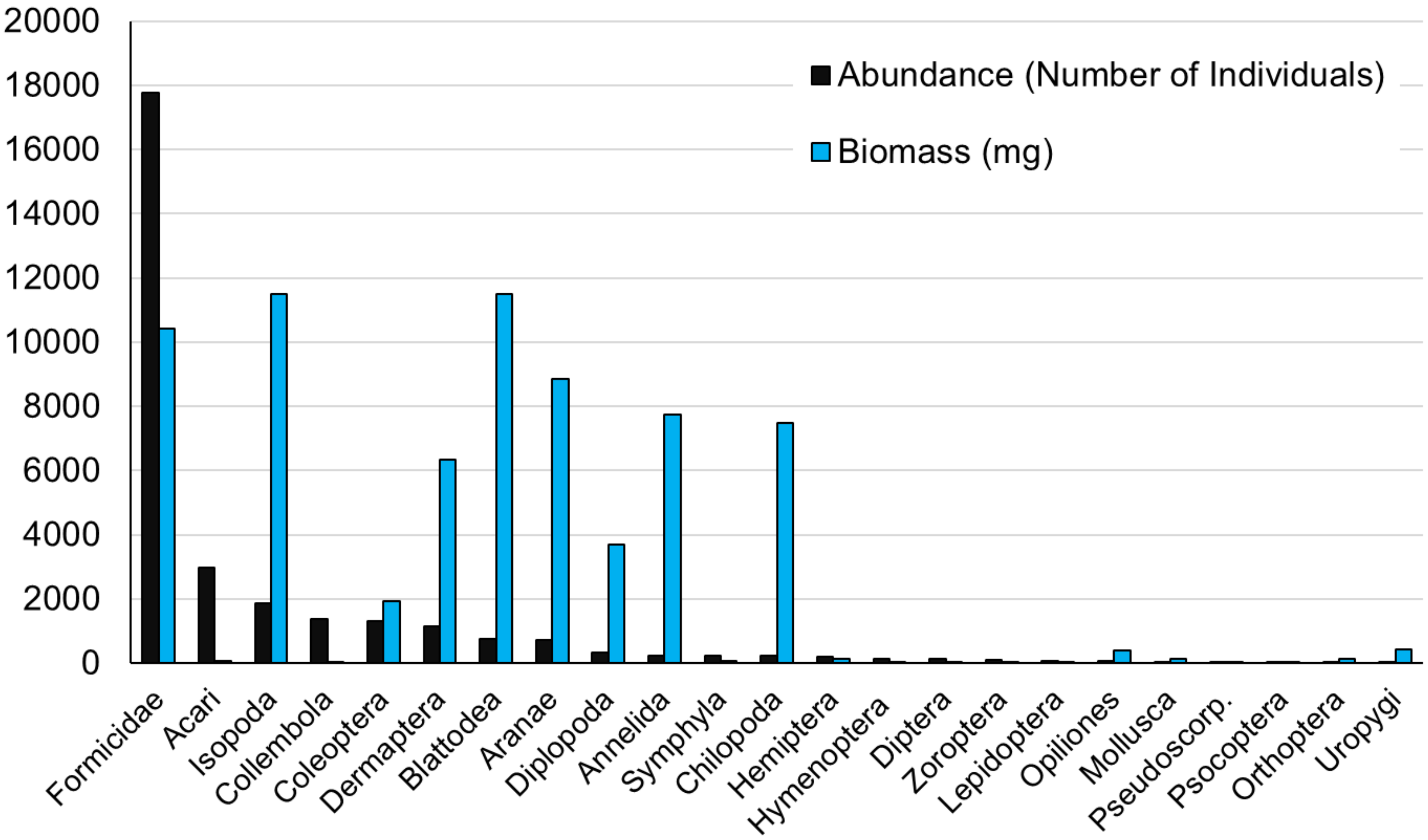


Figure 5.15 Relationship between abundance (number of individuals) of different taxonomic groups and biomass contributions (mg) of each group.

Plot 3 contained 51% of the total biomass (36,608 mg) recorded from this study, followed by Plot 4 (18%, 13,116 mg), Plot 1 (16%, 11,300 mg) and Plot 2 (14%, 10,077 mg). On average, ferns in Plot 3, including transplanted ferns, contained more biomass per fern (2,816 ± 1426mg) than ferns in Plot 4 (1,009 ± 326mg), Plot 1 (869 ± 156mg) and Plot 2 (775 ± 212mg). While the four plots made substantially different contributions to the total biomass recorded, as with abundance, the mean biomass per fern, including the transplanted ferns, did not significantly differ between the plots (Figure 5.16, One-way ANOVA, F = 1. 122, df = 3, p = 0.35).

Using the approximate mean biomass per fern of naturally occurring oil palm ferns (869 mg per fern, as in in Plot 1), as well as the mean number of ferns per hectare (35 ferns ha^{-1}) presented earlier an approximate total of 30,415 mg of invertebrate biomass per hectare may be supported by bird's nest ferns in mature or old growth plantations at Sabahmas. Further to this, using the approximate total number of ferns in mature or old growth plantation across the estate (227,850 ferns), and the mean biomass per oil palm fern (869 mg), it was calculated that as much as 198,001,650 mg, or 198 kg, of functional invertebrate biomass could be contained in bird's nest ferns across Sabahmas.

As with the abundance data, the biomass data was re-analysed separating the ferns from Plots 3 and 4 into transplanted ferns and vacant ferns. On average, the transplanted ferns contained significantly more biomass per fern (6878 ± 3111mg) than the vacant ferns in Plots 3 and 4 (730 ± 146mg) (Figure 5.17, One Way ANOVA, F = 8.83, df = 3, p < 0.000). The mean biomass of vacant ferns in Plots 3 and 4 (730 ± 146mg) did not significantly differ to the vacant ferns in Plot 2 (775 ± 212 mg), as well as the oil palm ferns in Plot 1 (869 ± 156 mg) (Tukey p = 0.767). This indicated that all of the vacant ferns across the experiment plots were colonised successfully. For both focus groups of taxa (cockroaches and centipedes) it was apparent that animals had not only colonised the vacant ferns from the plantation itself but from the transplanted ferns (see Section 5.3.3.3 and Section 5.3.3.4).

While the transplanted ferns retained high levels of invertebrate biomass, the difference between the transplanted fern that contained the most biomass (03:02, 18,080mg), and the transplanted fern that contained the least biomass (03:03, 664mg), was substantial at 17,416 mg. The transplanted fern which contained the least biomass (03:03) at the end of the experiment had fallen four times from its respective trunk, needing reattachment upon return visits to the plantation.

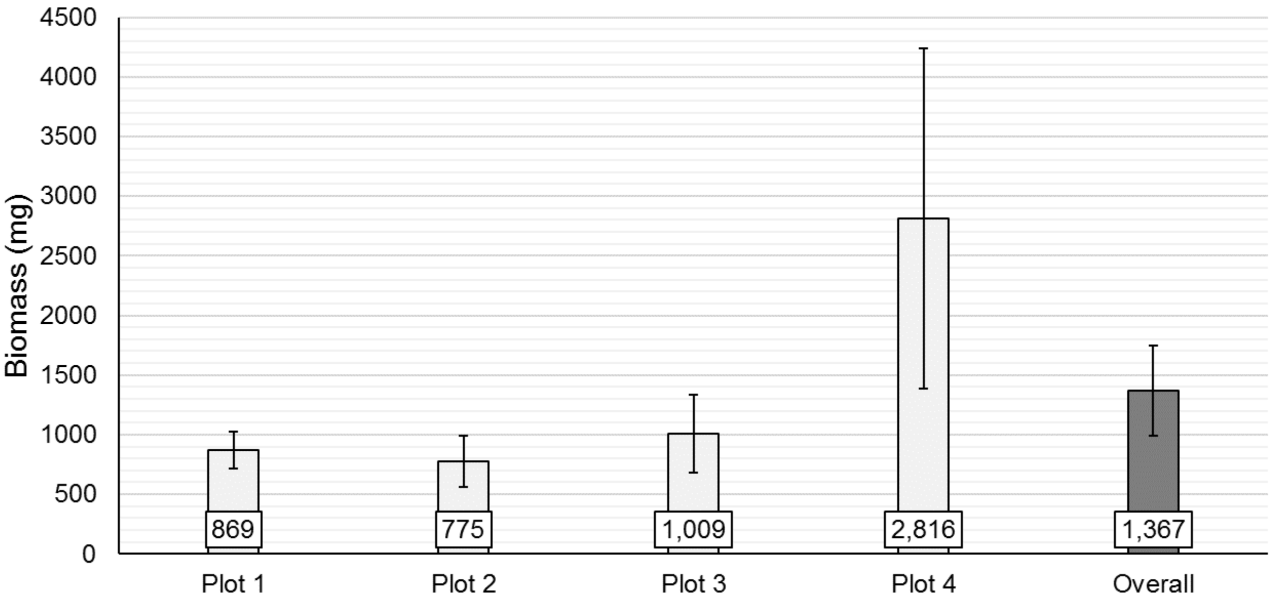


Figure 5.16 Mean biomass per fern (mg), including transplant ferns, with standard error across each of the experimental plots (F = 1. 122, df = 3, p = 0.35) and overall mean.

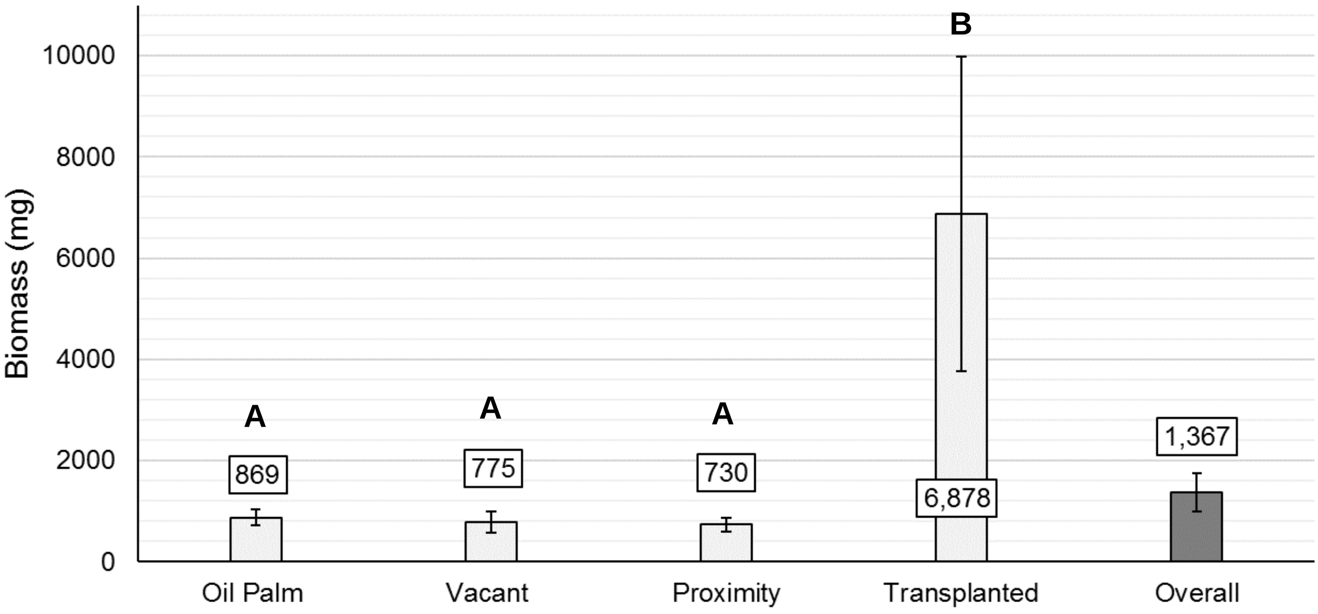


Figure 5.17 Mean biomass per fern (mg) for oil palm ferns, vacant ferns colonised by oil palm fauna, ferns in proximity to transplanted ferns, and transplanted ferns with standard error. Bars with different letters denote significant differences (F = 8.83, df = 3, p < 0.000).

5.3.3.3 COCKROACH COMMUNITY ASSEMBLY

Abundance and biomass are useful for inferring the relative functional importance of taxa (Wardhaugh, 2013), yet they provide no information regarding community structure or species specific interactions. Understanding the diversity, structure and specific interactions between functionally important groups, such as cockroaches, can provide insight into the decomposer trophic level. In total, 758 cockroaches were collected from 19 recognisable taxonomic units (RTU's) across 5 families (Appendix III). Cockroaches ranged in body length from 0.6mm to 44.7mm (mean = 5.7 ± 0.2mm), corresponding to a range of individual biomasses between 0.01mg and 64.2mg (3.0 ± 0.5mg). Generally, nymphs were the smallest, but adults of the genus *Anaplecta* were especially small, less than 4mm long on average. Two *Panesthia* specimens, a genus of giant cockroaches, were by far the largest recorded, at 36.4 mm and 44.7 mm in length.

One Way ANOVA's revealed no difference in Species Richness (S) (F = 2.085, df = 3, p = 0.12), Shannon's diversity index (H) (F = 1.094, df =3, p= 0.36), Simpson's diversity index (D) (F = 1.123, df = 3, p = 0.35) and Pielou's evenness index (J') (F = 1.03, df = 3, p= 0.39) between the plots. Indeed, Bray Curtis analysis and non-metric multidimensional scaling (nMDS) of the community assemblage data confirmed that there was no distinct separation in the cockroach community when the ferns were sorted by plot (Figure 5.18). *C*–Score analysis did not detect significant checker boarding between the plots (Table 5-3). Likely these results were due to the occurrence of species such as *Bolta* sp, *Margattea* sp 1, *Margattea* sp 2 and *Pycnocelus* sp which were common across all of the ferns.

Table 5-3 *C*–Score test results and their significance level (*p* value) for the overall cockroach community, and those of the individual plots.

Plot *n*	*C* – Score	*p* Value
1	$C_{obs} = 5.16 > C_{sim} = 4.90$	0.09
2	$C_{obs} = 3.70 < C_{sim} = 3.80$	0.13
3	$C_{obs} = 3.67 < C_{sim} = 3.69$	0.51
4	$C_{obs} = 2.67 > C_{sim} = 2.58$	0.34
Overall	$C_{obs} = 5.16 > C_{sim} = 4.90$	0.44

As with the abundance and biomass data, analyses were also conducted with the ferns in Plots 3 and 4 separated into transplanted ferns and vacant ferns. While no differences in Pielou's evenness (J') (p = 0.145) or Simpson's diversity (D) (p = 0.694) were observed, Species Richness (S) (F = 2.93, p = 0.046) and Shannon's diversity index (H) (F = 5.92, p = 0.02) were significantly different between transplanted ferns and the other ferns. This time, Bray

Curtis analysis and nMDS of the fern cockroach communities clustered the transplanted ferns, but no distinct grouping was apparent between the other ferns (Figure 5.19). SIMPER analysis revealed an average similarity in community composition of 46% between the transplanted ferns, likely because species such as *Eucorydia* sp, *Diploptera* sp and *Sundablatta* sp, were recorded in transplanted ferns, but near absent from the other ferns. In fact, the only other ferns to support any of these species were vacant ferns in Plots 3 and 4 indicating that these 'forest' cockroach species had dispersed from the transplanted ferns into the vacant ferns in their proximity. SIMPER analysis showed an average dissimilarity of 75% in the cockroach community composition across the ferns, this was driven to a large extent by variation in the abundance of species common to all of the ferns (*Bolta spp*, *Margattea spp* and *Pycnocelus spp*.). Eigen vectors for these species were added to the ordination in Figure 5.19 to illustrate the directions that these species pulled the data during the nMDS. Again, *C*–Score analysis of the cockroach communities did not reveal significant checker boarding, either in the transplanted ferns ($C_{\text{obs}} = 0.41$, $C_{\text{sim}} = 0.42$, $p = 0.61$), or in the vacant ferns in Plots 3 and 4 ($C_{\text{obs}} = 5.05$, $C_{\text{sim}} = 5.12$, $p = 0.41$).

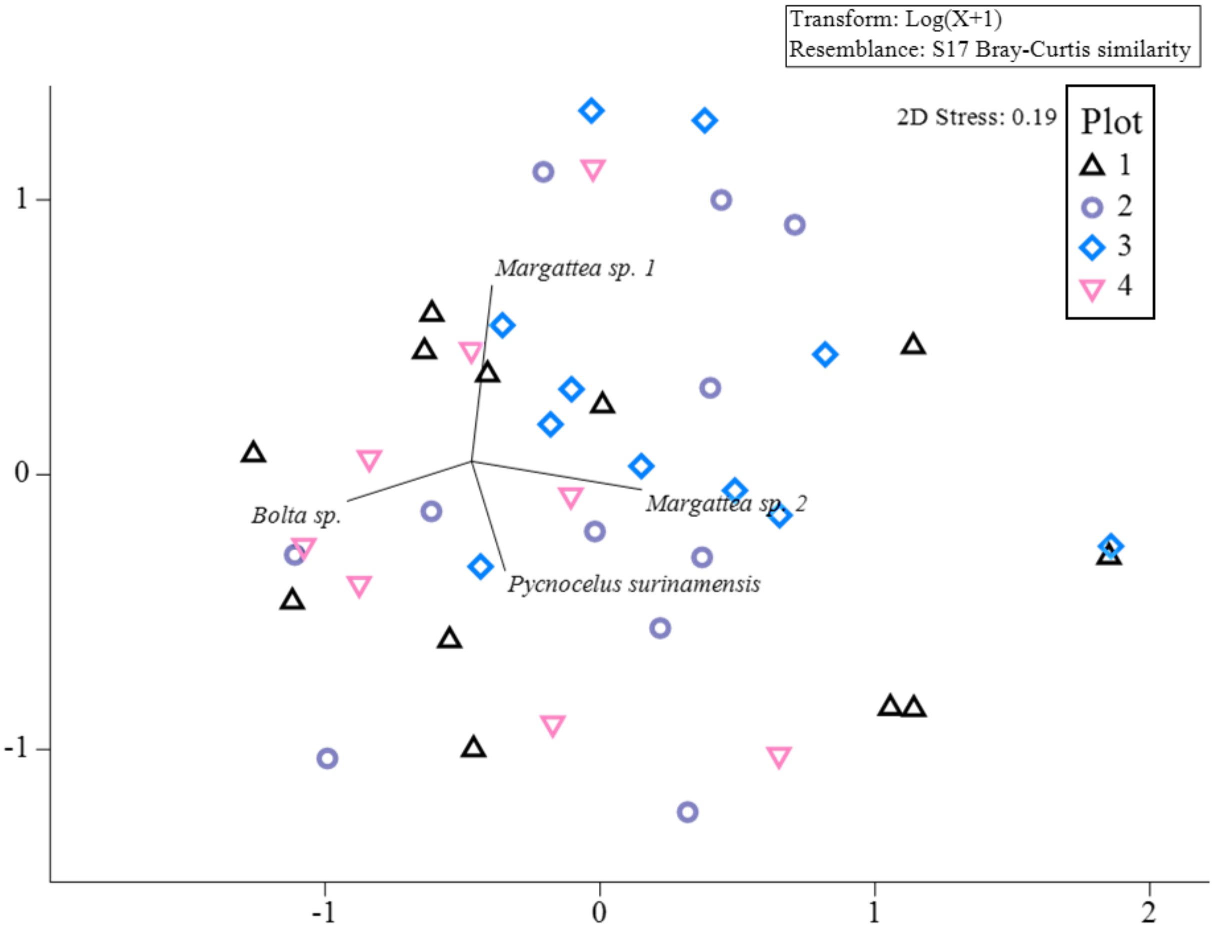


Figure 5.18 Non-metric multidimensional scaling (nMDS) of the community composition of cockroaches in ferns by plot.

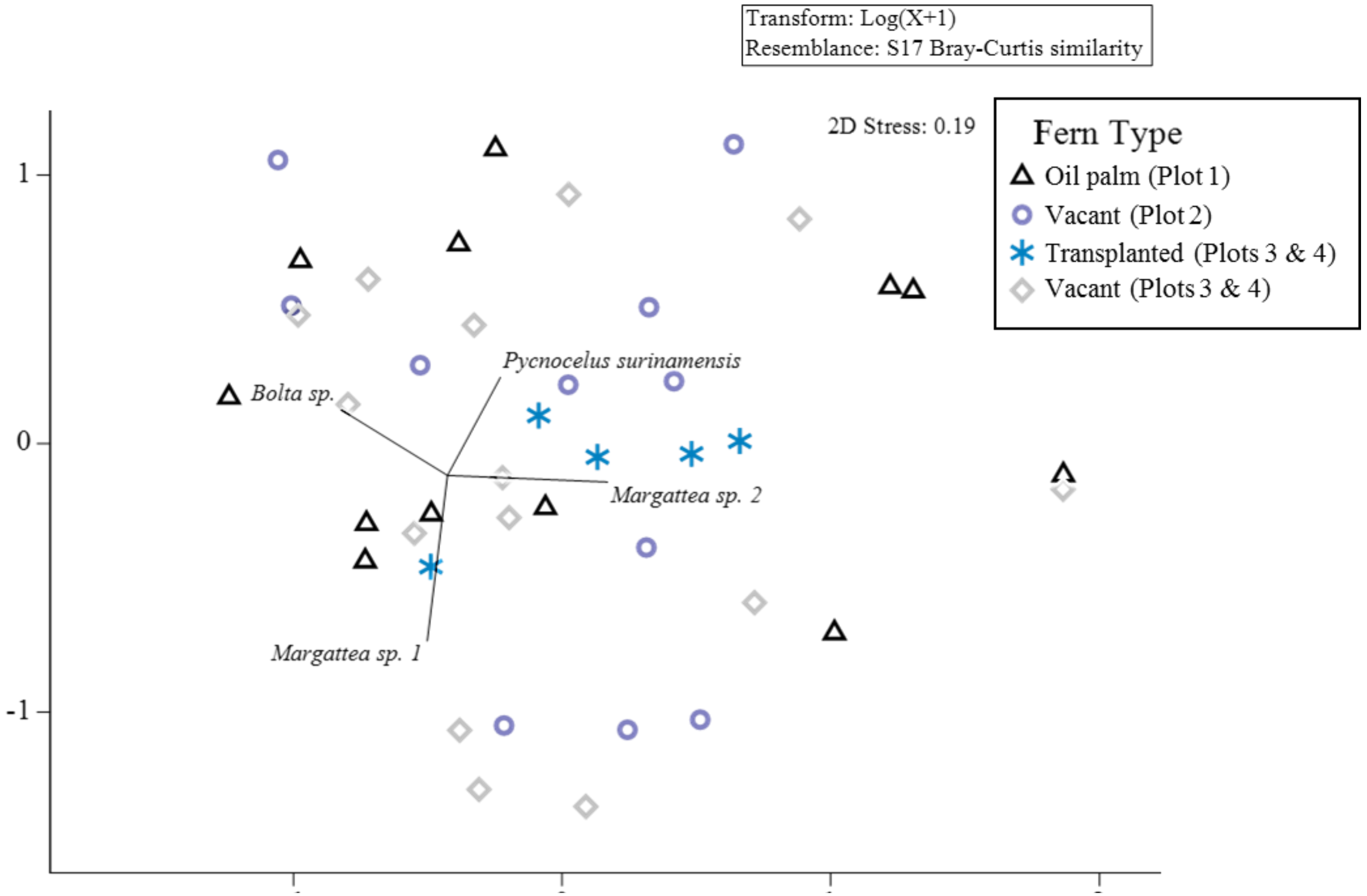


Figure 5.19 Non-metric multidimensional scaling (nMDS) of the community composition of cockroaches in bird’s nest ferns by fern type. Oil palm ferns are represented by black upward pointing triangles. Vacant ferns colonised by oil palm fauna (Plot 2) are shown as purple circles. Ferns in proximity to transplanted ferns are silver diamonds, and transplanted ferns are blue six pointed stars.

5.3.3.4 CENTIPEDE COMMUNITY ASSEMBLY

The functional significance of centipedes in bird's nest ferns, as well as the importance of bird's nest ferns as nesting sites for centipedes was explored in great deal in Chapter 4. Active centipede nests were also recorded from three ferns in this study (two transplant and one oil palm). As with the centipede nests in rainforest canopy ferns (Chapter 4), all nests belonged to centipedes of the family Scolopendridae, two belonged to *Otostigmus multidens* and the other belonged to an undetermined *Otostigmus* sp. A total of 229 centipedes from 10 recognisable taxonomic units (RTU's) across five families were collected [Scolopendridae, Scolopocryptopidae, Cryptopidae, Mecistocephalidae, and Henicopidae]. The centipedes ranged in body length from 2.2 mm to 46.2 mm (14.0 ± 0.6 mm), corresponding to a wide range of individual biomasses between 0.25 mg and 701 mg (59.4 ± 7.6 mg). The largest were *O. multidens* (46.2mm), *Ethmostigmus rubripes* (45.9mm) and *Scolopocryptops melanestoma* (40.5mm), all of which belong to the Order Scolopendromorpha.

Interestingly, centipedes were significantly larger in oil palm ferns (Plot 1, 19.1 ± 1.7mm), than those in the other plots (Plot 2 = 14.1 ± 1.2mm, Plot 3 = 12.7 ± 1.4mm, Plot 4 = 12.5 ± 0.7mm, One Way ANOVA log body size, $F = 7.40$ $p < 0.001$). Separation of the ferns in Plots 3 and 4 into transplanted ferns and vacant ferns revealed that the centipedes in the vacant ferns of Plot 3 and 4 (10.4 ± 1.1 mm) were the smallest across the study. While the centipedes in the transplanted ferns were somewhat larger (14.2 ± 1.2 mm), they remained significantly smaller than those from the oil palm ferns in Plot 1 ($p = 0.021$).

One way ANOVA's revealed no significant differences in centipede Species Richness (S) ($F = 1.83$, df = 3, $p = 0.16$), Shannon's diversity (H) ($F = 1.98$, df = 3, $p = 0.14$), Simpson's diversity (D) ($F = 0.60$, df = 3, $p = 0.62$) or Pielou's evenness (J') ($F = 0.08$, df = 3, $p = 0.97$) when the ferns were sorted by plot. However, Bray Curtis analysis and nMDS (Figure 5.20) showed a fair degree of separation of the centipede community between the plots. SIMPER analysis confirmed this with an average dissimilarity of 79% in species composition, driven largely by discrepancies in the abundance of three species common to all of the ferns. *Mecistocephalus punctifrons*, *Cryptops sp.* 1 and *O. multidens* accounted for 28%, 24%, and 22% of the variation, respectively. Interestingly, *C*–Score analysis of the centipede community structure across all ferns was significantly lower than would be expected by chance ($C_{obs} = 19.4 < C_{sim} = 20.5$, $p = 0.02$, Table 5-4). A significantly low *C*–Score is indicative of species aggregation rather than segregation (Ellwood et al., 2016).

Table 5-4 *C*–Score test results and their significance level (*p* value) for the overall centipede community and those of the individual plots.

Plot *n*	***C* – Score**	***p* Value**
1	$C_{obs} = 4.16 < C_{sim} = 4.31$	0.49
2	$C_{obs} = 3.00 < C_{sim} = 3.15$	0.33
3	$C_{obs} = 2.86 < C_{sim} = 2.99$	0.41
4	$C_{obs} = 2.67 > C_{sim} = 2.58$	0.33
Overall	$C_{obs} = 19.4 < C_{sim} = 20.5$	**0.02***
*p is significant at 0.05 or less		

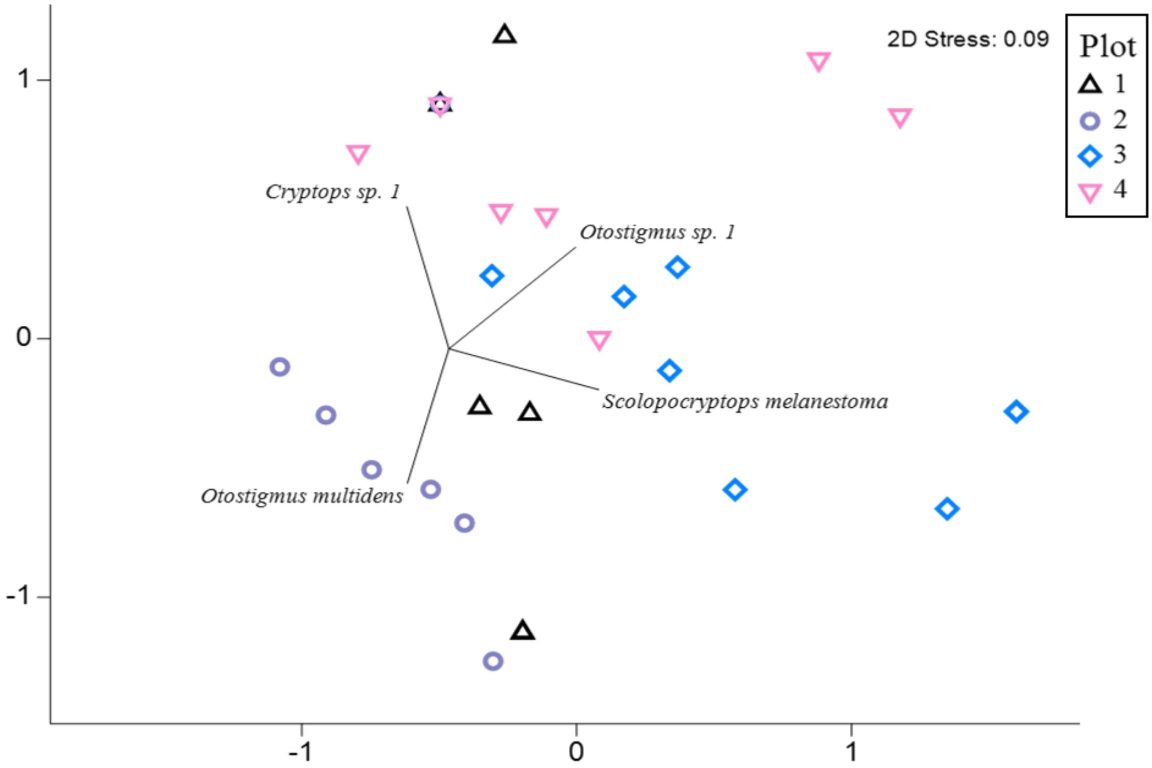


Figure 5.20 Non-metric multidimensional scaling (nMDS) of the centipede community in bird’s nest ferns by plot.

One Way ANOVA’s revealed highly significant differences in Species Richness (S) (F = 20.96, df = 3, $p < 0.001$) and Shannon’s diversity (H) (F = 8.18, df = 3, $p < 0.001$) between transplanted ferns, and the other ferns in the experiment. However, no significant differences were recorded for Simpson’s diversity (D) (F = 0.252, df = 3, p = 0.86) or Pielou’s evenness (J’) (F = 0.87, df = 3, p =0.47). Bray Curtis analysis and nMDS of the centipede community clumped the transplanted ferns, with SIMPER analysis showing an average similarity of 58% between the transplanted ferns. Interestingly, *Otostigmus sp.* 1 and *S. melanestoma* (Figure 5.21) were only recorded from transplanted ferns, and the vacant ferns in Plots 3 and 4. This would indicate that animals which arrived in the plantation via the transplanted ferns, were able to disperse across the oil palm plantation into the vacant ferns in proximity to the transplanted ferns. No significant *C*–Scores for the centipede community were recorded in either the transplanted ferns ($C_{obs} = 0.40$, $C_{sim} = 0.45$, $p = 0.61$) or vacant ferns in Plots 3 and 4 ($C_{obs} = 7.7$, $C_{sim} = 7.8$, $p = 0.68$).

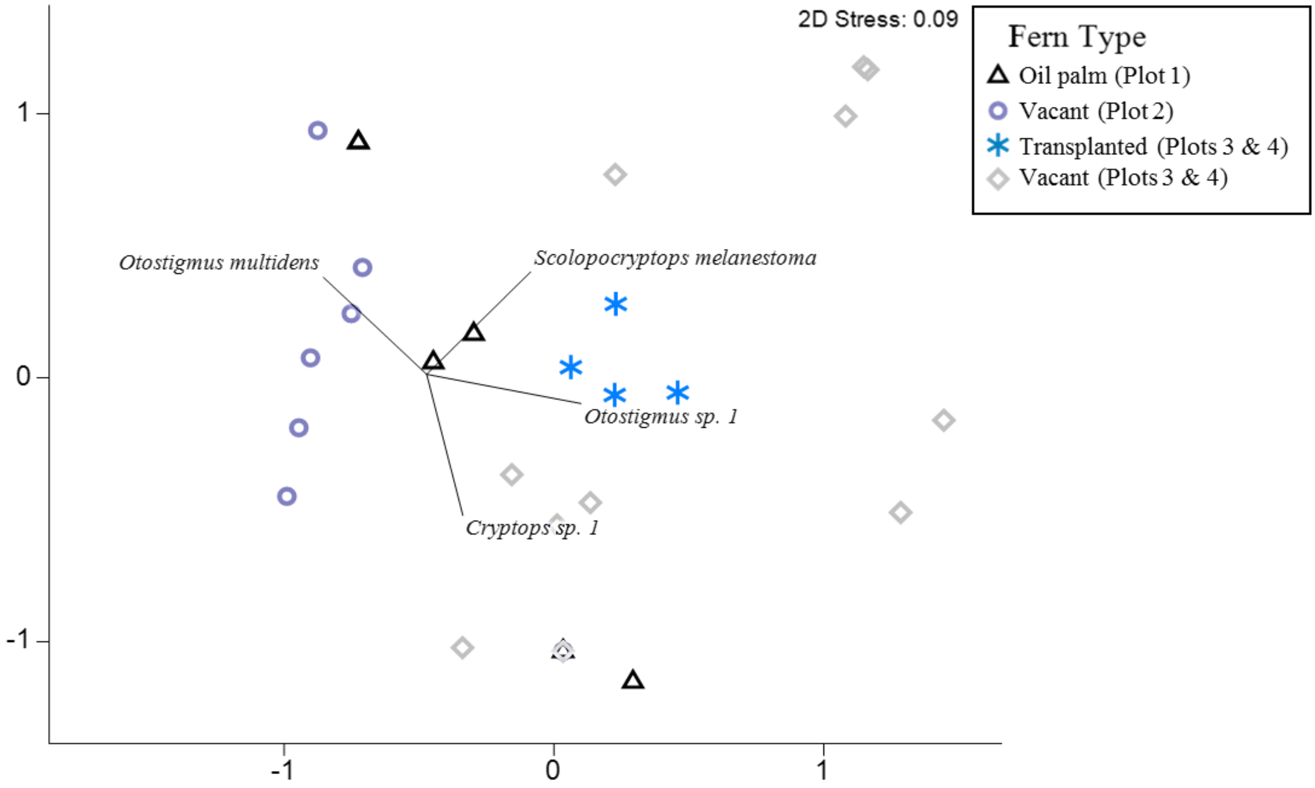


Figure 5.21 Non-metric multidimensional scaling (nMDS) of the community composition of centipedes in bird's nest ferns by fern type. Oil palm ferns (Plot 1) are represented by black up triangles. Vacant ferns in Plot 2, which were colonised by oil palm fauna, are represented by purple circles. Transplanted ferns are represented by blue stars, and vacant ferns in Plots 3 and 4, are represented by silver diamonds.

5.4 DISCUSSION

5.4.1 FERN SURVEYS

This study recorded bird’s nest ferns at much lower densities in oil palm (35 ha^{-1}) than was previously thought (112 ha^{-1}) (Turner and Foster, 2009). At even the most populated old growth plantation site, the abundance at Sabahmas (81 ferns), was an order of magnitude lower than that recorded by Turner and Foster (2009) (971 ferns ha^{-1} in a 26 year old plantation). Nor did the ferns appear to establish quickly in immature and young sites, as not a single fern was recorded in plantations less than six years old at Sabahmas. Epiphyte removal was once a standard practice in oil palm plantations, as they were thought to reduce harvest efficiency (Piggot, 1996). However, a study by Prescott *et al*. (2015) showed that epiphyte removal did not affect oil palm yield. Thus, it became a recommendation that epiphytes be left in plantations to increase structural complexity and provide refuges (Prescott et al., 2015, Dislich et al., 2017). Indeed, it is a standard practice at Sabahmas to avoid disturbing bird’s nest ferns, and other epiphytes because the plantation managers are aware of their importance for biodiversity (Sabahmas Estate Manager, pers. comm.).

By dividing the number of oil palm trees per hectare (144 ha^{-1}) by the fern density (35 ha^{-1}), it can be calculated that approximately 1 in 4 oil palms on Sabahmas would support a bird’s nest fern (144 ha $^{-1}$ / 35 ha^{-1} = 4.1). Because approximately 6,510 hectares of land at Sabahmas is under mature or old growth plantation (Sabahmas Estate Manager, pers. comm.), some 227,850 ferns may occur on the estate. By using the mean density of ferns per hectare from Turner and Foster (2009), as many as 729,120 ferns could occur on the estate (112 ha $^{-1}$ x 6,510 hectares = 729,120). The actual number of ferns most likely lies somewhere between the two estimates. Either way, we cannot afford to overlook the contribution of naturally occurring bird’s nest ferns to biodiversity maintenance in oil palm plantations. Their role in creating a mosaic of microhabitats across the oil palm landscape is probably crucial for the survival, and certainly critical for the dispersal, of decomposers and other functionally important invertebrates.

Although little is known of the natural reproductive biology of bird’s nest ferns (Srivastava and Uniyal, 2013), some work has examined their growth rate under artificial conditions (Khan and Kayani, 2008). Bird’s nest ferns are adapted for outbreeding, but their ability to sporophyte through intragametophytic selfing (self-populate), and the fact that they are wind dispersed, is likely what makes them such successful colonisers (Srivastava and Uniyal, 2013). Bird’s nest ferns are sexually mature when they begin to produce spores on the underside of their leaves (Khan and Kayani, 2008). Our study provided reassurance that bird’s nest ferns are well equipped to disperse through oil palm plantations, as one third of the ferns recorded were sexually mature (*n* = 221 / 705, 31.3 %). Given their ability to self-populate, under favourable conditions a single sexually mature fern could be responsible for the rapid development of a substantial population of ferns. Indeed, the oil palm landscape could provide a unique opportunity to study the dispersal ability of bird’s nest ferns. For bird’s nest ferns to become truly useful conservation tools, they must be able to establish themselves naturally in oil palm plantations. A well-developed series of ferns throughout the oil palm would provide a network of micro-corridors enabling invertebrates to traverse the landscape, and move between forest fragments and riparian reserves. Transplanting large, sexually mature ferns would not only contribute disproportionately to overall invertebrate biodiversity, as we have seen in this chapter, but an additional benefit of introducing mature ferns would be an increase in natural fern abundance across the landscape, as well as an increased opportunity for outbreeding.

5.4.2 CAN BIRD’S NEST FERNS BE USED AS CONSERVATION TOOLS?

In order to build a case in favour of bird’s nest ferns as conservation tools in oil palm plantations, several key questions needed to be answered: (1) Could the ferns be successfully introduced to oil palm? (2) Could they harbour biodiversity in plantations? (3) Could ferns, transplanted from the rainforest and containing rainforest fauna, successfully retain high levels of invertebrate diversity in plantations? And (4) could these animals disperse across the oil palm landscape?

Question one considered the feasibility of introducing bird’s nest ferns into oil palm plantations. Through this experiment, 52 bird’s nest ferns were successfully installed into the oil palm plantation at Sabahmas. In the first instance, the successful introduction of new ferns into the plantation hinged on our ability to attach the ferns, and for those ferns to remain attached to the oil palm tree trunks. While it was not difficult to attach the ferns to the palms at the onset of the experiment, upon return visits to the plantation over the course of the experiment, ferns often needed reattachment. However, we noted that on each visit, loose palm fruits were on the ground in the plot. Most likely the ferns were knocked from the palms during the harvesting of fresh fruit bunches (FFB’s). The initial concern was that such a disturbance, especially of the transplanted ferns, would result in the death of either the fern, or the animal inhabitants. However, it was brought to our attention that bird’s nest ferns are occasionally knocked from oil palm trunks during harvesting (Sabahmas Estate Manager, pers. comm.). At Sabahmas, the estate offices and the residential areas were decorated with a plethora of large and healthy bird’s nest ferns. These were all ferns that had been knocked from oil palms during harvesting, and had been reassigned as ornamentals. This provided reassurance that the ferns would be hardy enough to survive being knocked from the palm, and therefore fallen ferns were reinstalled rather than removed. Further reassurance came over the course of the experiment, as it became evident that the harvesters had learned how to avoid knocking the ferns from the palms, as the rate at which ferns needed reattachment decreased significantly over time (Figure 5.8, $R^2 = -0.943$, $p = 0.005$). As well as being biologically significant, this showed that the harvesters and plantations managers were taking this research seriously.

Indeed, between the sixth and final visit to Sabahmas, not a single fern had fallen from the palms. Further to this, several of the ferns (which had never fallen from the palms), had developed their own sturdy attachments, and needed to be prised off of the trunks at the end of the experiment. The answer to the first major question of whether bird's nest ferns could successfully be introduced into oil palm plantations is therefore yes. Bird's nest ferns can be installed into plantations, and in time the ferns will develop their own attachments to the palms, but care must be taken to avoid knocking them from the trees before they can attach themselves. In this sense, the long-term success of this venture will depend on total buy in from producers, and the support of the harvesters.

In primary rainforest, bird's nest ferns are aerial compost heaps (Fayle et al., 2008) and decomposers congregate in their suspended soils (Ellwood et al., 2009). It is likely that the relative importance of the ferns to ecosystem function is heightened in plantations. The ferns continue to provide a refuge for biodiversity (Turner and Foster, 2009, Fayle et al., 2010), yet in plantations the ferns represent one of the few microhabitats to provide nutrient and resource rich conditions. Our study supported this, showing that the control ferns, which were naturally occurring oil palm ferns, supported on average 532 invertebrates, and some 869 mg of biomass per fern. Multiplying these values by a mean density of 35 ferns ha $^{-1}$ revealed that around 18,620 individuals, and 30,418.5 mg of invertebrate biomass could be contained in bird's nest ferns in a hectare of oil palm. This is a substantial contribution to above ground functional biomass, and given the importance of birds nest ferns in thermal mitigation (Chapter 2), decomposition (Chapter 3) and as a resource for predators (Chapter 4), the ferns are likely the functional hotspot in oil palm plantations. The fact that we observed centipedes nesting in oil palm ferns also suggests that ferns, and the predators they support could even play a role in integrated pest management.

An increase in the number of bird's nest ferns in the oil palm landscape is likely to have a trophic cascade effect, in that the introduction of new litter intercepting habitats would lead to an increase in decomposer populations. As these animals colonise the new habitat, there would be an increase in above ground nutrient cycling (mediated by decomposers), leading to nutrient enrichment of the ground soils below the ferns (Turner et al., 2007). Predators would also benefit from an increase in prey abundance. Evidently, the establishment of new microhabitats benefited resident oil palm invertebrates as all of the vacant ferns in Plot 2 were successfully colonised. These vacant ferns could only have been colonised by oil palm animals given their substantial separation from the transplanted ferns, and while the mean number of animals (376 ± 155) and biomass (775.1 ± 211.7 mg) per fern was lower than those of the oil palm control ferns, this difference was not significant. The term 'beggars can't be choosers' may apply quite aptly to animals living within oil palm plantations. These animals are mostly generalists, of an opportunistic nature (Foster et al., 2011, Gray et al., 2017), so new microhabitats will be coveted (Rantalainen et al., 2005). The successful colonisation of the vacant ferns in Plot 2 provides direct evidence that even the action of introducing ferns (with no animals) into oil palm would provide an inherit benefit to the invertebrates that use them.

The vacant ferns in Plots 3 and 4 were available to colonisers from both the oil palm landscape, and the transplanted rainforest ferns. These ferns were successfully colonised, but until each and every one of the taxa collected in this study have been processed to the morphospecies level, we cannot be certain of the extent to which the animals that colonised these ferns were from the rainforest via transplanted ferns or from the oil palm landscape. However, some direct evidence that the animals colonising these ferns had originated from the transplanted ferns can be taken from the earthworms (Oligochaeta, Annelida). In Plot 3, one fern (3:1), which had been installed on the central tree between the four transplanted ferns, contained several large earthworms. These earthworms are not known from oil palm plantations (Turner and Foster, 2009, Foster et al., 2011), but are found in bird's nest ferns in primary forest (Ellwood et al., 2002). Most likely, animals colonised the vacant ferns in Plots 3 and 4 from both the transplanted ferns and from the wider oil palm landscape. This would explain why ferns in Plots 3 and 4 contained more animals than the vacant ferns in Plot 2, which could only have been colonised by oil palm animals, although the difference was not significant. The answer to the second key question posed in this chapter, of whether the ferns could harbour biodiversity in plantations, was again yes. While naturally occurring oil palm ferns support a relatively high abundance of invertebrates and functional biomass, in just six months, newly established vacant ferns were colonised to the extent that they contained similar numbers of animals and biomass as the control oil palm ferns.

The transplanted ferns contained significantly more animals (1841 ± 569 individuals) and more biomass (6878 ± 3111 mg) than the other ferns. Further to this, direct evidence that the transplanted ferns retained significantly high levels of biodiversity can be obtained from our focal groups, the cockroaches and centipedes. Species richness, that is, the number of species represented in an ecological community (Gotelli and Colwell, 2001), was significantly higher for both groups in the transplanted ferns. Several species of cockroach, including *Panesthia* spp., *Rhabdoblatta* sp. and *Sundablatta* sp., and the centipede *Ethmostigmus rubpripes*, were recorded only in transplanted ferns. Cockroaches are exclusively decomposers, whereas centipedes are exclusively predators, meaning that these animals represent very different trophic positions. Given that species richness was highest for both of these groups in the transplanted ferns, it is quite conceivable that the same would be observed across other taxonomic groups, and if this were true for all taxonomic groups, then the overall difference in species richness between transplanted ferns, and the other ferns, would be substantial. In response to my third major question, of whether transplanted ferns containing rainforest fauna could successfully retain high levels of invertebrate diversity in plantations, the answer is yes. For both focal groups, the transplanted ferns supported a greater species diversity. The fact that certain species were only present in transplanted ferns suggests that these ferns continued to support rainforest fauna in the oil palm landscape.

Two of the transplanted ferns (03:03 and 03:04) contained fewer animals, and less biomass than the other transplanted ferns at the end of the experiment. Both of these ferns had fallen from their respective oil palms on four occasions over the course of the experiment, and this likely led to losses of their animal inhabitants. These ferns, which had both been in excess of 50kg fresh mass at the onset of the experiment, appeared to have lost substantial biomass themselves by the end of the experiment. Although both of these ferns contained fewer animals, and less biomass compared with the other transplanted ferns, they still contained more individuals and more biomass than the other ferns in the experiment. Thus the success of transplanting rainforest ferns hinges on ensuring minimal disturbance to the fern and its animal inhabitants.

Species present in vacant ferns adjacent to transplanted ferns, but absent from oil palm control ferns (Plot 1) and vacant ferns (Plot 2), confirmed that dispersal from transplant ferns had taken place. Two such species were the cockroaches *Eucorydia* sp. and *Diploptera* sp., absent from Plots 1 and 2, yet were present at relatively high abundances in the transplanted ferns. They were also recorded in the vacant ferns in Plots 3 and 4, confirming that these species had dispersed across the plantation from the transplanted ferns into the vacant ferns. Similarly, the centipedes *Otostigmus* sp. 1 and *Scolopocryptops melanestoma* were absent from the oil palm control ferns in Plot 1, and from the vacant ferns in Plot 2. Yet they were both prevalent across the ferns in Plots 3 and 4. These centipedes were probably foraging between the transplanted ferns and the vacant ferns in Plots 3 and 4. Certainly the abundance and biomass data illustrated that the transplanted ferns retained a significantly high level of biodiversity in oil palm plantations. However, the information derived from our focal taxa provides the answer to the final question underpinning the use of ferns as conservation tools. Could transplanted animals disperse across the oil palm landscape? Wonderfully, the answer is yes. The occurrence of species of cockroaches and centipedes throughout the ferns in Plots 3 and 4, while being distinctly absent from Plots 1 and 2, suggests very strongly that animals were able to disperse out of the transplanted ferns across the oil palm plantation. However, we can only attain a true understanding of the extent to which animals dispersed from the transplant ferns upon completion of a full assessment of the taxonomic groups.

Cockroaches and centipedes provide ideal model taxa for exploring species assembly rules in oil palm plantations, because these animals represent distinct, functionally significant trophic levels. Cockroaches are decomposers, feeding on decaying organic matter derived from producers and consumers (Bell et al., 2007), and centipedes prey on decomposers (Gao et al., 2017). Until now, the functional significance of cockroaches to decomposition in oil palm has been overlooked. While previous work has shown that cockroach abundance is higher in oil palm relative to forest (Foster et al., 2011, Turner and Foster, 2009), it was unexpected that they would be the most important contributors to overall biomass in the ferns (11,508 mg, 16 %). Decomposers contributed the bulk of biomass recorded in this study, with exclusive decomposers such as cockroaches (Blattodea), woodlice (Isopoda), earthworms (Oligochaeta), millipedes (Diplopoda), Symphyla and springtails (Collembola) accounting for approximately 34,550 mg (49%) of the total 71,100 mg of biomass recorded. Many species of ants (Formicidae), beetles (Coleoptera) and earwigs (Dermaptera) are also exclusively decomposers, yet because these groups were not identified to the level of species, the true contribution of decomposers to overall biomass is likely much higher.

Several cockroach species such as *Bolta* sp, *Margattea* sp and *Pycnocelus surinamensis* overlapped all plots, occurring in many of the ferns from each plot. *P. surinamensis* (Chapter 3) is a widespread invasive species that does well in oil palm plantations (Pellens and Grandcolas, 2002). The prevalence of these species across the ferns from each of the plots is indicative of a multidirectional transfer of animals between the ferns and the oil palm landscape. Invasive species such as *P. surinamensis* do well because they tend to have stronger competitive ability than the animals they displace (Gurevitch and Padilla, 2004, Davidson et al., 2011). However, null model analysis did not reveal competitively structured cockroach communities across the ferns in this study. Whilst this does not mean that competitive interactions were entirely absent (Connor and Simberloff, 1979, Connor and Simberloff, 1986, Ellwood et al., 2009), it does suggest that other potential biotic or abiotic factors were more important in determining species assemblages (Kraft et al., 2015, Cadotte and Tucker, 2017). Where competitive interactions are not the most important ecological force at play, other key factors such as predation may be more important in determining the structure of communities (Menge and Sutherland, 1976, Petermann et al., 2015, Thakur et al., 2017).

The importance of bird's nest ferns to centipedes, and in turn the prevalence of the centipedes in bird's nest ferns, was explored in detail in Chapter 4. As regulators of decomposer populations (Formanowicz Jr and Bradley, 1987, Gao et al., 2017), centipedes exert top down control (Lawrence and Wise, 2017), although their role as predators of pests has likely been underappreciated in agricultural landscapes. Understanding the effect of habitat disturbance on top predators is key to understanding the effect of habitat disturbance on food webs (DeLong et al., 2014, Rusch et al., 2015). The results presented here have revealed that centipedes in bird's nest ferns naturally occurring in oil palm plantations (Plot 1, 19.1mm) were significantly larger than those collected in any of the other ferns, and indeed larger than those collected from the rainforest canopy (Chapter 4, mean 15.1mm). The largest centipedes collected in this study did not exceed 50mm in length, whereas those from the forest canopy were up to 120mm (Chapter 4). However the individuals recorded here were still juvenile, for instance *Ethmostigmus rubripres* was recorded here below 50 mm in length, whereas an adult specimen is typically 140 mm (Lewis, 1981). Previous studies have suggested that habitat disturbance can supress predator body size (Jellyman et al., 2014), yet centipedes are seemingly larger in oil palm plantations. Centipedes actively forage (Guizze et al., 2016) when prey abundance is unreliable (Formanowicz Jr and Bradley, 1987). In this sense, a large body size is advantageous in landscapes such as oil palm plantations where predators need to roam greater distances between resources (Kapustjanskij et al., 2007). Large animals also desiccate more slowly (Lighton and Quinlan, 1994), and have a better chance of overcoming and consuming prey where it is encountered (MacNulty et al., 2009).

Regardless of shifts in community structure through habitat disturbance, predator prey interactions remain a key ecological interaction (Konopik et al., 2014, DeLong et al., 2014). As generalist predators, centipedes switch between prey populations as they fluctuate (Formanowicz Jr and Bradley, 1987, Gao et al., 2017). This functionally important group has received relatively little attention under forest conversion, although one study revealed that centipede abundance and species diversity were consistent between rainforest and oil palm (Klarner et al., 2017). Typically, predators show negative spatial associations with one another due to competition (Hickerson et al., 2005, Hickerson et al., 2018), yet across the oil palm ferns, *C*–Score analysis revealed significant aggregation of centipedes in bird's nest ferns. Aggregation is the complete opposite of what one would expect if competitive interactions structured the community (Ellwood et al., 2009). However, as we have already seen in Chapter 4, bird's nest ferns promote resource sharing between this predatory group, and species aggregation is a clear indication of resource sharing (Ellwood et al., 2016). In fact, this observation, together with this line of reasoning, confirm the increased importance of birds nest fern resources in oil palm.

It is widely accepted that the establishment of oil palm plantations leads to significant losses in biodiversity (Foster et al., 2011, Barnes et al., 2014, Ghazali et al., 2016, Vijay et al., 2016). However, after the conversion process is complete (Gray et al., 2017, Turner et al., 2008), mature plantations are microclimatically stable (Luskin and Potts, 2011) and can harbour significant levels of diversity (Fitzherbert et al., 2008). The introduction of bird’s nest ferns into mature oil palm plantations provides an inherent benefit to the animals living within the landscape. The results in this chapter provide evidence that transplanting bird’s nest ferns and their faunal inhabitants from the rainforest can improve biodiversity in oil palm plantations. These results have revealed that the introduction of a single transplanted fern was sufficient to increase the abundance, biomass and diversity of fauna in a given area. Bird’s nest ferns are umbrella species, and introducing ferns, either vacant or transplanted along with their animals, into oil palm plantations could represent a unique opportunity for conservation by accelerating habitat restoration and by increasing habitat connectivity throughout the oil palm landscape. And so in answer to the final and most important question – yes, bird’s nest ferns can and should be used as conservation tools in oil palm plantations.

5.5 SUMMARY

- Bird’s nest ferns occur at lower abundances in oil palm plantations than previously thought. However, naturally occurring bird’s nest ferns can still support as many as 18,620 invertebrates and around 30,418 mg of biomass in a hectare of mature plantation.
- Bird’s nest ferns can be successfully installed into plantations, providing additional resources for animals already living there. Ferns can also be successfully transplanted from rainforest into oil palm plantations, and the animals associated with the ferns not only survive the move but can disperse across the oil palm landscape.
- The success of the installation is somewhat dampened if the ferns are frequently disturbed, but harvesters can learn to avoid knocking the ferns from the palms. In time the ferns will develop their own attachments to the trunks.
- Competitive interactions do not appear to govern species assembly in oil palm, therefore other factors such as predation pressure or environmental filtering may better explain community structure and species assembly.
- Centipede predators are significantly larger in plantations than in primary forest, and this may accommodate wider foraging for scattered resources. As in Chapter 4, widespread resource sharing was observed in the ferns.

6 SYNTHESIS OF FINDINGS AND FUTURE WORK

CONTEXT

The dense tropical rainforests of Borneo are a hotspot of species richness and endemism. Yet these incredibly important habitats are increasingly threatened by anthropogenic disturbances such as agricultural expansion. The demand for palm oil has disabeen a major driver of forest loss in recent decades, as rainforests across Southeast Asia have been replaced with oil palm. My research has deepened our understanding of bird’s nest ferns as refuges, capable of buffering environmental conditions for treasure troves of invertebrates in the rainforest canopy and more importantly in oil palm plantations. In Chapter 2 I defined the unique soil properties which allow the ferns to buffer microclimate. Further to this, I revealed that the ferns’ ability to store water represents a significant functional role in water capture, providing a degree of flood mitigation. Invertebrates represent some 90% of global biodiversity and while bird’s nest ferns protect these animals from climatic extremes, the tolerance of invertebrates to climate change and the consequences of anthropogenic disturbance remain poorly understood. Chapter 3 takes a major step towards solving these issues, because having quantified physical conditions in the ferns I used cockroaches as model animals to show how stable isotopes can integrate the physical conditions within the ferns with the physiology of their animal inhabitants. Linking the physiology of the animals with the physical conditions within the ferns has advanced the fern model system, and will provide a new direction for studies of insect physiology as a means to quantify species’ vulnerability to habitat disturbance and climate change. In Chapter 4 I focused my efforts on filling a knowledge gap concerning the role of predators in shaping rainforest canopy communities. I revealed unexpected levels of resource sharing by top invertebrate predators within the ferns, and that predation may be more important than competition in structuring rainforest canopy communities. In Chapter 5 I revealed the critical importance of the ferns as biodiversity refuges in oil palm plantations, and established the evidence base for using the ferns as conservation tools to return native biodiversity to the oil palm landscape. This final chapter will briefly synthesise the key findings of my thesis, provide an overview of the impact of my research beyond academia, and outline some of the strategic lines of enquiry that this project will follow in the future.

6.1 BIRD’S NEST FERNS AS THERMAL BUFFERS

In Chapter 2, I conducted an in-depth study of the ability of bird’s nest ferns to buffer the harsh physical conditions associated with the high canopy, revealing that it is the physical properties of the fern soils that are responsible for the ferns ability to thermo-regulate. My studies revealed that fern soils have a high water holding capacity (40%), low bulk density ($0.41 g/cm^3$) and high total porosity (84.4%). Essentially, this means that fern soils are able to absorb nearly half of their dry mass as water, but because of their low bulk density and high total porosity, the soils will never become completely waterlogged. This is incredibly important, first for the animals that inhabit the ferns, because it means that during heavy rainfall events they will not need to evacuate for risk of flooding, and second for both faunal and microbial organisms, because it means that the fern will always be well aerated and never anaerobic. Soils with low bulk densities also tend to have high material strength (Blazejczak et al., 1996), which explains why the ferns form strong attachments to their substrates, and why some of the transplanted ferns in Chapter 5 needed to be prised from the oil palm trees. Using my calculated value of bulk density, and the biomass of bird's nest ferns in a hectare of forest canopy (Ellwood et al., 2002), I was able to calculate that bird's nest ferns store approximately 865 litres of water per hectare of rainforest canopy. However, my calculated values for fern soil properties were derived from ferns harvested in the low canopy. Ferns in the low canopy do not need to store water for microclimatic buffering to the same extent as those in the high canopy or in oil palm. Therefore I may have underestimated the water storage capacity of the bird's nest ferns in a hectare of rainforest canopy, if ferns in the high canopy are better able to store water. Certainly the role of the ferns in water storage has never been appreciated, and the importance of above-ground water capture in flood prevention has never even been considered for oil palm plantations.

In Chapter 2 I revealed that bird's nest ferns regulate their own temperature by dissipating heat energy to their environment through latent heat, and this was evidenced by increased relative humidities in proximity to the ferns. In fact, bird's nest ferns in oil palm plantations buffer microclimate to such an extent that over a 24 hour period the mean temperature inside the fern soil core was not significantly different from the rainforest low canopy, and within 0.1°C of fern temperatures in the high canopy. This means that the animals residing in bird's nest ferns in oil palm plantations will experience similar temperatures as those living in ferns in primary rainforest. On this basis, bird's nest ferns should be considered critically important microhabitats in oil palm plantations, because they allow animals to evade climatic extremes of the wider environment. This was one of the key observations underpinning my decision to establish the ferns as conservation tools in oil palm plantations in Chapter 5.

6.2 STABLE ISOTOPES IN INVERTEBRATE PHYSIOLOGY

In Chapter 3 I deepened our understanding of how the oxygen isotopic composition ($\delta^{18}O$) of insect chitin is a reflection of the environmental conditions under which an insect has lived. By collecting *Periplaneta australasiae* (Australian cockroach) and *Pycnoscelus surinamensis* (Suriname cockroach), two pest species from sites with different microclimatic conditions across the Eden Project Rainforest Biome (RFB), I was able to show that significant differences in the microclimate of a habitat would result in significant differences in the $\delta^{18}O$ of insect chitin. The $\delta^{18}O$ of chitin was significantly positively correlated with ambient air temperatures ($R_s = 0.886$, $p = 0.019$), meaning that as ambient air temperatures increased, so too predictably did the $\delta^{18}O$ signature of chitin. However, the negative correlation between $\delta^{18}O$ and ambient relative humidity was significant to an even greater extent ($R_s = -0.943$, $p = 0.005$). I have therefore shown categorically that the $\delta^{18}O$ signature of chitin responds to changing temperature and humidity.

The $\delta^{18}O$ of insect chitin was entirely a reflection of environmental conditions, independent of genetic relatedness. Differences in $\delta^{18}O$ were reflected the microclimatic conditions experienced by the cockroach, but this was determined by the way in which the cockroaches interacted with their microhabitat. Where significant differences occurred in the climatic conditions between habitats, as seen in the Eden Project, this gave rise to significant differences in the $\delta^{18}O$ signature of chitin. Regardless of their genetic relatedness, all coming from the same species, *Periplaneta australasiae* showed significant differences in $\delta^{18}O$ when there were significant differences in climatic conditions between the collection sites, where conditions were homogeneous between collection sites in the RFB, so too were the $\delta^{18}O$ signatures of *Periplaneta australasiae*. The same was observed among the seven cockroach species analysed from the five large bird's nest ferns in Borneo. Chapter 2 had already shown the extent to which bird's nest ferns regulate their own microclimate, and I was therefore confident that the cockroaches inhabiting the ferns would have experienced similar microclimatic conditions. Further to this, these large ferns (leaf diameter >2m) would have had greater water storage capacity, and consequently their thermal buffering capabilities should have been even greater than those ferns studied in Chapter 2. Regardless of phylogenetic relatedness, there were no signficiant differences in the $\delta^{18}O$ of cockroaches from the Bornean ferns. However, different physiologies and life history strategies lead cockroaches to use their habitat in different ways, as in the case of *Periplaneta australasiae* and *Pycnoscelus surinamensis* at the Eden Project. When cockroaches use their habitats differently, and this leads them to experience different microclimatic conditions, their $\delta^{18}O$ signatures will reflect these habitat preferences. This chapter provided conclusive evidence that the $\delta^{18}O$ signature of insect chitin responds to climatic conditions alone, as predicted by Ellwood *et al* (2011) and illustrated by van Bergen *et al* (2016). This knowledge of the relationship between $\delta^{18}O$ and microclimate is now sufficient for $\delta^{18}O$ to be implemented widely as a measure of species resilience or vulnerability to habitat disturbance and climate change.

6.3 PREDATORS AS SHAPERS OF ECOLOGICAL COMMUNITIES

Bird's nest ferns support high abundances of centipedes, and are used by centipedes as canopy nesting sites. Prior to my investigation, centipedes from tropical rainforests were virtually unknown because so few studies have focused on the ecology of centipedes under natural conditions. While little was known of centipedes on the forest floor, nothing was known of centipedes in the rainforest canopy. My study of canopy centipedes has revealed that consideration for the significance of centipedes to ecosystem function needs to be revised because of the impressively large biomass that centipedes contribute to the canopy environment. Biomass is linked closely with ecosystem function. Beyond their functional significance, I identified each and every member of the canopy community, and was therefore able to reveal a distinct vertical stratification in rainforest centipede species. The rainforest high canopy was dominated by large centipedes belonging to the family Scolopendridae, while the low canopy was dominated by smaller centipedes of the family Cryptopidae. Although these centipedes were of different families, they all belonged to the Order Scolopendromorpha, and at the taxonomic level of Order the centipede community was structured consistently throughout the forest canopy.

I used *C*-Score analysis (Stone and Roberts, 1990, Gotelli, 2000) to show that this vertical stratification was not a result of competition between different species, but most likely because of species specific abilities with regard to accessing the rainforest canopy. From what is known of centipede behaviour I had expected that their aggressive nature would lead to competitive interactions between species. However, the lack of competition between species of centipedes was quite surprising because it indicated complementary and shared resource use. Mine is the first study to show resource sharing between top invertebrate predators, although invertebrate predators have been largely understudied (Klarner et al., 2017). Nevertheless, given the high abundance of large centipedes and other predators such as spiders in the rainforest canopy, predation may actually be the most important ecological force structuring canopy invertebrate communities. If this is the case, our understanding of species interactions in canopy ecosystems needd serious revision. My findings would explain several other studies that suggested that competitive interactions may not necessarily structure canopy communities (Ellwood et al., 2009, Wardhaugh et al., 2014, Ellwood et al., 2016, Pedley et al., 2016) as well as those in disturbed habitats such as oil palm plantations (Foster et al., 2011, Wood et al., 2017).

6.4 BIRD'S NEST FERNS AS CONSERVATION TOOLS

Bird's nest ferns occur at lower natural abundances in oil palm plantations than previously thought. My study, based on surveys of 40 hectares of oil palm plantation, revealed an average population density of 35 ferns ha^{-1}, compared with the ferns 112 ha^{-1} estimated from a previous study of 20 hectares of plantation (Turner and Foster, 2009). It is possible that the natural density of bird's nest ferns in oil palm plantations may be influenced by proximity to forested areas, or sources of moisture such as rivers. Additionally, the Sebrang Oil Palm Estate where Turner and Foster (2009) conducted their study, is situated on the coast between the 1,225 km^{2}

Tabin Forest Reserve and the Celebes Sea. Sabahmas is inland, and although the nearest forested area is a narrow offshoot of the Tabin Forest Reserve, the decreased air movement that would result from increased distance inland may reduce the efficiency of spore dispersal. Nevertheless, bird's nest ferns still represent critically important hotspots for invertebrate diversity and biomass in oil palm plantations, and a density of 35 ferns ha^{-1} could still support up to 18,620 invertebrates and around 30,418 mg of functional biomass in a hectare of mature plantation.

I devised a stepwise approach to fill key knowledge gaps, and to build a concrete, scientifically underpinned evidence base for bird's nest ferns as conservation tools in oil palm. First, I showed that bird's nest ferns could be installed successfully into plantations, providing additional resources for animals already living within the plantation. Then I revealed that bird's nest ferns and their animal inhabitants could be successfully transplanted from rainforest into oil palm plantations, and not only did the animals associated with the ferns survive the translocation, but these animals were able to disperse across the oil palm landscape. In doing so I revealed that many of the animals associated with bird's nest ferns in the rainforest high canopy are able to persist in oil palm plantations, and that if a network of bird's nest ferns were installed across the oil palm landscape, perhaps more native fauna would be able to use the habitat. However, the success of installing ferns can be dampened if the ferns are frequently disturbed during fresh fruit bunch (FFB) harvesting. On a positive note, oil palm harvesters can avoid knocking the ferns from the palms, allowing newly installed ferns to develop their own natural attachments to the oil palm trunks.

As I observed with the high canopy centipedes in Chapter 4, competitive interactions did not govern centipede species assembly in the oil palm plantation. Interestingly, centipedes significantly larger in oil palm plantations than in primary rainforest. This is likely to enable these predators to forage over greater distance for scattered resources, and to ensure that where prey is found it can be overcome. As in Chapter 4, *C*-Score analysis of the centipedes in the experiment ferns found no evidence of competition, but actually significant aggregation was detected indicative of resource sharing instead. There is an interesting parallel here with facilitation in plants. As conditions become more stressful, plant species tend not to compete, but rather facilitate the establishment and growth of other species (Wang et al., 2012). In the challenging oil palm environment, perhaps it is more energetically expensive and damaging to compete, and so apex invertebrate predators do not compete. If this is true, then the rules typically governing ecological communities may not apply when environmental conditions are sufficiently challenging, such as those in the rainforest high canopy, or in disturbed habitats such as oil palm plantations. This may provide direct evidence of environmental filtering in action.

6.5 FUTURE WORK

While Chapter 2 explored the buffering capabilities of bird's nest ferns, a simple calculation based on bulk density, water-holding capacity and dry biomass of fern soils indicated that the functional role of the ferns in above-ground water storage has been grossly underappreciated. Flooding is a major issue in many agricultural landscapes, especially in oil palm plantations, where sites on flat lowland areas can be flooded for a large proportion of the year. The cost of installing extensive drainage systems, and the cost accrued by flood damage could be mitigated by installing ferns as natural flood defence in plantations. Given that the 50 ferns ha^{-1} in rainforest canopy could store some 865 litres of water (Chapter 2), the installation of a fern on every palm in a hectare of oil palm (144 palms ha^{-1}) could nearly triple the volume of water captured and held above the ground in oil palm plantations during rainfall events. Future studies, which not only consider but quantify the role of bird's nest ferns and other epiphytes in above ground water storage, would reveal not only the importance of these plants to water cycling processes, but provide plantation growers with quantitative evidence of the benefits that bird's nest ferns could provide in oil palm.

I also revealed in Chapter 2 that bird's nest ferns show consistent and therefore predictable thermoregulation in response to climatic variation in the macroenvironment. At the Eden Project, my model ferns significantly buffered microclimate as per their wild Bornean relatives. On this basis it will be possible to model the ferns' evolutionary adaptations to thermoregulate. For example, based on our understanding of the ferns' soil properties and the buffering capabilities they provide, we should be able to develop a microclimate model predicting the temperature regime of the ferns under a range of climate change scenarios. If global temperatures continue to rise as predicted (Sokolov et al., 2009, Raftery et al., 2017), we need to be able to predict whether the ferns will continue to provide stable microclimatic conditions across habitats, allowing species to evade the impacts of climate change. If indeed the ferns buffer rainforests and oil palm plantations alike against climate change, then they should be prioritised in conservation efforts, and the # of ferns in plantations and other disturbed habitats should be actively increased to ensure that these climate refuges are available for sensitive species.

Now that we have shown conclusively that stable isotopes of oxygen ($\delta^{18}O$) in insect chitin are a reflection of climatic conditions, we can begin to investigate how these signatures will respond more widely to habitat disturbance and climate change. By measuring the $\delta^{18}O$ signatures of insect species from communities along disturbance gradients, we can integrate levels of evaporative enrichment with thermal tolerance into a model for predicting the point at which particular species will disappear from communities under increasing disturbance (Figure 3.28). Further to this, future studies of $\delta^{18}O$ in chitin should consider other taxonomic groups such as the predators, because they too are functionally significant and may also show isotopic convergence in response to microhabitat. In such cases, the $\delta^{18}O$ in chitin would provide a universal metric for quantifying the response of all tracheated arthropods to climate change and future disturbance.

Chapter 4 revealed the impressive abundance of top invertebrate predators in the rainforest canopy. However, we now need to quantify the precise influence of these predators in structuring ecological communities in canopy food webs. The role of top down control (Schneider and Brose, 2013) in regulating ecological interactions and associated function has already been explored in some depth for the forest floor. While my research has shown that the abundance of centipedes in the forest canopy will be influencing the community at large, we now need to reveal the precise influence of these top predators on other members of the canopy community. Future studies should consider the role of centipedes and other predators in the structuring different trophic levels within ecological communities, especially when environmental conditions are less than favourable. Indeed, the next step for understanding the importance of predators will be to decipher their specific influence on biodiversity, and reveal the knock-on effects of predation on ecosystem function in the canopy environment.

Finally, Chapter 5 provided the evidence base for using bird's nest ferns as conservation tools in oil palm plantations. However, this was just a pilot study using 52 bird's nest ferns in a relatively small area of oil palm plantation. Nevertheless, the results of this experiment suggest that introducing bird's nest ferns into the oil palm landscape would have a positive effect on biodiversity. We now need to determine whether returning native biodiversity to oil palm plantations will improve specific ecosystem functions such as decomposition and nutrient cycling. Future studies should work to quantify the interplay between biodiversity and ecosystem function in the oil palm landscape, and determine whether increasing structural complexity and restoring native biodiversity can improve the ecological outlook of plantations. This research will not cease upon the completion of this PhD thesis, but rather the results presented here will provide the springboard for future studies of bird's nest ferns, the biodiversity they support, and their role in functional processes in both natural and anthropogenic landscapes such as oil palm.

6.6 IMPACT BEYOND ACADEMIA

At the start of this project, a great deal of time was spent working alongside staff at the Eden Project, procuring and installing bird's nest ferns into the biome, trialling different microclimate monitoring system (MMS) set ups, and testing cockroach collection techniques. During this time, I worked closely with the Eden Project's Communication and Design team to write their Palm Oil Master Document. Master documents represent the Eden Project's stance on an issue, and are circulated to all staff members, encapsulating the precise details of what the Eden Project wishes to communicate to the public on a given topic. Based on the information presented in the Palm Oil Master Document, UWE Bristol and the Eden Project jointly commissioned a palm oil exhibit to be situated within their RFB. The exhibit opened in May 2017, reinforcing the message of supporting sustainable palm oil, and for consumers to become aware of the difference between RSPO certification and non-certified products. The Eden Project receives more than one million visitors each year and is now expanding, with a new site in the North of England, and several sites announced in China. Advising the Eden Project's stance on the oil palm issue was one of the most important opportunities to arise over the course of this project given that more than a million people visit each year.

In 2018, the Royal Society of Biology (RSB) and ITN Productions partnered to produce a feature called 'Addressing Global Challenges'. The focus of the news and current affairs-style programme was to explore innovations in the biosciences, and capture the length and breadth of the practical applications of breakthroughs in the field (RSB, 2018). My project featured in their production, specifically content based on Chapter 4 (centipedes) and Chapter 5 (oil palm transplants); essentially, we considered the importance of underappreciated animals as drivers of ecosystem function, and the role of bird's nest ferns in restoring functionally important biodiversity in degraded landscapes.

In 2018, UWE Bristol became the first university in the UK to take a stance on the palm oil issue, releasing a 'Statement on Palm Oil'. In the statement they acknowledge the effect of non-sustainably managed plantations on biodiversity, and the role that certification has to play in bringing plantations up to both social and environmental standards. They commit to ensuring that the university will use its teaching and research activities to raise awareness of the issues associated with palm oil to students, employees, partners and the public. UWE Bristol's commitment to source only products derived from Roundtable on Sustainable Palm Oil (RSPO) certified oil by 2020 was underpinned by the research presented here. Other UK universities are now following UWE Bristol in demanding sustainably sourced palm oil. This pioneering directive of UWE Bristol, and the change in policy and practice of other British universities, as well as public engagement highlighting the palm oil issue, are all evidence of the impact of this project beyond academia.

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8 APPENDICES

8.1 APPENDIX I

List of all species, and recognisable taxonomic units (RTU's) of centipedes recorded from bird's nest ferns in Borneo, with additional note of the significance of these specimens. The results from these studies of centipedes are reported in Chapters 4 and 5.

Species / RTU	**Family**	**Order**	**Type Specimen Collected From**	**Note**
Ballophilus sp. Cook, 1896	Ballophilidae	Geophilomorpha	Primary Rainforest	See group specialist, Luco Bonato in Italy.
Cryptops sp. 1 Leach, 1815	Cryptopidae	Scolopendromorpha	Primary Rainforest	*Paracryptop*s was known from Borneo, but *Cryptops* not known from Borneo.
Cryptops sp. 2 Leach, 1815	Cryptopidae	Scolopendromorpha	Oil Palm	
Ethmostigmus rubripres, Brandt, 1840	Scolopendridae	Scolopendromorpha	Oil Palm	
Lamyctes sp. 1 Meinert, 1868	Henicopidae	Lithobiomorpha	Primary Rainforest	This family was not known from SE Asia
Lamyctes sp. 2 Meinert, 1868	Henicopidae	Lithobiomorpha	Oil Palm	
undetermined Lithobiidae	Lithobiidae	Lithobiomorpha	Primary Rainforest	This family was not known from Borneo
Mecistocephalus cf. *punctifrons* Newport, 1843	Mecistocephalidae	Geophilomorpha	Primary Rainforest	
Mecistocephalus sp 1 Newport, 1843	Mecistocephalidae	Geophilomorpha	Primary Rainforest	See group specialist, Luco Bonato in Italy
Mecistocephalus sp 2 Newport, 1843	Mecistocephalidae	Geophilomorpha	Oil Palm	See group specialist, Luco Bonato in Italy
Otostigmus angusticeps Pocock, 1898	Scolopendridae	Scolopendromorpha	Primary Rainforest	There are no records of this family from Borneo.
Otostigmus multidens, Lewis 2001	Scolopendridae	Scolopendromorpha	Oil Palm Plantation	

Otostigmus sp. 1 Porat, 1876	Scolopendridae	Scolopendromorpha	Primary Rainforest	Head missing, could not identify.
Otostigmus sp. 2 Porat, 1876	Scolopendridae	Scolopendromorpha	Primary Rainforest	
Otostigmus sp. 3 Porat, 1876	Scolopendridae	Scolopendromorpha	Oil Palm	
undetermined Schendylidae	Schendylidae	Geophilomorpha	Primary Rainforest	See group specialist, Luco Bonato in Italy
Scolopendra subspinipes Leach, 1815	Scolopendridae	Scolopendromorpha	Primary Rainforest	One of the most aggressive species of centipede.
Scolopocryptops melanestoma, Newport, 1845	Scolopocryptopidae	Scolopendromorpha	Oil Palm	
undetermined Scutigeridae*	Scutigeridae	Scutigeromorpha	Primary Rainforest	Undescribed species, likely Borneo endemic.
undetermined Thereuoneminae (sub-family)	Scutigeridae	Scutigeromorpha	Primary Rainforest	Could not place.

*continued from previous page

8.2 APPENDIX II

Full list of taxonomic groups recorded from the bird's nest ferns collected for the study of centipedes in the rainforest canopy as presented in Chapter 4.

Acari - Mites
Annelida - Worms
Araneae – Spiders*
Blattodea - Cockroaches
Chilopoda – Centipedes*
Coleoptera – Beetles
Collembola - Springtails
Dermaptera - Earwigs
Diplopoda - Millipedes
Diptera - Flies
Formicidae - Ants
Gastropoda - Snails
Hemiptera – True Bugs
Hymenoptera (other) – Wasps and Bees
Isopoda - Woodlice
Lepidoptera – Butterfly and Moth Larvae
Mantidae – Mantis
Opiliones - Harvestmen
Orthoptera – Crickets
Pseudoscorpiones
Solfugida – Sun Spiders*
Strepsiptera – Two winged parasites
Symphyla
Thysanoptera - Thrips
Trichoptera - Caddisflies
Zoroptera – Angel insects
Psocoptera – Bark and Booklice
Phthiraptera - Lice
Isoptera - Termites
Uropygi – Whip Scorpions*
Phasmatodea – Stick Insects

*Exclusive predators

8.3 APPENDIX III

List of all species, and recognisable taxonomic units (RTU's) of cockroaches recorded from bird's nest ferns in Borneo. Many RTUs are assigned to species complex as identification to species level would require destructive sampling of internal anatomy. The results from this study are reported in Chapter 5.

Species / RTU	**Family**	**Type Specimen Collected From**
Episymploce spp. Bey-Bienko, 1950	Blatellidae	Oil Palm Transplant Fern
Margattea spp. Shelford, 1911	Blattelida	Oil Palm Transplant Fern
Shelfordina terminalis Brunner von Wattenwyl, 1898	Blatellidae	Oil Palm Transplant Fern
Bolta / *Margattea* spp. Shelford, 1911	Blatellidae	Oil Palm Transplant Fern
Blatella sp. Caudell, 1903	Blatellidae	Oil Palm Transplant Fern
Eucorydia sp. Hebard, 1929	Corydiinae	Oil Palm Transplant Fern
Diploptera cf. ethyrocephala Princis, 1950	Blaberidae	Oil Palm Transplant Fern
Haanina adusta Hebard, 1929	Blaberidae	Oil Palm Transplant Fern
Anaplecta sp. Burmeister, 1838	Blattelidae	Oil Palm Transplant Fern
Parasymploce spp. Hebard, 1929	Blattelidae	Oil Palm Transplant Fern
Undetermined Blattidae, Latreille, 1810	Blattidae	Oil Palm Transplant Fern
Panesthia sp. 1 Serville, 1831	Blaberidae	Oil Palm Transplant Fern
Panesthia sp. 2 Serville, 1831	Blaberidae	Oil Palm Transplant Fern
Pycnoscelus surinamensis, Linnaeus, 1758	Blaberidae	Oil Palm Transplant Fern
Undetermined Blattinae (sub-family) Latreille, 1810	Blattidae	Oil Palm Transplant Fern
Rhabdoblatta sp. Kirby, 1903	Epilamprinae	Oil Palm Oil Palm Fern
Subdablatta spp. Hebbard, 1929	Blattelidae	Oil Palm Transplant Fern
Methana spp. Stal, 1877	Blattidae	Oil Palm Transplant Fern
Hemithyrsocera spp. Saussure, 1893	Blattelidae	Oil Palm Vacant Fern

*sp. refers to a single identifiable species whereas spp. refers to what may be a species complex with either one species with a degree of plasticity in appearance, or more than one cryptic species.