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Firefly (Coleoptera: Lampyridae) Diversity and Distribution in Malaysia: Ecological Explanations and Conservation Requirements

By:

Nada Badruddin

A thesis submitted in partial fulfilment of the requirements for the degree of

Doctor of Philosophy

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:) Firefly

Firefly
Small your light
It takes the glow of many
To mark the night.
What wisdom do you know,
What can you speak,
Of regions far beyond your realm?

Firefly help me listen
For your whisper in the night.
~ Bill Grace ~

ABSTRACT

Tropical forests support most of the biodiversity of the world, yet many groups including the fireflies (Coleoptera: Lampyridae) are still poorly understood. The research question addressed in this study is on the influence of logging and elevation on species diversity, distribution and abundance of tropical fireflies. Throughout the research, whether and how firefly community composition varied with habitat characteristics were identified. The use of a robust, quantitative analysis framework (iNEXT) to estimate firefly species richness and diversity was explored. A total of 229 transects in 26 forest compartments in Dungun Timber Complex and 110 transects at every 50 m elevation bands along a 1,900 m elevation gradient on five mountains located across the main mountain range of Peninsular Malaysia were sampled. From the sampling conducted, 23 species of fireflies, 17 of which are new record for Peninsular Malaysia and five new to science were identified. The males and reliably associated females of one of the new species, *Pygoluciola dunguna* was taxonomically described. Effect size of age of forest since logging was not found to be significant however twice logged forest showed a significantly lower recovery of firefly species. Canopy closure, leaf litter depth and number of water bodies were found to moderate their community composition and proximity to primary forest showed a large positive effect size on the firefly species diversity in forests recovering from logging. Fireflies were found to be restricted to certain elevational range of mountains and turnover of species was significant among forest types across elevations. This research is a first attempt, at least in Southeast Asia, to place focus on this sensitive, vulnerable, low diversity and low abundance taxa. While further benefits would be gained with increasing collections in wider range of habitats, these data have enabled a better understanding of tropical firefly and placed a good foundation for future firefly biodiversity and conservation work in the tropics.

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To the fantastic four, the most energetic field assistants I have known. Thank you Jafni (Uyang), Ashraf (Bob), Baz and Afad. What an experience it has been- got stuck in the forest because a bull elephant decided he need to express his feelings that night; a tree fell so close to us but we did not know where to run because it was pitch dark, toasting buns on sticks in the forest while waiting for dusk to settle down; two red spots, green spots, yellow spots when we accidently pointed our headlights at the “wrong” directions. Memories I hope will always be remembered.

To my Mama and Papa, I am blessed to have you. To my mother-in-law, thank you for taking care of the children while I was away in the forests hunting for fireflies. To my late father-in-law, the quiet of the two, your sudden passing almost two years ago while I was finalising my field work in Malaysia, has left a scar yet I am glad all of us were there on the day of your demise.

At one point in time I did question myself if this work will be possible as I have very limited field experience and resources for working with inland forest fireflies. But one person has always been there, through thick and thin. He was there to encourage me that all can be done and the targets achieved if we plan, and persevere on. And to never forget that the best planner is always Allah - have faith and courage and all will work out in the end. My dearest Saiful Azhari, I will never, ever be able to repay you. A mere thank you will not be enough to show how much you have done for me and our children. Finally, to my loving Alfie, my sweetheart Myiesha, my determined Firas, my cheeky Dhiya and my little gentleman Rifqie- you are the coolness of my eyes and the warmth of my heart. We have accomplished this together, now let’s go for yet another adventure!

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CHAPTER 1

Introduction

1.1. Background and thesis objectives

This thesis focuses on species diversity and the distribution of tropical forest fireflies (Coleoptera: Lampyridae) in Peninsular Malaysia. The work looks into how firefly diversity changes with habitat variables important to its life history that vary across gradients of forest age after logging and across forest type transitions as elevation increases towards mountain tops.

The work was conducted in Malaysia, a megadiverse country (Mittermeier et al., 2005) situated in Southeast Asia. This region experiences some of the highest rates of recent forest loss via high human population densities and rapid expansion of oil palm, *Elaeis guineensis* and other crops including rubber, *Hevea brasiliensis* (Abdullah & Hezri, 2008; Phalan et al., 2013; Wilcove et al., 2013). Many locations in this region are categorised as biodiversity hotspots (Myers et al., 2000). Although forest of Southeast Asia contributes only a fifth of the world's rainforest, it has amongst the highest concentration of endemic species (Myers et al., 2000; Sodhi et al., 2004) and floristic species richness compared to the Amazonia and west and Central Africa (Whitmore, 1995).

In spite of growing interest to determine the drivers behind the high biodiversity observed in the tropical forests, many species groups are understudied (Ballesteros-Mejia et al., 2013; Jetz et al., 2012; Magurran, 2017) including insects (Ballesteros-Mejia et al., 2013; Dunn, 2005; McKinney, 1999). Fireflies (Coleoptera: Lampyridae) are among the insect groups with limited information, although they have been fascinating scientists and non-scientists alike because of their ability to produce light. They are culturally valued and widely recognized among the general public (Tetsuro Hosaka et al., 2016; Mendonca et al., 2012; Pichetvit, 2014).

Their charismatic light displays appeal to the public and concerns of their decline is increasing (Firebaugh & Haynes, 2016; Khoo et al., 2012; Nada et al., 2009; Nallakumar, 2003). Very little is known about firefly biodiversity and what moderate their distributions. Fireflies occupy diverse habitat types across the globe (M. V. Macedo et al., 2016; Nagelkerken et al., 2008; Santos et al., 2016; Takeda et al., 2006) and inhabit a wide range of ecological niches (Ballantyne et al., 2015; Fu, Ohba et al., 2005; Thancharoen et al., 2007; Wattanachaiyingcharoen et al., 2016). They also have diverse courtship communication (Lewis & Cratsley, 2008; Ohba, 2004)and exhibit diverse behavior at immature and egg-laying stages (Ballantyne et al., 2015, 2016; Branham, 2010).

Fireflies of the tropical forests can be grouped based on their light displaying behavior, either solitary or aggregative flashing. Aggregative fireflies are relatively better studied because they occur in large numbers (Jusoh et al., 2013; Ohba & Wong, 2004), are easier to sample and have economic contribution via firefly watching ecotourism (Jamil & Suzana, 1999; Nurancha et al., 2013). The solitary fireflies on the other hand are not well studied even though they are more diverse in morphology, behavior and habitat requirements (Branham & Wenzel, 2003; Jeng et al., 1998; Nak-Eiam et al., 2011a; Yuyong Wang et al., 2007). Solitary firefly habitat requirements are linked to their reproductive behavior and the requirements of larvae. A mature canopy and sub-canopy structure provide mating habitats (De Cock et al., 2014; Faust & Faust, 2014; Koji et al., 2012). Leaf litter and water source provide habitat for eggs and larvae, as some are aquatic or semi-aquatic (Fu, Wang et al., 2005; Takeda et al., 2006; Yuyong Wang et al., 2007).

Like any low abundance taxa, firefly survival could easily be threatened by detrimental changes of their environment. They are sensitive to changes of habitat and have been shown to reduce in numbers where breeding and mating areas are disturbed. Their population decline is linked to habitat loss, water pollution and light pollution (Koji et al., 2012; Picchi et al., 2013; Wong & Yeap, 2012). Therefore, there is a need for a rapid and reliable approach to estimate firefly species richness and diversity, especially in the tropical regions where information on species diversity especially of low abundance and low diversity taxa is still lacking.

Expanding information on solitary firefly species diversity, and the impact of logging and elevation on their distribution is the core objective of this thesis. The thesis covers four research chapters that combine to meet this overall objective:

1. The second chapter assessed the accuracy and precision of a newly developed species diversity estimator, iNEXT (Hsieh et al., 2016), to estimate species richness and diversity of tropical firefly communities. Solitary fireflies are a low diversity, low abundance taxa with patchy local distributions. Can iNEXT work well with this taxon? The data in this chapter focuses on accuracy and precision of estimates along environmental gradients and aids understanding of the value of iNEXT as previous assessments primarily focus on taxa which are much more diverse and abundant (Cristiane Costa et al., 2017; Onodera et al., 2017; Sharpe et al., 2017). Crucially, this chapter also validates the use of iNEXT in the following chapters.

2. While the impact of logging in the tropics on the diversity and species composition of well-studied, abundant, and taxonomically well-defined taxa is increasingly clear, there is limited information on taxa that are low in abundance or difficult to study such as the fireflies. The third chapter attempts to identify the possible effects of logging history and associated changes in habitat variables on species richness and diversity of tropical fireflies. Comparison of diversity estimates in once logged and twice logged compartments on firefly species richness was also investigated.
3. In the fourth chapter, fireflies were studied in mountainous forests along elevational gradients. It is known that studies across elevation enables rapid assessment of species diversity for multiple habitats in a shorter temporal scale. Here, species turnover (beta diversity) of the fireflies among five mountains and among five forest types across and elevational gradients were assessed. Species richness-habitat relationship of fireflies was also assessed to identify possible association.
4. During this study, five new species to science and twelve new records to Malaysia were discovered reflecting the potential of further discoveries and the limited information available thus far on fireflies. In the fifth chapter, a new species of the rare genus in the firefly family, *Pygoluciola dunguna* was described based on its morphology and distribution in various forest types (Nada & Ballantyne, 2018).

In the following sections, the natural history of solitary fireflies and the habitat they require are introduced. This is followed by a brief overview of secondary (logged) forests influence on the biodiversity of insects and recovery of species after logging ceased. The possible effects of this temporal gradient in disturbance towards firefly biodiversity are also described. This is followed by a brief overview of insect biodiversity research along elevation gradients and the five key elevational forest types of Malaysian mountains where firefly diversity (beta diversity) could be related to. The effect of the habitat variables along this spatial gradient on firefly diversity is also described. Finally, an overview of methods for estimating biodiversity and an introduction on iNEXT, the emerging, advanced method for estimating species richness and diversity which is used throughout the thesis, is presented.

1.2. Fireflies (Coleoptera: Lampyridae)

There are an estimated 2,000 species of fireflies from 100 genera (Lloyd, 2002) occupying diverse habitat types within the tropical and temperate regions of the world (Branham, 2010). Their habitats range from open grasslands (Lloyd et al., 1989; Takeda et al., 2006) to dense rainforests (Santos et al., 2016; Viviani & Santos, 2012); from mangroves (Nagelkerken et al., 2008; Wong & Yeap, 2012) to apex of mountain ranges (Macedo et al., 2016; Wattanachaiyingcharoen et al., 2016). This fascinating insect has been captivating ecologists, evolutionary biologists and conservation biologists through their ability to produce light (Buck, 1988; De Cock et al., 2014; Lewis & Cratsley, 2008). They are also emerging as a tool for conservation and education (Faust, 2004; Kobori, 2009; Lloyd, 1997; Mendonca et al., 2012); and as indicator species promoting environmental awareness through citizen science projects (Bonney & Dickinson, 2012; Chow et al., 2014; Xing, 2012).

Fireflies of the tropical forests can be grouped by their light displaying behaviour as either solitary flashing or aggregative flashing (Buck, 1938; Lloyd et al., 1989; Wong & Yeap, 2012). Preliminary studies conducted in the lowland dipterocarp forest within Forest Research Institute Malaysia campus in 2011 and 2013 (Nada, Mohd Salleh, Farid et al., 2014) showed the species richness of the solitary fireflies in the area was higher (ten possible species from seven genera) compared to the aggregative fireflies in estuarine or mangrove areas (one to three species from a genus) (Wong & Yeap, 2012). This finding supports the importance of further exploration into varied habitats to understand the diversity of fireflies. Determination of firefly species richness and diversity is among the first few steps that would help to identify important firefly habitat conservation areas and strategies.

The solitary fireflies (Figure 1.1), although more diverse in morphology (Lau et al., 2007; Wu et al., 2010), behaviour (Branham & Wenzel, 2003; De Cock & Matthysen, 2005) and habitat requirements (Fu, Ohba et al., 2005; Nak-Eiam et al., 2011b; Takeda et al., 2006); are not well studied due to their presence in difficult terrain, occurrence in low number, have solitary behavior and less touristic value. These factors limit our understanding of their diversity. However, like any low abundance taxa, their survival could be easily threatened by detrimental changes to their environment. Fireflies have been shown to reduce in population size where breeding and mating areas are disturbed (Hagen & Viviani, 2009; Lloyd, 2005), linked to water pollution and habitat loss as a result of agriculture expansion and urbanisation (Koji et al., 2012; Picchi et al., 2013; Wong & Yeap, 2012). Light pollution has recently been found to impact fireflies negatively by decreasing the probability of them securing a mate, thus affecting their breeding and survival (Firebaugh & Haynes, 2016; Hagen et al., 2015; Ineichen & Ruttimann, 2012; Thancharoen et al., 2008).

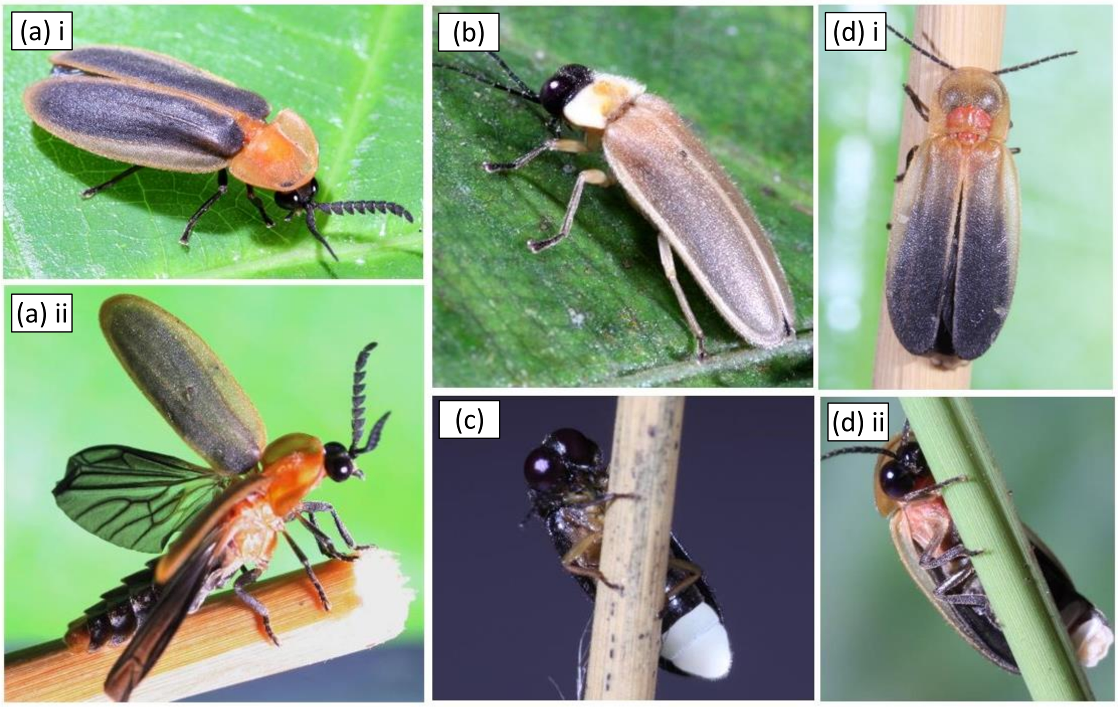

Figure 1.1: Adult fireflies (Coleoptera: Lampyridae): (a) i-ii Male of *Pyrocoelia* sp., (b) female of *Abscondita pallescens*, (c) male of *Luciola pallidipes* and (d) i-ii male of *Diaphanes* sp.

Fireflies require different niches of the habitat in order to complete their lifecycle. As larvae (Figure 1.2), they are predators, active at night preying on snails, slugs and earthworms (Fu & Meyer-Rochow, 2012; Fu et al., 2006; Jeng et al., 2000; Viviani, 2001). They can be terrestrial, aquatic or semi-aquatic (Ballantyne & Lambkin, 2013; Ballantyne et al., 2015). Terrestrial larvae crawl among leaf litter or on the ground among shrubs (Ballantyne et al., 2013; Jeng et al., 2001; Yuyong Wang et al., 2007), semi-aquatic larvae remain mostly stationary at stream edges in contact with water (Ballantyne et al., 2013; Fu & Ballantyne, 2008) and aquatic larvae swim near the water surface or dwell at the bottom of streams or ponds (Fu, Ballantyne et al., 2012b; Takeda et al., 2006; Thancharoen et al., 2007). The habitats of the aquatic or semi-aquatic larvae are confined to water body area including shallow flowing stream or stagnant water (Fu, Ohba et al., 2005; Takeda et al., 2006). Terrestrial larva seek refuge under leaf litter or among cracks of soil (Yuyong Wang et al., 2007; Wattanachaiyingcharoen et al., 2016) and semi- and aquatic larvae rest between aquatic vegetation roots or stems (Fu, Wang et al., 2005) when inactive.

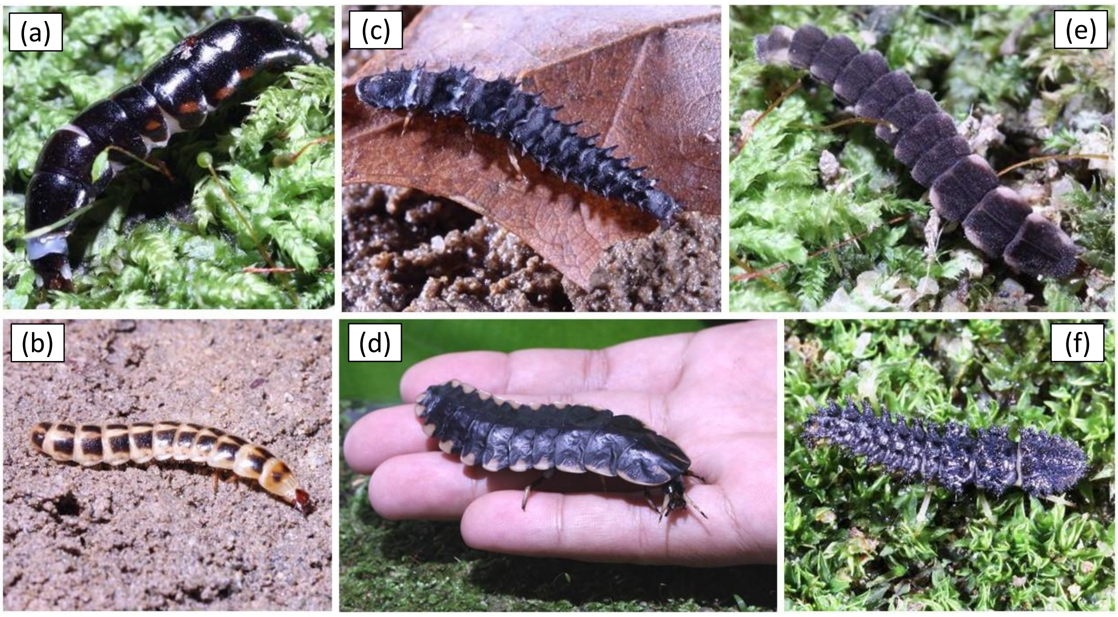

Figure 1.2: Firefly larvae: (a) *Drilaster* sp. larva and (b) *Stenocladius* sp. larva are diurnal fireflies. (c) A possible larva of *Pygoluciola dunguna* **sp. nov.**, (d) a *Lamprigera* sp. larva, (e) a possible *Diaphanes* sp. larva and (f) a possible Luciolinae larva.

Transformation to adult firefly happens during the pupal stage. Diverse pupation strategies are also seen in fireflies. Aquatic fireflies, i.e. *Luciola cruciata* would emerge from the water as the larva is ready to pupate before moving to nearby suitable ground and construct a cocoon from clump of wet soil (Takeda et al., 2006). The terrestrial firefly, *Pteroptyx tener* excavates an underground chamber for it pupation (Nallakumar, 2003) while *Pyractomena borealis* uses tree trunks to anchor itself before pupating within the cracks of the bark or on the surface (Faust, 2012).

As adults, fireflies utilise tree canopies, herbaceous plants or tall grass as their display and mating sites. These courtship and mating sites consist of trees lining riverbanks (Jusoh et al., 2011; Sartsanga et al., 2018), herbaceous plants (Faust & Faust, 2014; Katoh et al., 2009; Yuyong Wang et al., 2007) or grass blades in open area (De

Cock et al., 2014). A diverse range of courtship communication is also observed in fireflies. Courtship comprise either bioluminescent signals, bioluminescent signals and pheromone; or pheromone only (Lewis & Cratsley, 2008). The display of light signals could either be during flight or while positioned on leaves or grass blades, depending on species (Case, 1980; De Cock et al., 2014; Faust, 2012; Faust & Faust, 2014; Koji et al., 2012). Several genera with flightless females (brachypterous females) attract potential males by light signals and the release of pheromone (De Cock et al., 2014; Yuyong Wang et al., 2007). Courtship attraction by pheromone occurs in diurnal fireflies (Gronquist et al., 2006; Ming & Lewis, 2010). Diurnal fireflies from the subfamily Ototretinae (Coleoptera: Lampyridae) including *Drilaster* and *Stenocladius* have light emitting larvae (Figure 1.2 a-b) but once the adults emerge from the pupal stage, they only produce weak light or are barely luminescent, and therefore rely on pheromone as courting signals (Janisova & Bocakova, 2013).

1.3. Logging in tropical forest and its effect on biodiversity

Most tropical forests are situated within developing countries. Extraction of the natural resources or alteration of forests to other landscapes for socio-economical purposes are often unavoidable (Pia Katila et al., 2014). Some of the highest rates of recent forest loss occur in developing regions of Southeast Asia, with high human population densities and rapid expansion of oil-palm (*Elaeis guineensis*) and other crops including rubber (*Hevea brasiliensis*) (Abdullah & Hezri, 2008; Phalan et al., 2013; Wilcove et al., 2013). Although deforestation has decreased since 2010 (Keenan et al., 2015), degradation of remaining areas of tropical forest is expected to continue to increase (Sloan & Sayer, 2015). This includes from timber extraction (Geist & Lambin, 2002).

Timber extraction or logging is a major cause of forest degradation (Johns, 1997; Nepstad et al., 1999). The alteration of forest structure, tree stratification and composition by logging affects the local temperature, moisture, light penetration, soil and leaf litter conditions. Compaction and erosion caused from skid trails, logging roads and loading bays disturb soil properties (Ampoorter et al., 2011; Cambi et al., 2015; Hattori et al., 2013). The alteration of soil also deplete soil nutrient availability (Imai et al. 2012; Shariff et al. 1989). Tree felling cause collateral damage to neighbouring trees and contribute to forest gaps and canopy damage. The heterogeneous extraction of timber in tropical forests, where certain areas in the same forest blocks remain untouched while other sections are heavily timbered, causes forest fragmentation (Broadbent et al., 2008). Increase light penetration to the ground from larger canopy gaps increase soil temperature, and increase growth of understorey plant (F. R. C. Costa & Magnusson, 2003; F. V. Costa et al., 2015; Lebrija-Trejos et al., 2011). The decreasing canopy closure and leaf litter depth changes the breeding and feeding habitats of forest insects such as butterflies, dung beetles and ants (Ewers et al., 2015; França et al., 2017; T Hosaka et al., 2014; Molina-Martínez et al., 2016; Whitworth, Villacampa et al., 2016), and species composition of the dragonflies of logged forests was altered due to the removal of riparian vegetation in logged forests (Calvão et al., 2016).

Logging has a varying effect on the capacity for insect species to recover after it has ceased. Species recovery for abundant insects were found to begin in the first few years after logging. A post-logged forests of ages between 20 and 40 years have been shown to support almost similar species richness as that of primary forests for ants (Dunn, 2004). Nyafwono *et al.* (2014) found that high abundance and species richness of butterfly occurs in the intermediate stage of the forest succession. Although species recovery occur in successional secondary forest, old-growth specialist species were found to be present in highest number within primary forest as oppose to secondary forest (Basset et al., 2017; Gibson et al., 2011; Intachat et al., 1999).

The alteration of the forest environment impacted from logging could influence the biodiversity of fireflies. Larger canopy gaps increase light penetration to the ground, increasing soil temperature, decreasing leaf litter availability and increasing growth of understorey plants (F. R. C. Costa & Magnusson, 2003; F. V. Costa et al., 2015; Lebrija-Trejos et al., 2011) Soil temperature and leaf litter alterations could negatively affect microhabitats of the firefly larvae, their prey and the flightless firefly females. The increase in height and density of understorey plants may positively or negatively influence the adult firefly mating success. Understorey plants are resting and mating locations for many firefly species therefore presence of understorey plants may promote mating success in fireflies. However, the denser undergrowth of the logged forest could form a barrier for the firefly visual communications.

1.4. Tropical forest across elevations, its habitat changes and biodiversity

Tropical forest is relatively understudied and is even more poorly researched at higher elevations. A large percentage of highly threatened endemic species occur along elevational gradients of the tropical montane environments (Myers et al., 2000). Species occurring in tropical forests of higher elevation face bigger threats than their temperate counterpart due to narrower thermal tolerance and more restricted distribution (Janzen, 1967; Sheldon et al., 2018). Biodiversity of species is expected to decrease as climate change is predicted to cause warming and drying in the tropics, with high chance of significant community turnover (Cusack et al., 2016). Therefore, understanding species turnover across elevations helps to predict the outcome of climate change towards species biodiversity.

Studying biodiversity across elevational gradients also allows rapid assessment of organism diversity in various habitats (across climatic forest formations). Rapid assessment is particularly important for an understudied taxa with minimal species richness and distribution data especially in tropical region that are fast experiencing anthropogenic modifications (Bhardwaj et al., 2012; Veijalainen et al., 2014). The nature of elevation gradients, with compact environmental and geographical variation, provides a platform to increase our knowledge on patterns of biodiversity and its drivers more rapidly.

Studies on insect biodiversity turnover across elevation have mostly focused on indicator taxa with established systematics and ecological understandings, e.g. ants (Bishop et al., 2014; Samson et al., 1997), butterflies (Acharya & Vijayan, 2015; Molina-Martínez et al., 2016) and dung beetles (Menendez et al., 2014; Sheldon & Tewksbury, 2014). The turnover of species across elevations was also assessed based on association with changes in habitat as elevation increases, which underpin the ecology and life history of the insects. Ants species turnover along elevation gradients have been found to be strongly associated with tree basal area (Blatrix et al., 2016) and leaf litter depth (Bruhl et al., 1999); while for butterfly and dung beetle, with vegetation cover (Bhardwaj et al., 2012; Carneiro et al., 2014a; Chamberlain et al., 2015).

Fireflies are known to occur at low elevations of various habitat types (Ballantyne, 2001; Cleide Costa & Vanin, 2010; Koji et al., 2012; Nagelkerken et al., 2008). Limited information however, is available on its species along (M. V. Macedo et al., 2017; Silveira et al., 2016; B. W. Smith, 2009) and at high elevations (Fu & Ballantyne, 2008; Jeng et al., 2011; Wattanachaiyingcharoen et al., 2016). Change of temperature and availability of specific niche of the habitat as elevation increases may influence species turnover of fireflies across elevations. Fireflies have species specific light signal patterns to communicate (Lewis & Cratsley, 2008; Martin et al., 2015; Ohba, 2004) and temperature has been shown to modulate light flashing intervals, flash intensity and the offset of the firefly light display (Dreisig, 1975; Ueda et al., 1994). Their limited dispersal ability and availability of obligate prey and specific breeding locations (Ballantyne & Lambkin, 2013; Takeda et al., 2006; Wu et al., 2010; Yuma, 2007) may also influence their turnover along the elevational gradient.

Firefly presence along the elevation of Malaysian mountainous areas could be associated with the five main floristic zones along elevational gradients. Whitmore (1984) identified five floristic zones of tropical forest along elevational gradients based on his extensive work in tropical forest around South East Asia, specifically in the biogeographical region of Malesia. These five forest zones beginning from the lowest elevation are lowland dipterocarp, hill dipterocarp, upperhill dipterocarp, oak laurel and mountain ericaceous. Lowland dipterocarp forest occur within the elevations of 0-300 m a.s.l. with around half of the trees at the emergent layer comprise of dipterocarp trees of 30-50 m tall, and the young of the emergent trees occupy the main storey of the forest. Ground layer is abundant with herbaceous plant including fern, ginger and palm. In the lowland dipterocarp forest, lianas and large climbers are common.

At higher elevation of between 330 and 830 m a.s.l., a change in the emergent and main storey are observed and this zone is the hill dipterocarp forest. At this altitude, common lowland species are present at a lower number, instead it is being dominated at main and upper storey by *Shorea curtisii*, an important timber tree species belonging to the Red Meranti group. Hill dipterocarp forest is distinctively characterized by undulating and hilly terrain with moderate to steep slopes (Niiyama et al., 1999). The ground layer has less species and mainly being dominated by bertam palm, *Eugeinossa tristis*. The third forest type as the elevation increases is the upperhill dipterocarp forest, which could be present up to 1,200 m a.s.l. This forest is not distinctively different from hill and lowland dipterocarp in terms of the tree species, however the density, basal area and canopy layer is lower (Ghazoul, 2016). The emergent and main storey is also less distinct making the canopy more even.

As elevations increase upperhill forest transitions into oak-laurel forest (1,200-1,500 m a.s.l.) that is largely dominated by Fagaceae and Lauraceae. The forest is mainly of a two tree-layered forest as emergent tree is absent. Shrubs could consist of ferns and rattans while mosses and liverworts grow at the ground layer. Montane ericaceous (> 1,500 m a.s.l) comprise of one tree-layer structure of around 10 m in height. This forest is dominated by Ericaceae, Fagaceae and Laureaceae. The ground layer has thick humus layer and is heavily covered by mosses. In this forest orchids and rhododendron are common.

1.5. Estimating species diversity from incomplete samples

Species richness is a quantitative measurement of species number from a local area helping ecologists to identify fundamental properties of assemblages. Species richness estimates enable development of various models to predict species that coexist, at the focal area or at a larger spatial scale aiding conservation plans and their implementation (Adenle et al., 2015; Chazdon et al., 2009; Hooper et al., 2005; Porter-Bolland et al., 2012). Areas with high species richness are frequently selected as a high-priority conservation areas (Fleishman et al., 2005; Leishman & Lair, 2001), although high species richness areas does not necessarily support endemic, threatened or rare taxa (Kier et al., 2009; Orme et al., 2005; Reid, 1998).

Species richness, albeit the most used measurement of biological diversity, is a measurement with issues (Chao et al., 2014). It is sensitive to sampling size; therefore comparing observed species richness directly could be misrepresentative of the species estimates. Frequently this issue is overcome by rarefying or extrapolating the sampling size into a common size and the species richness is compared within this standardized range. This however does not equalise the sampling completeness and could give a misrepresentation of the communities sampled (Chao & Colwell, 2017; Chao & Jost, 2012).

Species richness also does not include information of relative species abundance, leaving the rare, less common species undetected and treats rare and common species as equals. This could lead to misinterpreting the ecosystem function and conservation of rare species. Over time ecologists suggested ways to combine species richness with proportions of each species in assemblages (Gotelli & Chao, 2013). However their statistical behaviour are largely left unstudied (Barrantes & Sandoval, 2009; Ghent, 1991).

Rarefaction and extrapolation by coverage-based standardisation instead of the traditional size-based method gives more meaningful and accurate information when identifying the degree of diversity differences between communities sampled (Chao & Jost, 2012). Colwell *et al*. (2012) overcome rarefaction and extrapolation problems associated with abundance and incidence data by successfully linking rarefaction curves with corresponding extrapolated curves into one smooth single curve. By doing so, issues of estimating species diversity based on the traditional rarefaction that discard a portion of a large sample in order to compare with smaller samples (Heck et al., 1975), were resolved. In the same period, Chao & Jost (2012) showed a method of extrapolation to a higher coverage rather than to larger sample size, providing more meaningful information of samples at equal quality and equal completeness.

Recently, Chao *et al.* (2014) revealed that Hill numbers (Hill, 1973) are a mathematically unified family of diversity indices that overcome the limitation of species richness as a measure of biodiversity. It unites several species diversity indices and combines species richness with relative abundance. Chao *et al*. (2014) elaborated further on the advantages of the Hill numbers approach over other diversity indices including resolving the inadequacies of species richness as a diversity measurement, while improving the characterisation of species diversity of an assemblage.

The most significant diversity measurement using the Hill number is it uses the effective number of species which helps researcher to interpret the data of species "directly" rather than generating indices value that are not able to be compared side by side. Within the Hill numbers, the transformed diversity indices of Shannon entropy and Simpson-Gini can be expressed in similar units as species richness. They simply differ among each other by an exponent q: the higher the order of q the more sensitive the measure to species relative abundance (Jost, 2006).

iNEXT (Hsieh et al., 2016) integrated the first three Hill numbers of species richness ($q = 0$), the exponential of Shannon entropy ($q = 1$) and the inverse Simpson concentration. For order $q = 0$, the effective number of species is counted as being equal, ignoring its relative abundances. The measure of $q = 1$ counts individuals equally meaning it counts species in proportion to their abundances or its effective number of common species of the assemblage. Finally, for order of $q = 2$, is interpreted as the effective number of the most dominant species in the assemblage (Chao *et al.* 2016). The greater the difference between these three numbers, the greater the dominance in the community (Jost, 2006).

This unified statistical framework integrates Hill numbers (Chao et al., 2014) with individual- and sample-based rarefaction/extrapolation (Colwell *et al.*, 2012) and standardisation based on sampling completeness developed by Chao & Jost (2012). This robust estimator of species diversity extends previous rarefaction and extrapolation models by measuring taxon diversity through incorporation of relative abundance. iNEXT estimates species richness at a certain level of sample completeness coverage, i.e. comparing estimated species richness of standardised samples with similar sample size or sample completeness. A great advantage of this is that estimation of species richness is still able to be compared between samples that have a common sample size or completeness, even without knowing the asymptotic value of the estimates (Chao et al., 2014).

CHAPTER 2

Assessing the accuracy and precision of iNEXT in estimating species diversity of cryptic taxa with low population densities - Fireflies of the Peninsular Malaysia as a case study

2.1. Abstract

Biodiversity measurement is important in basic ecology and nature conservation studies. One of the frequently used measurements, species richness, is highly dependent on sampling intensity. Most observed species richness usually underestimates actual species richness of a community, especially in areas of high heterogeneity and high diversity, and for a taxa with low abundance, cryptic behaviour/morphology or having low sampling detection. To address the discrepancies, several asymptotic or non-asymptotic extrapolation approaches have been developed. Another issue of estimating species richness is that it does not include the relative species abundance which could lead to misinterpreting the ecosystem functions and conservation priorities of rare species. To overcome this insensitivity to species abundances, many diversity indices have been developed. They are however understudied and seldom produce sensible and intuitive estimates. Hill numbers, a mathematically unified family of diversity indices were recently found able to overcome these limitations. iNEXT is a newly developed statistical framework, integrating Hill numbers with rarefaction/extrapolation and standardisation based on sampling completeness. To date, it was used to estimate species diversity for large samples of highly abundant and diverse taxonomic groups. This study assesses iNEXT performance in estimating species diversity of the solitary fireflies (Coleoptera: Lampyridae) of tropical forests, a model system representing taxonomic groups that are difficult to collect in large quantity due to low abundance, their cryptic nature, high habitat

heterogeneity and other factors hindering ecological fieldwork. Accuracy and precision of iNEXT estimation were assess based on species diversity of fireflies from different Malaysian forest types across an elevational gradient and a forest age gradient (recovery post logging). The accuracy of iNEXT in estimating firefly species richness was found to be high across multiple forest types and precision to vary according to forest types. However, because rarefaction and extrapolation of Hill numbers using iNEXT is reliable up to double the reference sample (number of fireflies collected within group), reliable estimate is still able to be conducted for comparing between firefly communities of different forests or to estimate the species diversity of each community.

2.2. Introduction

Biodiversity measurement is an important property for understanding biological communities (Chao & Chiu, 2016; Gotelli & Chao, 2013; Magurran, 2004). One of the frequently used measurements is species richness. It lies at the centre of many areas of ecological study, including understanding of and comparing diversity among community assemblages, determining changes in species compositions (Rosenzweig, 1995) and extinction rates (Scott et al., 1987) and developing ecological models of community structure (Gotelli & Colwell, 2011). It is also central to understanding human impacts on biodiversity, and guiding decisions regarding conservation investment and management practices (E. D. Brown & Williams, 2016; Weber et al., 2004).

However, species richness, as an index to measure biodiversity, is highly dependent on sampling intensity (Brose et al., 2003). Most biological surveys do not record all species present at the survey site (Gotelli & Colwell, 2011; Graça et al., 2017). As a result, observed species richness usually underestimates the true species richness of the community (Walther & Moore, 2005). The magnitude of discrepancy between observed and true species richness increases when sampling in areas with high habitat heterogeneity (Tews et al., 2004), high species diversity (Coddington et al., 2009) or high number of uncommon species (Reese et al., 2014). The uncertainty can also increase when sampling a taxa with cryptic behaviour/morphology or having low sampling detection (Gu & Swihart, 2004; MacKenzie et al., 2005).

To address the discrepancies between observed and true species richness, several asymptotic or non-asymptotic approaches have been developed (Chao & Chiu 2016). Both types of estimators have been devised for incomplete sampling where some species are left undetected. Both have also enabled comparison of estimated species richness from unequal sampling effort. The asymptotic approach estimates the asymptote of the species accumulation curve through i) fitting asymptotic equations to species accumulation curves; ii) fitting a lognormal abundance distribution and estimating the hidden or unsampled portion of the curve (known as parametric estimator); or iii) using nonparametric estimators which do not make any assumptions on the underlying distribution of the data (Colwell & Coddington, 1994).

In contrast, the non-asymptotic approaches estimate the species richness within the non-asymptotic portion of the species accumulation curve via rarefaction and extrapolation. This approach enables standardised comparison of species estimation between different assemblages. However, the classical rarefaction form of estimation involves discarding information from larger size sample in order to compare with smallest in a group of samples (Heck et al., 1975).

A breakthrough in rarefaction in estimating species came nearly 40 years later when Colwell et al. (2012) was able to link rarefaction curves with corresponding extrapolated curves into one smooth single curve. In the same period, Chao & Jost

(2012) developed a method of extrapolation to a higher coverage rather than to larger sample size which provides more meaningful information of samples at equal quality and equal completeness.

Another issue associated with estimating species richness is that it does not include information of relative species abundance. It treats the abundance of rare and the common species as equals (Lennon et al., 2004). This could lead to misinterpreting the ecosystem functions and conservation priorities of rare species (Fleishman et al., 2006). To overcome this insensitivity to species abundances, many diversity indices have been developed that combine species richness and their relative abundance (Gotelli & Chao, 2013). These indices however have poorly studied statistical properties that seldom produce estimates that allow sensible and intuitive comparisons (Barrantes & Sandoval, 2009; Ghent, 1991).

Recently, Chao et al. (2014) revealed that Hill numbers (Hill, 1973) are a mathematically unified family of diversity indices that overcome these limitations. Within the Hill numbers, the transformed diversity indices of Shannon entropy and Simpson-Gini can be expressed in similar units as species richness. They simply differ among each other by an exponent q and the higher the order of q the more sensitive the measure to species relative abundance (Jost, 2006). Species richness, represented by $q = 0$, is not sensitive to species relative abundance while the transformed Shannon entropy and Simpson-Gini indices represented by $q = 1$ and $q = 2$, respectively, are interpreted as the measure of “typical species” and the measure of “very abundant species” (Gotelli & Chao, 2013).

iNEXT (Hsieh et al., 2016) is a newly developed, unified statistical framework for species diversity estimation, integrated Hill numbers (Chao et al., 2014) with individual-and sample-based rarefaction/extrapolation developed by Colwell et al. (2012) and standardisation based on sampling completeness proposed by Chao & Jost (2012). This robust estimator of species diversity extends previous rarefaction and extrapolation models by measuring taxon diversity through incorporation of relative abundance.

To date, the iNEXT framework has most frequently been applied to estimate species diversity in surveys of very large numbers of individuals (thousands) from highly abundant and diverse taxonomic groups, such as tropical fish (Sharpe et al., 2017), dung beetles (Cristiane Costa et al., 2017), saproxylic beetles (Onodera et al., 2017) and microbial communities (Wurzbacher et al., 2017). While this is a positive development, there remains a need to assess the performance of this new statistical framework in estimating species diversity of other taxonomic groups that are difficult to collect in large quantity due to low population densities, the cryptic nature of individuals, high habitat heterogeneity and other factors that hinder ecological fieldwork such as terrain that is difficult to access or species that are active at night.

These features of species and field sites may limit our capacity to better understand diversity in taxa that are not abundant and diverse. However, efforts to understand their species structure and composition are vital because rare taxa are known to be more sensitive to negative influences, therefore more vulnerable compared to the highly abundant and diverse groups (Hooper et al., 2005; Hubbell, 2013; Prendergast et al., 1993; With & Crist, 1995). It is therefore critical to ensure this statistical estimator is able to perform equally well for both low and high abundance taxa.

Walther & Moore (2005) described several concepts associated with testing estimators of species richness. They specifically highlighted accuracy and precision. A good estimator of species richness should be able to accurately estimate the true value of species richness. Accuracy therefore is defined as the overall difference between estimated value and the true value. The more precise an estimator is, the less variation there is in the estimation. A good species richness estimator should also perform consistently for any types of community or habitat.

Here we provide an empirical assessment of how iNEXT performs for low density populations with cryptic individuals, sampled across different habitats. We focus on the solitary fireflies (Coleoptera: Lampyridae) as a model of rare and cryptic organisms in tropical forests. Our assessment is based on samples from forests of different logging histories and forests at different elevations, two major habitat characteristics in tropical rainforests. Our data suggest that iNEXT can be a robust estimator of species diversity of low abundant group of taxa, where it would otherwise be impossible without prior extensive sampling effort. The analyses provide insight into how habitat alters estimates and thus guidance for standardised protocols to maximise effectiveness for sampling to estimate species diversity of low abundance and potentially low diversity taxa.

2.3. Methods

We assess the accuracy and precision of iNEXT species diversity estimations using data from two firefly surveys conducted in tropical forest in Peninsular Malaysia. These two surveys sampled along i) elevational gradients (200 m to 1,900 m) from lowland dipterocarp to montane ericaceous forests , and ii) gradients in the age of secondary forest (from unlogged primary forest to 41 years since logging). These two datasets, with replicated sampling, capture much of the habitat variety of wet tropical forest types in this region of Malaysia.

2.3.1. Study areas

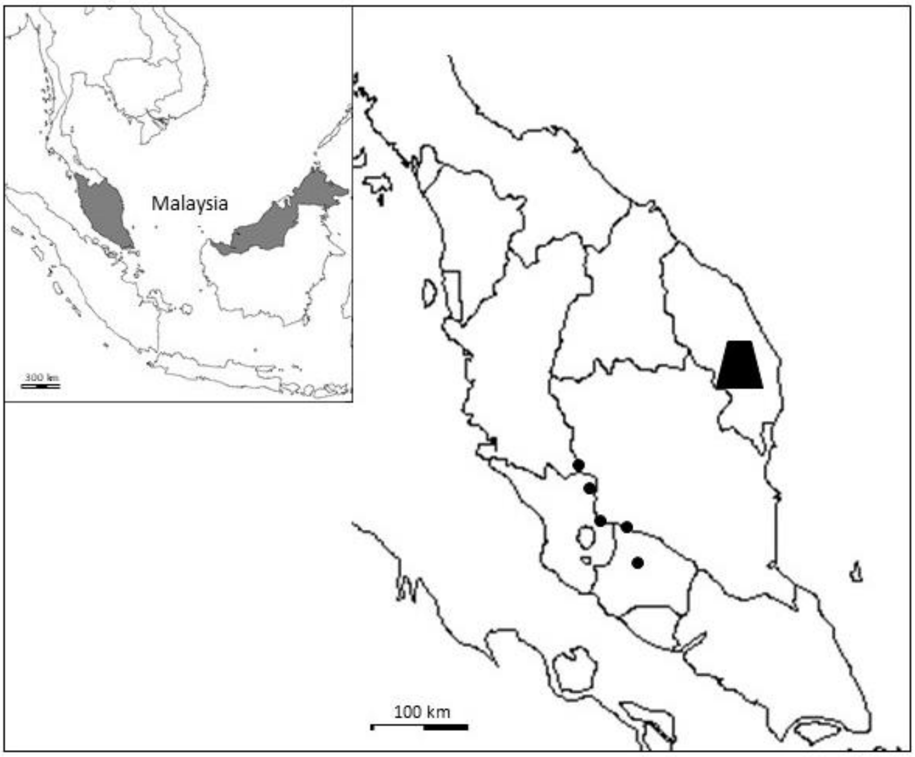

Figure 2.1: Locations of the five mountains sampled in 2015 are indicated by solid dots and the location of the logging area (DTC) sampled in 2016 is indicated by the trapezoid shape. Inset: Map of Malaysia in the Southeast Asian region.

The elevation gradient survey was conducted from May-July 2015, during the Southwest monsoon when the region experiences stable weather conditions (Jamaludin et al., 2010). We sampled five mountains along the main mountain range of Peninsular Malaysia, the Banjaran Titiwangsa, which extends 480 km from the Thailand and Malaysia border in the north towards the southern tip of the peninsula and separates the east and the west coasts. Mountain summits along this range have elevations between 396 m a.s.l. (above sea level) and 2,183 m a.s.l. Our five focal mountains have summits between 1,051 m a.s.l. and 1,933 m a.s.l. and cover a 135 km section of the range with minimum distances between individual surveyed mountains ranging from 12 km to 47 km.

The second survey was conducted at the Dungun Timber Complex (DTC), Terengganu, Malaysia in 2016 (Figure 2.1). This covers 108,974 ha between 200 m and 800 m a.s.l. Our sampling was confined to logged and natural, unlogged (primary) lowland dipterocarp forests (elevation: 0-300 m a.s.l.), with compartments having been logged between 1 and 41 years ago. From the 1960’s until 1982, logging here followed the Malayan Uniform System (MUS) which emphasizes sustained-yield timber production, but since 1982 logging has followed the Malaysian Selective Management System (SMS) which attempts to ensure the sustainability of multiple forest resources and acknowledges the importance of sustaining non-timber goods and ecosystem services. The first logging rotation under the Malaysian Selective Management System (SMS) occurred between 1982 and 2007, with the second rotation commencing in 2008 – but many compartments have only been logged once (Mohd Hakimi et al., 2014). In this study we sampled only in forest compartments that were logged once.

2.3.2. Field sampling

The elevational gradient study sampled a total of 110 transects (80 m in length to prevent overlap of transects between bands) between 200 m and 1,900 m a.s.l. These transects extended into all five types of climatic climax tropical forest, as described by Whitmore (1984): lowland dipterocarp forest (0-330 m a.s.l.), hill dipterocarp forest (330-830 m a.s.l.), upper dipterocarp forest (830-1,350 m a.s.l), oak laurel (1,200-1,500m a.s.l.) and montane ericaceous forest (1,500-2,100m a.s.l.). There were between 9 and 50 transects per elevation band/forest type (Appendix Table 2.1).

In the post-logging forest study, 164 transects (100 m in length) were sampled from seven large forest blocks (average size = 18,163.50 ha). Each forest block consisted of between 7 and 131 forest compartments, each logged in different years, with the earliest being logged in 1969. We categorised compartments into ages post-logging of 0-5, 6-15, 16-25 and more than 25 years after logging. 93.6% of transects sampled were within logged areas that underwent the logging regime of Malaysian Selective Management System. Only 11 transects were within forests that underwent the Malayan Uniform System representing forest logged more than 25 years ago.

For both surveys, fireflies were collected at night (~5 transects/night) while walking along a length of transect. Fireflies across elevation were generally sampled on transects consisting of nature trails of 1 m wide or less, at every 50 m altitude increase from the lowest possible band of 200 m a.s.l. to the highest possible at 1,900 m a.s.l. Each transect was 80 m in length to prevent overlap of transects between bands. The lowland dipterocarp forests of Dungun were sampled along randomly positioned 100 m transects with at least 100 m gap from each other. In both studies fireflies were collected from the 3 m belt on each side of the transect.

We used an active search method, i.e. sweep nets for adults and hand searching on the ground for larvae. Fireflies fall into two main groups – light producing adults that are active at night (mainly of the Luciolinae and Lampyrinae subfamilies) and those in which adults have reduced light organs and therefore are active during the day (Ototretinae subfamily). Both groups have light emitting larvae that are active at night and thus our sampling methods enabled both groups to be collected during a single sampling period, providing a rapid collection method for all firefly life stages. There are numerous other methods used for sampling fireflies including the use of light lure (Pacheco et al., 2016), pheromone traps (De Cock et al., 2014), intercept traps and Malaise traps (Hyvärinen et al., 2006; Macedo et al., 2016). However, based on pilot trials, these collection methods were ineffective or overly time consuming.

The sampling of fireflies began at nautical twilight and ended approximately three hours after, depending on the difficulty of movement on the terrain. We detected fireflies by their emission of light whilst in flight, on the ground or on plants. Two people (each with sweep nets) sampled each transect with headlamps switched off every 3 metres for at least one minute to detect fireflies (including larvae on the ground) – if no fireflies were detected after one minute headlamps were switched on and surveys progressed to the next stopping point. All specimens were immediately preserved in 70% ethanol.

2.3.3. Firefly identification

Adult fireflies in the Luciolinae subfamily were identified to species level using firefly taxonomic identification keys (Ballantyne et al., 2013; Ballantyne & Lambkin, 2013; Fu, Ballantyne et al., 2012b). Adult fireflies in the Lampyrinae subfamily and larvae of the Ototretinae subfamily were assigned to genera using Jeng et al. (1999, 2000, 2001), Kawashima et al. (2005) and Wang et al. (2007) taxonomic identification keys and descriptions before being assigned into morphospecies as species level guides are not available. The traits used to identify morphospecies are those typically used for species level identification of fireflies, i.e. the range of diameter of eye sockets, distance between the eyes, lateral length and colouration of the elytra or exoskeleton, shape and size of the light organ and the length of the antenna (Ballantyne et al., 2015; Fu, Ballantyne et al., 2012b).

2.3.4. Data analysis

2.3.4.1. Estimating species diversity using iNEXT

Firefly species diversity estimations in both focal studies were derived using the iNEXT programme, version 2.0.15 in R (Hsieh et al., 2018). We used all specimens that were identified to taxonomic species level or to morphospecies, with the exception of larvae of nocturnal fireflies – whilst these were identified to morphospecies we could not determine if these belonged to the same species for which we had obtained an adult specimen.

iNEXT integrates the sample-size-based (Colwell et al., 2012) and coverage-based (Chao & Jost, 2012) methods of rarefaction and extrapolation with Hill numbers to form a unified statistical framework in estimating species diversity. iNEXT can handle abundance and incidence data; we used abundance data and associated species diversity estimates. iNEXT will construct two types of rarefaction-extrapolation curves, i.e. sample-size- and coverage-based. Both sampling curves are linked together by a third curve known as a sample completeness curve. The sample completeness curve is useful to get information of sample completeness variation between treatments. For the purpose of our study, we analysed iNEXT performance based on the sample-size-based rarefaction and extrapolation curves. iNEXT also generates the confidence intervals for the interpolated and extrapolated estimation using a bootstrap approach specifically developed for Hill numbers (Chao et al., 2014).

2.3.4.2. Calculating the accuracy of iNEXT species diversity estimates

The developers have integrated three rarefaction/extrapolation curves to characterise the species diversity of an assemblage based on the three Hill numbers of q = 0, 1 and 2. In the output, the transformed Shannon entropy is referred as Shannon diversity (q = 1) and transformed Simpson-Gini index is referred as Simpson diversity (q = 2). To quantify the accuracy of iNEXT in estimating the species diversity measures, we used a cross-validation, 'leave one out' approach (Efron & Gong, 1983). For a group of transects in a given age after logged group or elevation forest types, we estimated the difference between the sampled species richness value of left out transects and the iNEXT estimates of all the others at the number of observations represented by each left out transect. Our surveys are based on multiple transects within various forest types, allowing us to ‘leave one transect’ out multiple times and use iNEXT to estimate species richness, Shannon diversity and Simpson diversity each time using the remaining transects that ranged from 3 to 21 transects per forest type.

We used these data to calculate the mean absolute error (MAE) as a measurement of accuracy. This calculation was reviewed by Walther & Moore(2005) to be less sensitive to outliers than the alternative mean squared error. Smaller values of MAE indicate better accuracy. We implemented the cross-validation method within each of five major forest types along the elevational gradient, and within each of five forest groups in the logging study. We used these data to explore graphically whether elevation or forest age since logging influenced iNEXT accuracy.

2.3.4.3. Calculating the precision of iNEXT species diversity estimates

To measure precision of iNEXT, we referred to the standard error (SE) of the asymptotic estimates of the Hill numbers calculated by iNEXT for each elevational forest types and each forest age group. The standard error by definition measures how precisely the sample mean estimates the population mean. The objective was to explore patterns of precision in iNEXT estimates of species diversity and whether precision varied across the different habitat types.

2.3.4.4. Scaling the accuracy and precision measures

The accuracy and precision measures were scaled in order to make meaningful comparison of the performance of estimations between different forest types and between different studies. The scaling was calculated based on Walther & Moore (2005). The MAE values were scaled by dividing the values with their respective estimated species richness, Shannon diversity and Simpson diversity, returning the scaled mean absolute error (SMAE). The precision measures were scaled by dividing the SE values with their respective diversity estimates and expressed in percentages. We also conducted Pearson correlations to assess if precision and accuracy of iNEXT species diversity estimates were associated with the number of fireflies collected within each forest type. This analysis combined data from the elevational and forest age gradients in order to maximise the sample size.

2.4. Results

2.4.1. Outcome of sampling

A total of 100 specimens were collected during the elevational study and 262 specimens were collected during the logging study. A total of 23 species were identified from both studies which included 5 new species to science (Appendix Table 2.2). We found 13 species from five genera in Luciolinae, with five species are new to science; 7 species from two genera in Lampyrinae and 3 species from two genera in Ototretinae subfamilies.

Fireflies were collected on less than half of transects (elevational study: 40.0%, 44 transects; logging study: 45.7%, 75 transects). Where fireflies were collected species richness per transect was low, with most transects having only one species and maximum observed species richness being four (Figure 2.2). Table 2.1 summarises the outcome from the firefly sampling in both study areas.

Table 2.1a: Descriptive habitat, transect and species data from the Elevational study on five mountains. Estimated species richness was calculated using iNEXT and grouping data from across the mountains into climatic forest formations.

Habitat type	Total transect number	Transects with collections (%)	Number of individuals collected (mean ± SE)	Observed species	Unique species to elevational study	Estimated species richness, mean ± SE
Lowland dipterocarp	9	5 (55.56%)	25 (2.78 ± 1.01)	10	1	22.00 ± 16.47
Hill dipterocarp	50	21 (30.30%)	37 (0.74 ± 0.19)	10	1	11.46 ± 2.24
Upper dipterocarp	32	11 (44.74%)	18 (0.56 ± 0.21)	6	1	6.99 ± 2.11
Oak laurel	11	3 (47.06%)	5 (0.46 ± 0.25)	5	0	13.00 ± 8.07
Montane ericaceous	8	4 (54.29%)	15 (1.88 ± 0.85)	6	4	7.87 ± 3.51

Table 2.1b: Descriptive habitat, transect and species data from the Logging study. Estimated species richness was calculated using iNEXT and grouping data from across the compartments into year bands.

Habitat type	Total transect number	Transects with collections (%)	Number of individuals collected (mean ± SE)	Observed species	Unique species to logging study	Estimated species richness, mean ± SE
00-05 years	32	13 (40.63%)	48 (1.50 ± 0.50)	7	1	14.83 ± 11.43
06-15 years	33	10 (30.30%)	35 (1.06 ± 0.61)	7	0	16.71 ± 9.82
16-25 years	33	17 (44.74%)	51 (1.34 ± 0.36)	11	1	14.92 ± 5.20
More than 25 years	33	16 (47.06%)	66 (1.94 ± 0.73)	8	0	12.43 ± 7.09
Unlogged	33	19 (54.29%)	62 (1.77 ± 0.57)	7	0	7.49 ± 1.31

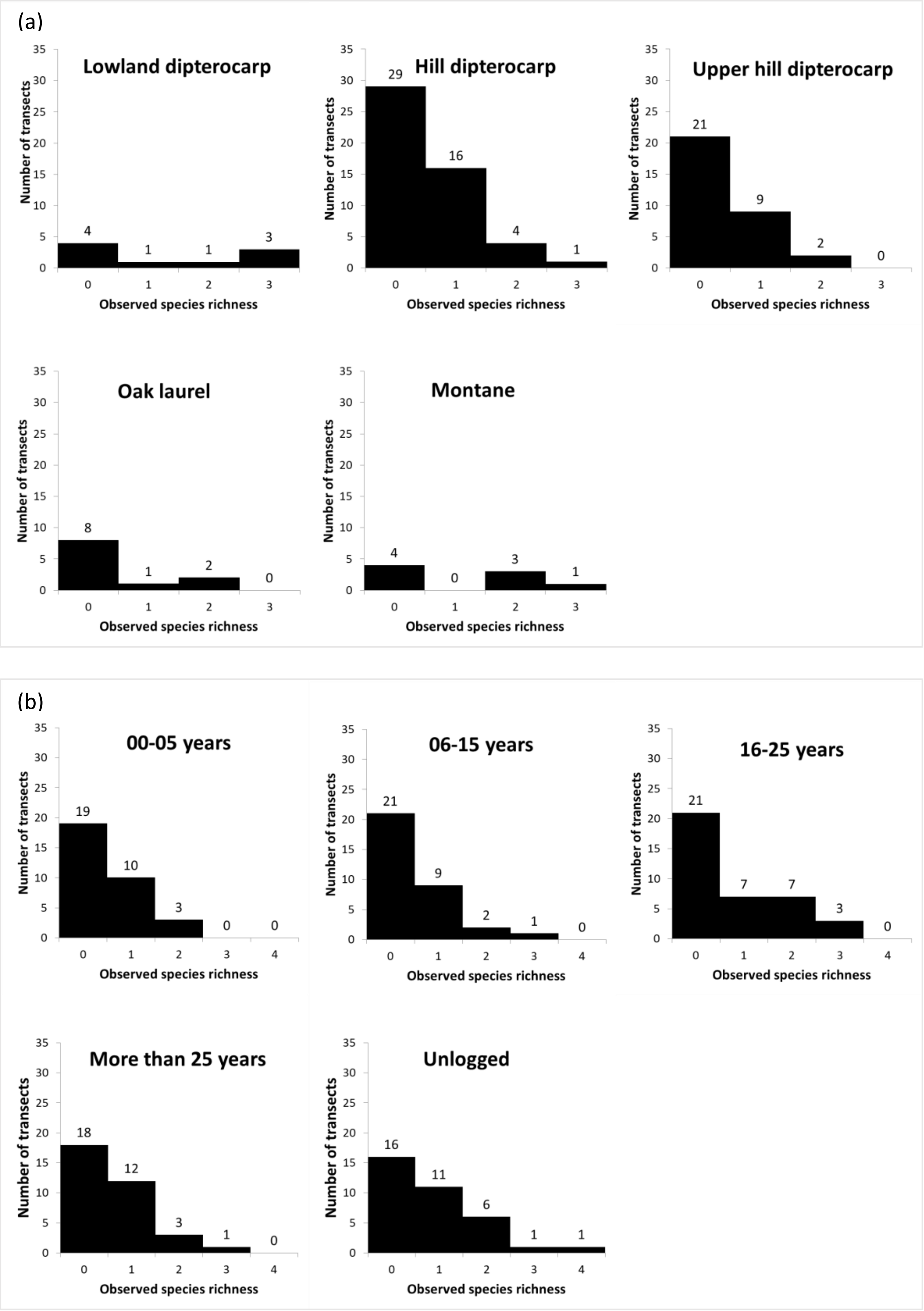

Figure 2.2: Histograms of the number of transects according to number of firefly species collected during (a) the elevational study, grouped by forest type and (b) the logging study, grouped by time since logging durations.

2.4.2. Accuracy

2.4.2.1. Accuracy according to forest types

The MAE values for the elevational gradient study ranges between 0.000-1.356 (species richness), 0.530-2.588 (Shannon diversity) and 0.673-2.736 (Simpson diversity); while in the logging study the ranges are 0.462-1.064 (species richness), 0.865-2.188 (Shannon diversity) and 1.109-1.829 (Simpson diversity). In assessing the accuracy of iNEXT estimations between forest types, the scaled mean of absolute error (SMAE) values were referred upon.

The SMAE for species richness in all habitat types are the lowest compared to corresponding Shannon and Simpson diversity (Figure 2.3). There was no consistent increase in accuracy of all three diversity measurements with elevational increase or with increase of age post-logging. iNEXT was able to estimate the diversity of forests in the elevational gradient study more accurately than for the forests in the logging study based on the lower overall SMAE values.

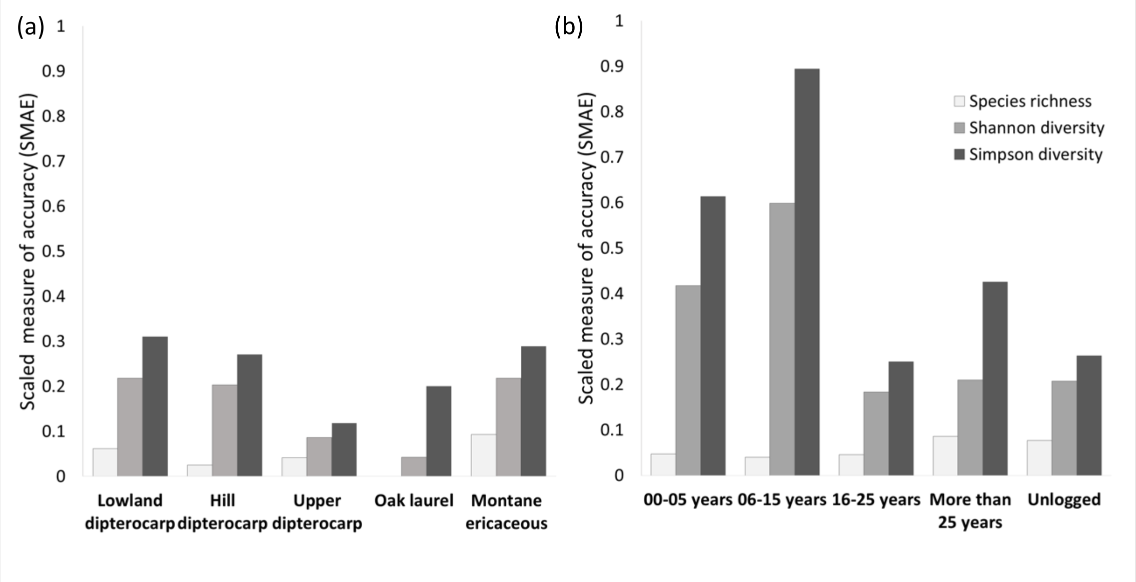

Figure 2.3: The scaled mean of absolute error (SMAE), representing the accuracy of iNEXT in estimating firefly diversity according to Hill numbers in (a) forest types along the elevational gradients and (b) forest ages in the logging compartments.

2.4.2.2. Accuracy according to diversity measures

Species richness estimations had the highest accuracy (reflected by the lowest average MAE) while the accuracy of Simpson diversity estimations were the lowest. The accuracy of species richness estimation were significantly higher than the accuracy of Shannon diversity (Paired samples T-test: *t*= 3.358, *df*= 18, *p*= 0.004) and Simpson diversity (Paired samples T-test: *t*= 4.010, *df*= 18, *p*= 0.001) estimations.

2.4.3. Precision

2.4.3.1. Precision according to forest types

The SE values for the elevational gradient study ranges between 2.108- 16.468 (species richness), 1.025-5.422 (Shannon diversity) and 1.113-2.758 (Simpson diversity); while in the logging study the ranges are 0.507-11.426 (species richness), 0.569-1.375 (Shannon diversity) and 0.303-0.993 (Simpson diversity). In assessing the precision of iNEXT estimations between forest types, the scaled precision measures were referred upon (Figure 2.4). There was no consistent increase in precision for the three diversity measurements with elevational increase or with increase of age post-logging. The precision of estimates were highest for Shannon diversity in the elevational study, and Simpson diversity was most precisely estimated for forests in the logging study.

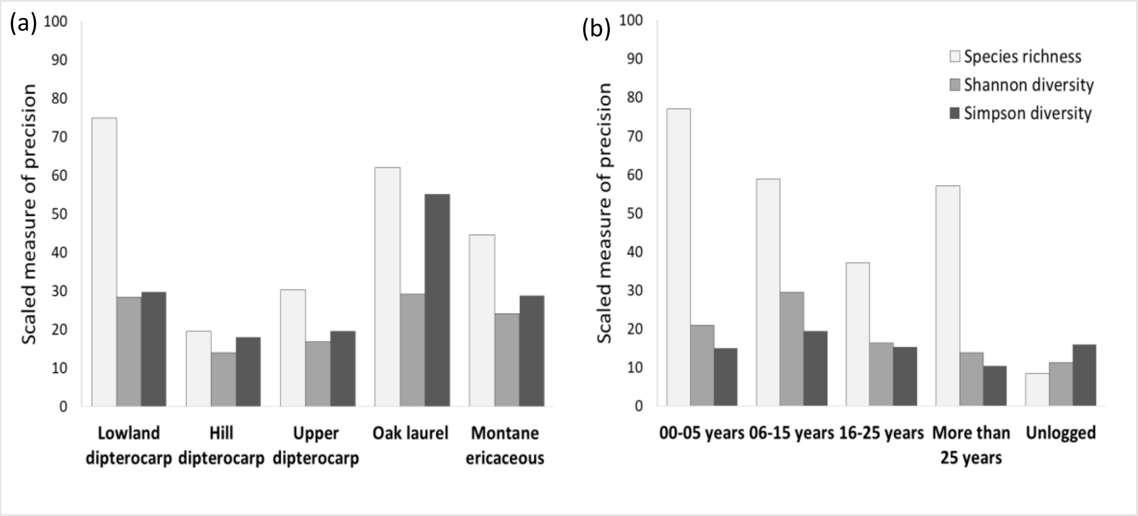

Figure 2.4: The scaled measure of the precision of iNEXT, based on the standard error of the estimate of species richness of species diversity of fireflies in (a) forest types along elevational gradient and (b) forest ages among logging compartments.

2.4.3.2. Precision according to diversity measures

Simpson diversity estimation had the highest precision (reflected by the lowest average of SE) while species richness were found to be the least precise estimates. The precision of estimations for Simpson and Shannon diversities was not significantly different (Paired samples T-test: *t*= 0.881, *df*= 18, *p*= 0.390), however the precision of species richness estimations were significantly lower than the precision of Simpson diversity (Paired samples T-test: *t*= 3.415, *df*= 18, *p*= 0.007) and Shannon diversity (Paired samples T-test: *t*= 3.012, *df*= 18, *p*= 0.012) estimations.

2.4.4. Influence of number of collections to the accuracy and precision of iNEXT

When combining data from the elevational gradient and the logging studies, the number of individuals collected was not associated with the accuracy of species richness (*p* = 0.203, *n* = 10), Shannon diversity (*p* = 0.408, *n* = 10) and Simpson diversity (*p* = 0.447, *n* = 10) estimations (Figure 2.5a-c); or with the precision of species richness (*p* = 0.534, *n* = 10) (Fig. 2.5d). This means the number of individuals does not influence the accuracy and precision of iNEXT in estimating the species richness; and it also does not influence the accuracy of iNEXT in estimating Shannon diversity and Simpson diversity.

However, there was a significant relationship between the number of individuals collected with the precision of Shannon (*p* = 0.030, *n* = 10) and Simpson diversity (*p* = 0.005, *n* = 10) estimations (Figure 2.5e-f). As the number of individuals increased, the precision of Shannon and Simpson diversity estimations also increased.

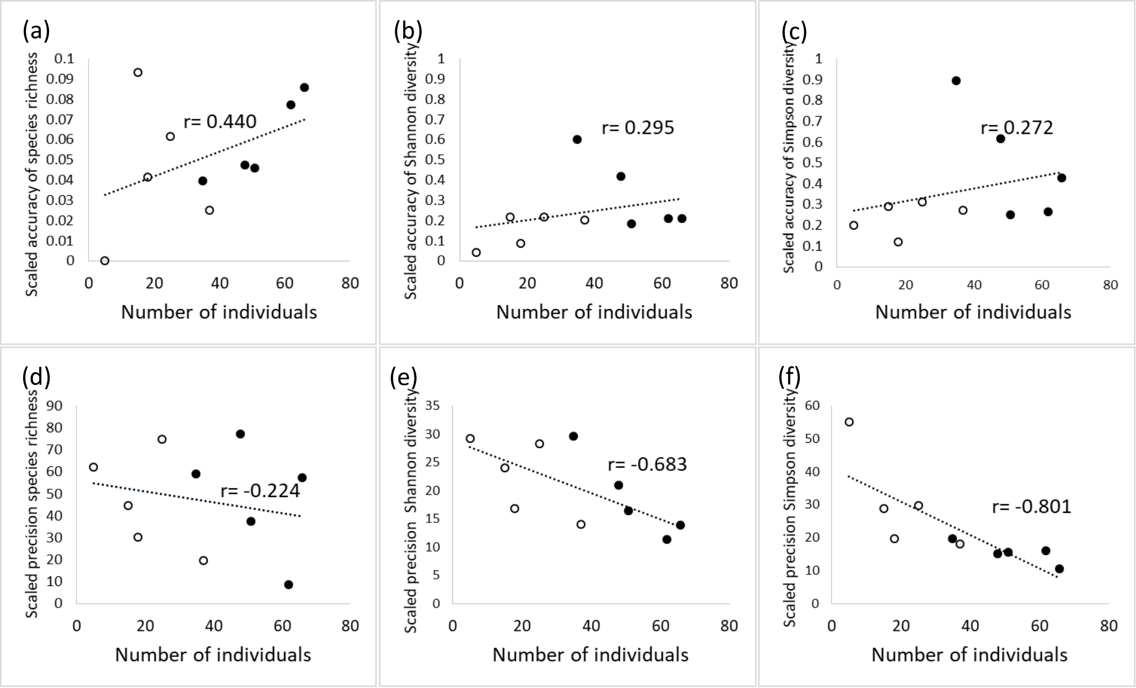

Figure 2.5: The Pearson correlations between the number of fireflies collected and (a-c) accuracy and (d-f) precision of iNEXT diversity estimates. Open circles are data points from the elevational gradient study. Closed circles are data from the logging study. Note: Lower value of scaled precision indicate higher precision of the estimates.

2.5. Discussion

In this study we aimed to evaluate the accuracy and precision of the iNEXT tool for estimating species richness and two widely used diversity measures applied to fireflies, a taxa of low diversity and low abundance. The data used to assess iNEXT were of fireflies collected from different Malaysian forest types across elevational and age gradientsafter logging). In combination, our sampling represents the major tropical forest types in Peninsular Malaysia. The accuracy of iNEXT in estimating firefly species richness, estimated via a ‘leave one out approach’, was found to be high across multiple forest types. The accuracy of iNEXT was highest in estimating the species richness, while the precision of iNEXT in estimating species richness was the lowest.

2.5.1. Characteristics of the firefly community

This study has provided further evidence supporting the cryptic and low abundant nature of the fireflies. They were found to occur in very low number at a given situation and were distributed sparsely across habitats. This was apparent from our study whereby only 362 fireflies were collected after c. 170 hours of sample effort from 274, 80 and 100 m- transects. The number of collections were comparatively low to similar spatial and time scale of sample effort for other invertebrates e.g. 2,695 dung beetles (Scarabaeidae) collected from 44, 150 m-transects (Cristiane Costa et al., 2017) or 1,617 skipper butterflies (Hesperiidae) collected within 231 hours of sample effort (Carneiro et al., 2014b). The high number of transects with no firefly collections (almost 60% of transects) further support the sparsity and uneven distribution of fireflies within their habitats. The pressure of habitat alteration, both natural and to accommodate human needs (Hamer *et al.*, 2015; Pavlacky *et al.*, 2015; Wells *et al.*, 2007; Goosem, 2007) means that a robust sampling technique and estimation of species richness is critical if we wish to understand the distribution and diversity of such cryptic and low abundance group of organisms.

Prior to this work, only 19 firefly species were confirmed to occur in Peninsular Malaysia consisting 7 aggregative and 12 solitary species (Jusoh, 2015). Our sampling regime involving fifty five, 3-person sampling nights found 17 new species for Peninsular Malaysia, of which 5 were new to science. This was surprising given that over 100 published studies have reported information on the identity of fireflies recorded in Malaysia, including from four studies conducted in the 21st century (Jusoh, 2015). The average undetected species in each forest types was 5.07 (range of 0.49 to 12.00) species per habitat.

Whilst many of these undetected species will occur in multiple habitat types it is clear that when summed across all surveyed sites there were a significant number of additional species undetected. Given that approximately 52% of the firefly species detected were new to Malaysia and nearly 22% were new to science it is highly plausible that new additions to Malaysia and possibly global firefly fauna await discovery in the areas studied. It thus seems that further intensive sampling in Malaysia and elsewhere in Southeast Asia will result in new information on the distributions of firefly species and discovery of additional novel species.

2.5.2. Accuracy and precision of iNEXT in estimating firefly species diversity measures

Across all habitat types mean absolute error (MAE) in firefly species richness estimates ranged from 0.288 to 1.356, suggesting that iNEXT was accurately predicting species richness to within one species of actual species richness. This measure of accuracy was also consistently high across all habitat types. The accuracy of estimations for Shannon and Simpson diversities were not as accurate, ranging between 0.530-2.588 for Shannon diversity and 0.673-2.736 for Simpson diversity. Across all habitat types, iNEXT was able to perform the best in estimating species richness. In combination these results suggest that iNEXT has the capacity to estimate firefly species richness with a high degree of accuracy regardless of the cryptic nature and low density of this taxonomic group.

Despite the high accuracy, the precision of iNEXT species richness estimates was sometimes low (large standard error), e.g. 22 estimated species with a standard error of 16.47 or 14.83 with a standard error of 11.43, but in other cases the precision was much higher, e.g. 7.19 and 11.46 species estimated with standard errors of 1.31 and 2.24, respectively. With less certainty reflected by large standard error or variation in estimation, it would not be possible to conclude any significant differences in species richness of fireflies between the forest types (Schenker & Gentleman, 2001). The limited precision of richness estimates in some habitats made it more difficult to generate firm conclusions regarding species richness patterns along environmental gradients.

iNEXT was able to estimate the Shannon diversity and Simpson diversity at a much higher precision in each habitat type compared to its estimation of species richness (scaled precision, Fig 2.4). The degree of precision in iNEXT estimations depends on the range of extrapolations and on the order of q. Extrapolation of species richness estimates ($q = 0$) is reliable up to double the number of collections while for $q \geq 1$, “the extrapolation can be safely extended to the asymptote” (Chao et al., 2014). In our assessment of precision, we compared the SE values at asymptotic portion of the extrapolation, therefore we are seeing a significantly lower precision of species richness estimates but a much precise Shannon diversity ($q = 1$) and Simpson diversity ($q = 2$) estimates.

Both accuracy and precision of iNEXT estimates of species richness were not influenced by number of individuals collected. The non-significant correlation between numbers of individuals collected with the accuracy and precision of iNEXT species richness estimation indicates that it was a reliable estimator of species richness even for low abundant taxa. However precision of Shannon and Simpson diversity estimates were found to have a strong relationship with the number of individuals collected (Figure 2.5e-f).

We compared iNEXT precision in estimating species richness, Shannon and Simpson diversities from three datasets used by the developer to assess iNEXT performance (Chao & Chiu, 2016; Chao et al., 2016; Hsieh et al., 2016). To do this, we plot the graphs according to number of individuals collected in relations to their respective scaled measures of precision for species richness, Shannon diversity or Simpson diversity (Figure 2.6). The comparison further supported our current finding that precision of Shannon and Simpson diversities estimates were strongly influenced by number of individuals collected (Shannon diversity: *p* = 0.018, *n* = 9; Simpson diversity: *p* = 0.006, *n* = 9).

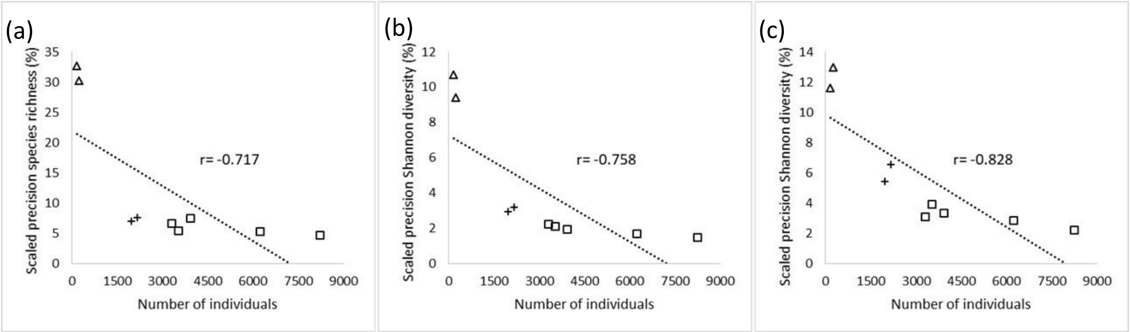

Figure 2.6: The Pearson correlations of the number of individuals collected made from three different studies using iNEXT tool with their precision values (low scaled precision values = high precision of estimate). a) original data from Ellison et al. (2010) of spiders in two canopy manipulation treatments (open triangles); b) original data from Magnago et al. (2014) of trees in two habitats (crosses); c) original data from Ibanez et al. (2016) of trees in five elevation groups (open squares).

Across both studies, iNEXT had high accuracy in estimating species richness of fireflies for primary forests (all the elevational gradient forest types and the unlogged forest). Primary forests may harbour the most diverse species of organisms in the tropical forests (Barlow et al., 2007; Gibson et al., 2011). They are also the undisturbed habitat, thus providing a reference point for assessing the effects of disturbance. Accurate estimate of species richness in primary forests will provide a reference of species richness when identifying any changes in other habitats (D. P. Edwards et al., 2011; Whitworth, Downie et al., 2016). Information derived from estimation of species richness in this study could be used as a reference for future firefly diversity study.

2.6. Summary

This study has increased our understanding of how iNEXT was able to estimate species diversity for low diversity and low abundance taxa. iNEXT was able to estimate species richness of fireflies in different habitat types at high accuracy, whereby its accuracy was tested in 10 different forest types. The precision of iNEXT however was inconsistent with large standard error differences and varying precision of estimates in different forest types. The low precision of estimation could be caused by the variation of the species within sites representing the forest types. In contrary, accuracy was highest in estimating fireflies of primary forests represented by the five forest types in the elevational study and the unlogged forest in the logging study which could be due to less variation of sites within the forest types. It is advantageous to reduce the standard error to achieve a greater precision of estimation. However for a taxa that is low in abundance, this would be impractical as this will require a much rigorous effort in the field with a much lower resulting samples collected, compared to other abundant occurring groups.

CHAPTER 3

Firefly species richness and diversity in tropical lowland dipterocarp forests recovering from timber extraction

3.1. Abstract

Tropical forests support substantial, and for their land area, disproportionate amounts of biodiversity. They are, however amongst the most threatened biomes on the planet. These threats primarily arise from expansion of agriculture, urbanisation and resource extraction, particularly timber. Such forest conversion places increasing pressure on remaining forested land to supply a growing demand for timber promoting further degradation. Consequently, an increasing proportion of forest concessions are being subject to multiple logging cycles. We focussed on assessing the biodiversity of a low abundance and difficulty to detect insect- the solitary fireflies (Coleoptera: Lampyridae) in once-logged, twice-logged and unlogged forest compartments in Malaysia. Fireflies have specialised biology and ecology requirements and have limited dispersal capacities which may limit their ability to colonise regenerating habitats. There were significant relationships and large effect sizes of canopy closure and distance to primary unlogged forest on firefly species richness. The firefly community composition within forests were significantly influenced by leaf litter depth and number of water bodies. Time since logging had a small to medium effect size on species diversity, however forest experiencing twice logged showed a significantly lower recovery of firefly species.

3.2. Introduction

Tropical forests support substantial, and for their land area, disproportionate amounts of biodiversity (Wilson, 1988). They are, however amongst the most threatened biomes on the planet (Cusack et al., 2016; Hoekstra et al., 2005). These threats primarily arise from expansion of agriculture, urbanisation and resource extraction, particularly for timber (Geist & Lambin, 2002). Rates of resultant forest degradation in the tropics have been estimated at ~500 million ha in 2005 (Ghazoul & Chazdon, 2017) of which, 326.4 million ha have been allocated as natural timber extraction areas (Blaser et al., 2005, 2011). Although deforestation has decreased since 2010 (Keenan et al., 2015), degradation of tropical forest is expected to continue to increase (Sloan & Sayer, 2015). The highest rates of recent forest loss typically occur in regions such as Southeast Asia, with high human population densities and rapid expansion of oil-palm, *Elaeis guineensis* and other crops including rubber, *Hevea brasiliensis* (Abdullah & Hezri, 2008; Phalan et al., 2013; Wilcove et al., 2013). Such forest conversion places increasing pressure on remaining forested land to supply a growing demand for timber promoting further degradation (Sist et al., 2014).

Consequently, an increasing proportion of forest concessions are being subject to multiple logging cycles (Blaser et al., 2011). These additional logging cycles remove additional timber but equally important, exert additional pressures including soil compaction and erosion (Cambi et al., 2015; Schmidt et al., 2015), leaching of soil nutrients (Chazdon, 2003; Imai et al., 2012) , higher temperatures and reduced humidity that can reduce microclimate suitability for some taxa (Scheffers et al., 2017) and increase fire risks (Cochrane, 2003; Lindenmayer et al., 2009). Tree felling also typically causes collateral damage to neighbouring trees, with resultant increased canopy openness promoting invasive vines that further adversely influence the growth and survival of the remaining trees and regenerating saplings (Fauset et al., 2017; Schnitzer et al., 2000). These indirect effects of logging frequently have substantial adverse impacts on biodiversity that can be more influential than the direct effects of tree removal (Delgado et al., 2007; F. A. Edwards et al., 2017; Vinson et al., 2015). Consequently, much attention has been given to developing reduced-impact logging techniques (RIL) that attempt to minimise these adverse indirect effects, although the precise nature of these alternative methods and their success can vary markedly and is not fully understood (Bicknell et al., 2015; W. A. Chaves et al., 2017).

Despite these adverse effects of logging, there is increasing evidence that logged tropical forests are able to support substantial amounts of biodiversity (Dunn 2004; Clarke et al. 2005; Edwards, Tobias, et al. 2014). Protection of such areas can contribute to conservation goals by preventing conversion to alternative land uses, such as plantations, that support less biodiversity than secondary forest (Edwards et al. 2011; Ewers et al. 2015). As secondary forests recover and mature, species richness and diversity can approximate those of primary forests, albeit with some shifts in species composition (Edwards et al., 2012, 2014; Hamer et al., 2003). The estimated time required for recovery to the diversity levels of primary forest is insufficiently documented, but estimated to be between 30-50 years for insects such as ground beetle, ants and butterflies (Hopp et al., 2010; Rocha-Ortega & Favila, 2013; Whitworth, Villacampa et al., 2016) and a complete recolonization of affected areas predicted to take around 50 to several hundred years (Bihn et al., 2008).

These studies are typically biased towards taxonomic groups that are easier to study because of their abundance and diversity - especially birds (Hamer et al., 2015; Rajpar & Zakaria, 2014b; Yap et al., 2007), butterflies (Hamer et al., 2003; Lawton et al., 1998; Nyafwono et al., 2014) and dung beetles (Bourg et al., 2016; França et al., 2017; T Hosaka et al., 2014). Whilst such taxa can act as biodiversity indicators for other taxa

(Azevedo-Ramos et al., 2005; Lawton et al., 1998) the validity of the indicator approach has been challenged (Hubbell, 2013). It is notable, however, that much of the range in these estimated biodiversity recovery times overlaps with the typical 20-40 year cutting cycles used in many countries (Blaser et al., 2011). This suggests that secondary cutting cycles may reduce the conservation value of the forest as it is rarely of sufficient age for biodiversity to recover and approximate that of primary forest. Secondary cut cycles shorter than 40 years also typically yield low amounts of timber (Huth & Ditzer, 2001; Ruslandi et al., 2017). This reduces the economic value of multiple cut forest concessions that may reduce financial arguments for not converting multiple logged forests to alternative land uses.

Our overall objective was to provide an analysis of biodiversity in logged forest focusing on a challenging taxonomic group: the solitary fireflies (Coleoptera: Lampyridae). Fireflies represent a challenging species to work with because though they are biologically diverse, they typically occur at low density. Despite their possible sensitivity to habitat and climate change and their potential to be an indicator species because their presence is easily noted, inland tropical forest fireflies have not been extensively studied and specifically in the context of logging related forest change. They are obligate predators of snails and slugs during their larval stage (Fu & Benno Meyer-Rochow, 2013; Viviani et al., 2012), with larval habitats of either aquatic, semi-aquatic or terrestrial (Ballantyne et al., 2016; Fu, Ballantyne et al., 2012b; Fu & Meyer-Rochow, 2012). The habitat of adults and larvae are not confined to the same microhabitats. Flying adult species are fully terrestrial, requiring herbaceous plants as their resting and mating places. Adults with flightless females are confined to the forest floors and also fully terrestrial (Fu, South et al., 2012; Jeng et al., 2011, 2001; Santos et al., 2016).

Ecological theory suggests that such specialization will increase solitary fireflies' sensitivity to environmental disturbance (Firebaugh & Haynes, 2016; Kazama et al., 2007). Furthermore, solitary fireflies also appear to have low dispersal capacities (Fu, South et al., 2012; Kakehashi et al., 2014) which may limit their ability to colonise regenerating habitats increasing the time required for their diversity to recover following disturbance events such as logging.

Our study site in Malaysia contains primary forest compartments, several once-cut forest compartments of various years since logging and several compartments cut twice in the past 41 years. In addition to these data on time since logging, we collected data on several habitat characteristics of the compartments. This allowed us to address two major questions. We started by analysing the relationship between time since logging, habitat characteristics and firefly biodiversity. We then explored if the form of this relationship was influenced by number of logging cycles. Answering these questions focused on both the effects of logging and on increasing our understanding of which habitat features were closely associated with diversity, which might be managed to reduced impact logging and maximise their value for firefly biodiversity.

3.3. Methods

3.3.1. Study area

Solitary fireflies were sampled at the Dungun Timber Complex (DTC) logging concession located on the east coast of Peninsular Malaysia (lat 4°40'45.32"N, long 103° 4'14.76"E). We sampled lowland dipterocarp forest within an elevational range of 0 - 111.95 m a.s.l. The site (108,974 ha) comprised unlogged and logged forest compartments. At DTC, logging from the 1960s to 1982 followed the Malayan Uniform System (MUS) which emphasized sustained-yield timber production (Suhaimi & Borhan, 2010). Since then logging has followed the Malaysian Selective Management System (SMS) which attempts to ensure the sustainability of multiple forest resources and acknowledges the importance of sustaining non-timber goods and ecosystem services. The first logging rotation under SMS occurred between 1982 and 2007, with the second rotation commencing in 2008 (Mohd Hakimi et al. 2014).

3.3.2. Field Sampling

Sampling was conducted in May to September 2016 along four to seventeen, 100 m -transects in each of 26 compartments (area: 61.0 – 445.3 ha, average: 285.2 ha; total transects: 229). All compartments in this analysis were either not logged in the past (categorised as primary unlogged), or have been logged once or twice (Appendix Table 3.1 and Appendix Figure 3.1). Compartments that were logged once had recovery age post-logging of 2 to 41 years (actual values since logging: 2, 2, 5, 5, 6, 10, 11, 20, 23, 24, 30, 31, 32, 32, and 41). Compartments that were logged twice had recovery age post-logging of 1 to 15 years (actual values since second logging rotation: 1, 2, 3, 3, 10, 10, 10, and 15) and experienced the first rotation of logging between 31 to 46 years ago (actual values since first logging rotation: 31, 32, 33, 33, 36, 36, 36, and 46). The age gap between the first and second logging rotations in these eight compartments were between 26 and 31 years. The three compartments that were unlogged were assigned values of 200.

All transects were located at least 100 m from the edge of a forest compartment and 100 m from logging roads in order to avoid edge effects (Benedick et al., 2006; Dambros et al., 2013). For each compartment, an entry point to the forest compartment was identified and from 100 m inwards as the starting point of the first transect. The starting position of subsequent transects in the forest depended largely on accessibility but were always 100 m from compartment boundaries, roads and other transects.

3.3.3. Firefly sampling and identification

Fireflies were collected at night along a three-metre strip either side of each 100 m transect; typically five transects were sampled each night. Sampling began at nautical twilight (approximately 20:00) and ended between three and four hours after, depending on logistical difficulties.

We used an active search method, i.e. sweep nets for adults and hand searching on the ground for larvae. Fireflies fall into two main groups – light producing adults that are active at night (mainly of the Luciolinae and Lampyrinae subfamilies) and those in which adults have reduced light organs and therefore are active during the day (Ototretinae subfamily). Both groups have light emitting larvae that are active at night and thus our sampling methods enabled both groups to be collected during a single sampling period. There are numerous other methods used for sampling fireflies including the use of light lure (Pacheco et al., 2016), pheromone traps (De Cock et al., 2014), intercept traps and Malaise traps (Hyvärinen et al., 2006; M. V. Macedo et al., 2016). However, based on pilot trials, these collection methods were ineffective or overly time consuming. The fireflies were detected by their emission of light whilst in flight, on the ground or on plants.

Two people (each with sweep nets) sampled each transect with headlamps switched off every 3 metres for at least one minute to detect fireflies (including larvae on the ground) – if no fireflies were detected after one minute headlamps were switched on and surveys progressed to the next stopping point. All specimens were immediately preserved in 70% ethanol.

Adult fireflies in the Luciolinae subfamily were identified to species level using firefly taxonomic identification keys (Ballantyne et al., 2013; Ballantyne & Lambkin, 2013; Fu, Ballantyne et al., 2012b). Adult fireflies in the Lampyrinae subfamily and larvae of the Ototretinae subfamily were assigned to genera using Jeng et al. (1999, 2000, 2001); Kawashima et al. (2005); Wang et al. (2007) taxonomic keys and descriptions before being grouped into morphospecies as species level guides are not available. The traits used to identify morphospecies were those typically used for species level identification of fireflies, i.e. the range of diameter of eye sockets, distance between the eyes, lateral length and colouration of the elytra or exoskeleton, shape and size of the light organ and the length of the antenna (Ballantyne et al., 2015; Fu, Ballantyne et al., 2012b).

3.3.4. Habitat characteristics recording

In addition to the time since logging, five key habitat characteristics that could influence firefly abundance and diversity were collected. These consisted of: i) canopy closure - anticipated to be lower in more recently logged forests, thus increasing temperatures and reducing humidity in forested areas (Gardner et al., 2018; Lebrija-Trejos et al., 2011), eventually reducing their suitability for fireflies (Kaufmann, 1965; Koji et al., 2012); ii) leaf litter depth - deeper leaf litter may accumulate as degraded forest recovers, providing more resources for snails which are obligate prey for the predatory larvae of many firefly taxa (Rios & Quinta, 2010; Yuyong Wang et al., 2007); iii) height of understorey plants - anticipated to increase and then decline as the forest regenerates (F. R. C. Costa & Magnusson, 2003); in many firefly taxa adults exploit this shrub layer for shelter and mating (Dreisig, 1975; Lall, 1994; Santos et al., 2016); iv) presence of water bodies - larvae of some firefly species are aquatic (Fu, Wang et al., 2005; Ho et al., 2010; Viviani et al., 2010), thus waterbody presence could influence the abundance and diversity of adult fireflies in our samples; and v) proximity to primary forest - being near to primary forest is anticipated to influence species recovery of post-logged forests (D. P. Edwards, Gilroy et al., 2014).

Canopy closure was recorded using a spherical, convex densiometer and counting the number of grid cells, maximum of 24, that had a clear view of the sky. Eight readings were taken (at the four cardinal points), converted to a percentage closure using equations from Lemmon (1956). Uncompressed leaf litter thickness was measured (to the nearest cm) at the corners of a 1m quadrat located in the three metre strip parallel to the transect (8 readings per transect). The height of the understorey plants was measured using a 150 cm long ruler with fifteen alternating 10 cm white and red bands. A person stood three metres away from the pole and counted the visible sections of the pole. The value was then deducted from the total 15, to give the approximate height of the understorey plants. Readings were taken at two points with the pole remaining in one point, while the observer moved parallel to the transect line (4 readings per transect). The height of understorey plant was taken in the 3-m strip of the transect line. These three habitat characteristics readings were recorded from 20 m and 60 m points along each transect.

The number of water bodies present up to 10 m away from the transect were recorded. All collection of habitat characteristics data were averaged by the number of transects sampled to represent the mean for each forest compartments. Forest compartment’s distance from the nearest primary unlogged forests were measured from the DTC forest compartment map provided by the Remote Sensing & GIS Unit of Forest Research Institute Malaysia (FRIM). The minimum distance measurement was taken from the centroid points of compartment sampled to the border of the nearest primary unlogged forest.

3.3.5. Data analysis

We investigated the effect of time-since-logging and the five habitat characteristics on the firefly species diversity and on species composition at community level. All analyses were carried out in R version 3.5. Our approach involved three steps. Step one was to estimate species diversity in each compartment among multiple transects. Step two was to analyse these estimates of diversity as a function of time since logging and habitat characteristics. Step three was to compare estimates of diversity between once and twice logged compartments of similar ages.

3.3.5.1. Species diversity

We estimated species richness, Shannon diversity and Simpson diversity at the forest compartment level using the iNEXT programme, version 2.0.15 in R (Hsieh et al., 2016, 2018). iNEXT has emerged as the most effective tool for estimating species diversity for the three most widely used measures, i.e. species richness (Hill number order q = 0), the transformed Shannon entropy (Shannon diversity, q = 1) and transformed Simpson-Gini index (Simpson diversity, q = 2). It is an integrated sampling, rarefaction, and extrapolation methodology to reliably estimate species diversity of a set of communities based on samples of equal completeness (as measured by sample coverage) instead of equal size.

We used iNEXT to construct a sample-size-based rarefaction and extrapolation curve for each forest compartments. We further formalised each estimate at 90% completeness. The estimation values at this level of completeness were used when performing analysis to identify effect size of habitat characteristics and when performing analysis of their influence on firefly community structure. Asymptotic estimation of species richness, Shannon diversity and Simpson diversity of fireflies were also retrieved from iNEXT to report on the estimated total species richness of fireflies for each compartment, including the diversity.

3.3.5.2. Effect size of forest age and habitat characteristics to species diversity

We estimated the effects of time since logging (once logged forests) and habitat characteristics on species richness and species diversity of fireflies using multiple regression. The effects of time since logging and mean habitat characteristic values on species richness, Shannon diversity and Simpson diversity were examined. The effects of time since logging and the variation in habitat characteristics within compartments on species richness and species diversity were also examined.

For each model, we made inference in two ways. First, we used Type II Sums of Squares to estimate the significance of the terms in the models with the Anova() function in the car package, version 3.0-0 in R (Fox, Weisberg et al., 2018). This is followed with an assessment of effect sizes using partial eta squared (Partial η^2) values using the heplots package, version 1.3-5 for R (Fox, Friendly et al., 2018).

For each of these models, we first tested whether second order polynomials (e.g. non-linear relationships between diversity values and habitat) were justified. We also ensured that residuals were normally distributed and that the constant mean-variance relationship was met in the residuals. The age of unlogged forest was assigned as 100 or 200 years old to test if the output of analysis could be influenced by the age assigned to unlogged forest categories.

3.3.5.3. Influence of habitat characteristics on species composition

We analysed whether community composition varied as function of time since logging and the five habitat characteristics using the mvabund package, version 3.13.1 in R (Yi Wang et al., 2018). The mvabund approach fitted a generalised linear model (GLM) to each species abundances with a common set of predictor variables and specifies the appropriate mean-variance relationship for abundance data (mean increases with variance in count data). The approach used resampling to test for significant community level change as a function of predictors and was preferred over methods that use distance-based metrics. We first fitted a model of abundance (count) data for all species as a function of forest age and habitat characteristics using the negative binomial distribution which produced highly satisfactory diagnostics (e.g. compared to a poisson distribution assumption).

3.3.5.4. Influence of once vs. twice logging on species diversity

The effect of once vs. twice logging on firefly species diversity were analysed using an analysis of covariance on a subset of the compartment data for which we had details on once and twice logged firefly species richness and that were of similar time since logging. We thus restricted analyses to time since logging of less than twenty years. We had data on eight compartments in the once and eight in the twice logged groups (Appendix Table 3.2).

The ANCOVA model was firstly fitted to test the hypothesis that the effect of time since logging on firefly diversity (species richness, Shannon diversity or Simpson diversity) varied by once vs. twice logged. Then, each habitat characteristicwas added individually to assess whether it explained any additional variation. The sample sizes precluded adding five variables to the baseline model. As above, Type II Sums of Squares was used to estimate the significance of the terms in the models with the Anova() function in the car package, version 3.0-0 in R (Fox, Weisberg et al., 2018).

The species richness of fireflies in the once and twice logged forests were estimated using iNEXT. The sample based estimates were extrapolated by iNEXT to double the reference sample (number of fireflies collected by group) to compare the quantitative differences in species richness between the two groups. Inference of species richness for both groups were made within the range of the doubling of the reference sample. Chao et al. (2014) gave a guideline for choosing a base sample size and base coverage when comparing between multiple assemblages or groups. A reliable estimate of species richness and comparison between groups can be conducted for any similar sample size less than the base sample size; and for any equally complete sample coverage that is less than the base coverage.

3.4. Results

3.4.1. Outcome of sampling

We sampled on average from 9 transects among 26 compartments (Appendix Table 3.1). A total of 16 species were recorded (Appendix Table 3.3), of which six were of fireflies with flightless females while one of the complete wing species was a diurnal firefly. This study also discovered four firefly species new to science (Appendix Table 2.2). The highest number of fireflies collected was made for *Pygoluciola dunguna* (n = 93), followed by *Curtos costipennis* (n = 72) and *Abscondita pallescens* (n = 64) (Figure 3.1a). The rest of the firefly species collections were between 1 and 26 individuals. *Abscondita pallescens* were found in 17 of the 26 compartments sampled (65.4% of total compartments sampled), followed by *Curtos costipennis* in 42.3% of the sampled compartments, and *Pygoluciola dunguna* in 38.5% of the total compartments sampled (Figure 3.1b). The number of species collected according to compartment ranged between 0-6 species (mean: 2.9), with 3-5 species (mean: 4.0) collected in each unlogged compartment, 0-6 species (mean: 2.8) collected in each once-logged compartment and 1-5 species (mean: 2.5) in each twice-logged compartment.

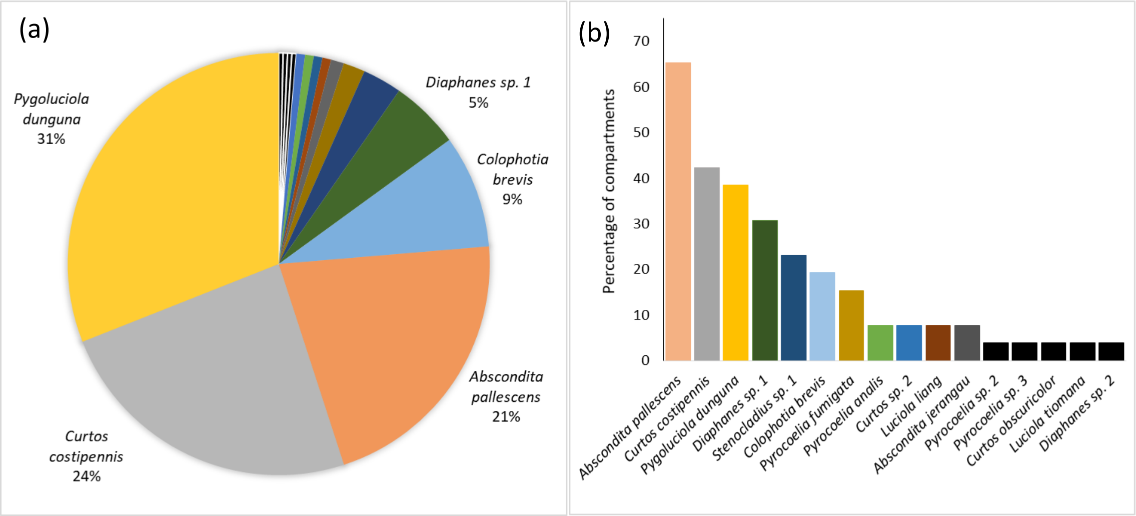

Figure 3.1: Relative abundance of firefly species collected as part of the logging study. (a) Percentage of firefly species collected as fraction of the total. Names of species representing <5% are not displayed. (b) Percentage of compartments in which different species were found indicating the most widely and narrowly distributed species.

Collections of adults were mainly made while they were in flight; while some were collected while they were mating, or while displaying their lights on leaves of understory plants. Collections of larvae were made at the shallow stream edges (possibly semi-aquatic/riparian larva); on forest floors among leaf litter, mossy grounds and small rocks (terrestrial larva); and on stems and leaves of forest understories (terrestrial larva).

3.4.2. Species diversity of fireflies

Species richness, Shannon diversity and Simpson diversity of fireflies estimated at 90% completeness and at asymptotic level for each compartment are reported in Appendix Table 3.4. Each compartment was estimated to support up to 13.8 species (mean: 3.95); with the common species averaging at 2.38 species (Shannon diversity) and dominant species of 1.92 species (Simpson diversity). The means of species richness and species diversity estimations (at 90% completeness) for unlogged forests were the highest compared to the other two forest groups (Table 3.1). iNEXT estimated species richness for each forest compartment ranging between 1-13.78 species, 0-5.84 species for Shannon diversity, and 1-6.88 for Simpson diversity (Appendix Table 3.4).

Table 3.1: Species richness, Shannon diversity and Simpson diversity estimates of fireflies according to groups of unlogged, logged once and logged twice compartments. Values are the range of estimates. Values in brackets are the means. All estimates are made by iNEXT at 90% completeness.

Forest groups	Species richness	Shannon diversity	Simpson diversity
Unlogged	2.64-4.78 (3.75)	2.34-4.43 (3.38)	2.20-4.16 (3.10)
Once logged	0.00-8.52 (2.76)	0.00-4.04 (1.59)	0.00-3.51 (1.48)
Twice logged	1.00-6.91 (2.79)	1.00-3.92 (1.94)	0.00-2.89 (1.46)

3.4.3. Effects of time since logging and habitat characteristics on species diversity

There were significant correlations between several habitat characteristics measured, i.e. leaf litter and canopy closure (p = 0.035, r = 0.500); canopy closure and understory height (p = 0.015, r = 0.562); and time since logging and canopy closure (p = 0.038, r = 0.539). In all analyses, polynomial relationships were not supported (all p > 0.5). All analyses were insensitive to the choice of 100 or 200 years old assigned to the unlogged compartments, with both inputs giving the similar analysis outcome (Appendix Table 3.5-b). Here the outcome of analysis with the unlogged compartments assigned as age 200 years old are reported. Species richness did not vary as a function of the variability of habitat characteristics within compartments (all p > 0.4). We focus on reporting how species richness and diversity varied as a function of mean values of habitat characteristics.

The relationships between time since logging and all the habitat characteristics measured, and species richness estimated from iNEXT are depicted in Figure 3.2. The relationship of species richness and canopy closure; and distance to primary forest were apparent from the graphs. Further analysis revealed these relationships were significant: firefly species richness was found to increase with increasing canopy cover (t = 2.443, p = 0.033) and decline with distance to primary forest (t = -3.02, p = 0.012) (Appendix Table 3.6). These two characteristics, however, have statistically non-significant relationships with Shannon or Simpson diversities (Appendix Table 3.5-a).

Time since logging was not found to be having a significant relationship with firefly species richness and diversity (F = 1.78, p = 0.21). Understory plant height, leaf litter depth and number of water bodies have non-significant relationships with all three diversity measures (p values: 0.09-0.10).

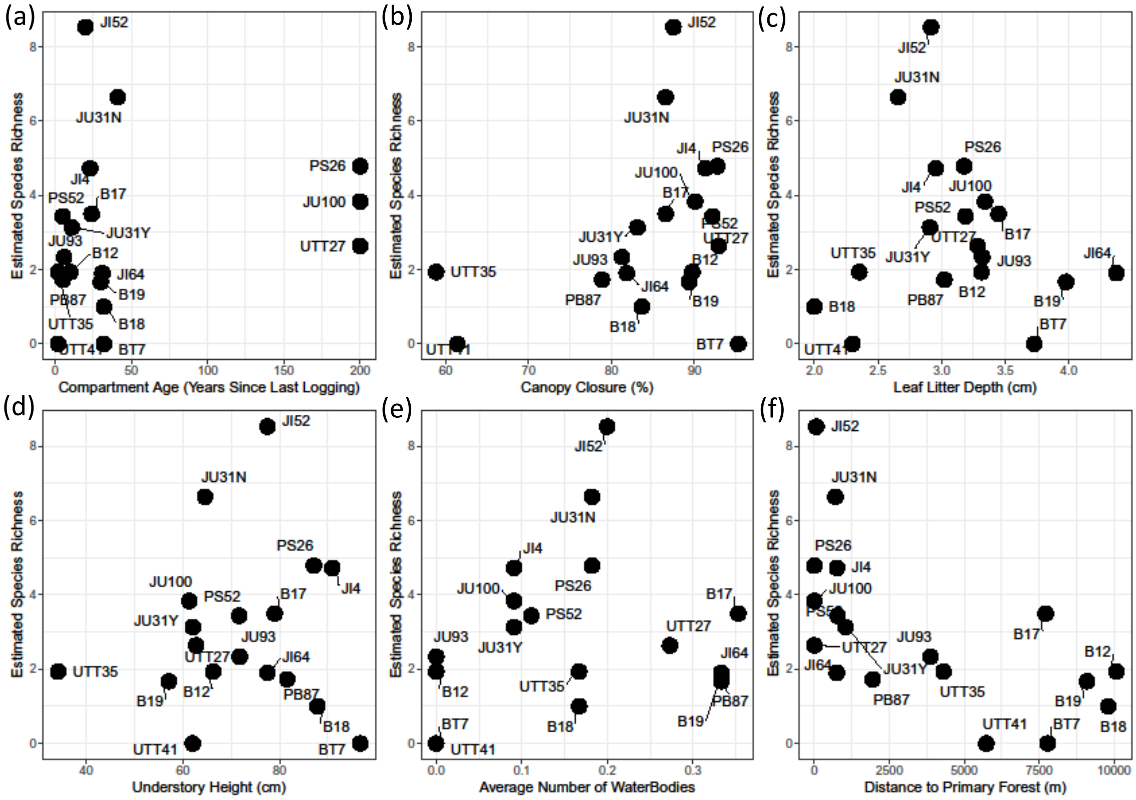

Figure 3.2: The relationships between species richness and six habitat characteristics measured in the study. Species richness estimates were provided by iNEXT at a coverage of 90%. Label on each datapoint corresponds to unique identifiers of the compartments.

The effect sizes were also estimated to complement the assessment of p-values. All six habitat variables showed a larger effect size on species richness than on Shannon or Simpson diversities of fireflies (Figure 3.3). Interestingly, the effect size of time since logging on the three diversity measures was not large with the size ranging from small to medium (Species richness: partial η^2= 0.14; Shannon diversity: partial η^2= 0.41; Simpson diversity: partial η^2= 0.11).

Instead, the effect size of distance to nearest primary forest on all diversity measures was largest, especially on species richness (Species richness: partial η^2= 0.45; Shannon diversity: partial η^2= 0.27; Simpson diversity: partial η^2= 0.15). This was followed by the effect of canopy closure on species richness and Shannon diversity (Species richness: partial η^2= 0.35; Shannon diversity: partial η^2= 0.13). The second largest effect on Simpson diversity was forest age (partial η^2 = 0.11), although the size was moderate. Number of water bodies, depth of leaf litter and canopy closure had negligible effects on Simpson diversity (partial η^2: 0.000001-0.0159), while negligible to small effects of understory height, number of water bodies and age after logging on Shannon diversity (partial η^2: 0.005-0.0454).

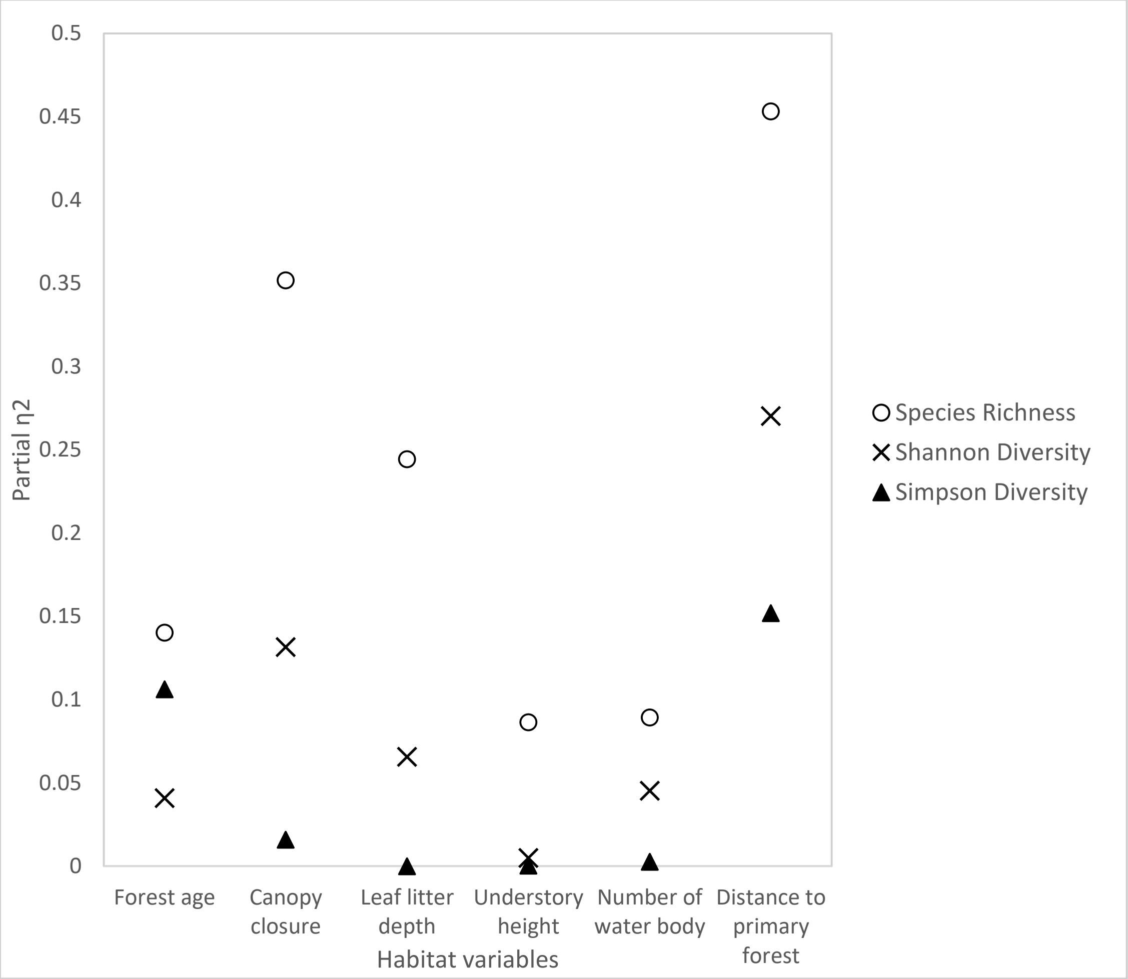

Figure 3.3: Effect sizes of the six habitat characteristics on species richness, Shannon diversity and Simpson diversity of fireflies. Effect sizes were estimated from the linear model predicting species richness and diversity as a function of habitat. Values > 0.3 are deemed large effects.

3.4.4. Influence of habitat characteristics on community composition

Community composition of the fireflies as a whole (multivariate test) varied significantly with the number of water bodies (p = 0.021) and leaf litter depth (p=0.038) (Table 3.2). Figure 3.4 shows that abundances of Sp. 9 (*Curtos costipennis*), 13 (*Pygoluciola dunguna*), 20 (*Diaphanes* sp. 1) and 22 (*Colophotia brevis*) appeared particularly variable along these two habitat gradients. The abundance of *Curtos costipennis* showed a decrease as leaf litter depth increase, while *Pygoluciola dunguna* abundance increases when leaf litter depth were approximately between 3 and 4 cm deep, and *Colophotia brevis* also showed an increase in abundance but when the leaf litter was deeper than 4 cm. The abundance of species *Pygoluciola dunguna* was found to increase as number of water body increased, while *Curtos costipennis* abundance also saw a change as number of water bodies increased.

Table 3.2: The habitat characteristic effects on firefly species composition was estimated with a multivariate model of abundance using the mvabund package in R. Significant variables ($p < 0.05$) are in bold.

Term	Res.Df	Df.diff	Dev	Pr(>Dev)
Forest compartment age	13	1	10.32	0.783
Canopy closure	10	1	13.68	0.254
Leaf litter depth	11	1	30.05	**0.038**
Understory height	12	1	22.54	0.106
Number of water bodies	9	1	37.67	**0.021**
Distance to primary forest	8	1	8.74	0.533

The univariate tests offer further insight into the effects of habitat on specific species. *Curtos costipennis* abundance varies significantly with water bodies (p = 0.02) and distance to primary forest (p = 0.002). *Pygoluciola dunguna* abundance varied significantly with time since logging (p = 0.006) and height of the understory (p = 0.04). *Diaphanes* sp. 1 abundance varied with height of understorey (0.043), number of water bodies (p = 0.03) and distance to primary forest (p = 0.012). *Colophotia brevis* abundance varied with leaf litter depth (p = 0.028).

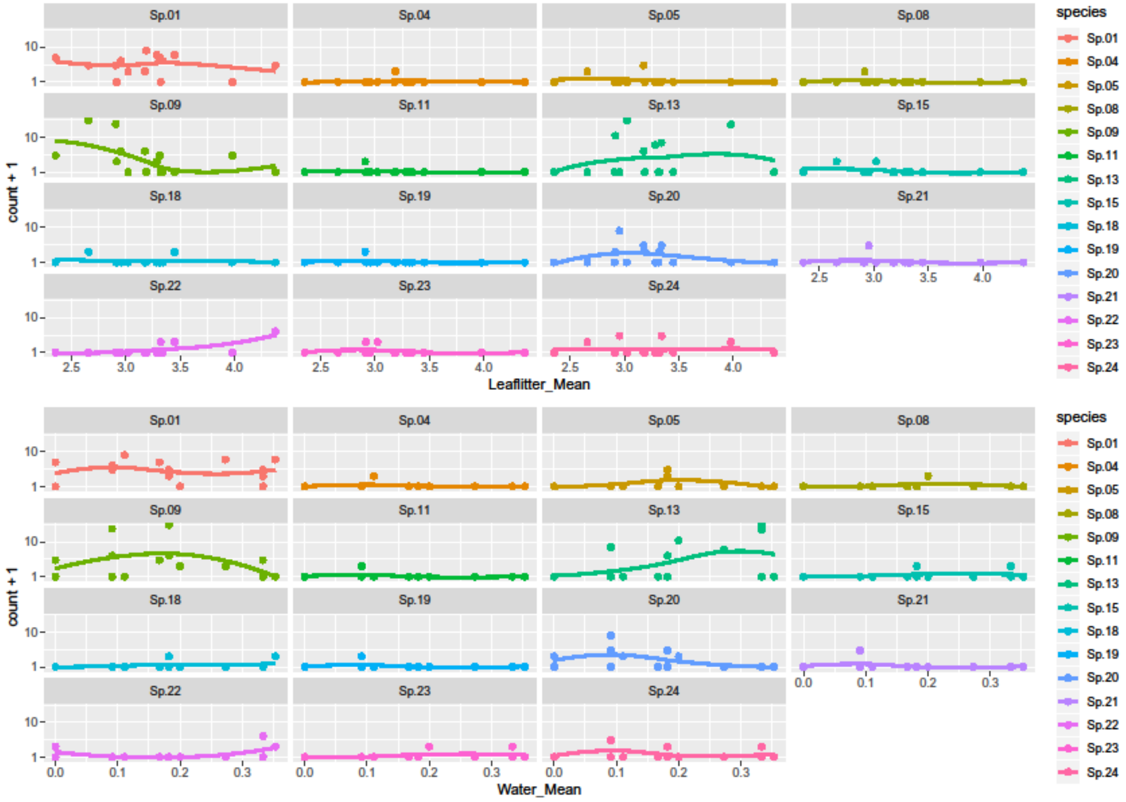

Figure 3.4: Influence of leaf litter depth and number of water bodies (significant terms, Table 3.2) on individual species of fireflies. Changes in species abundance along the gradients of these two habitat characteristics are more noticeable for Sp. 09, Sp. 13, Sp. 20 and Sp. 22. The multivariate models of abundance fit using the mvabund package for R deals simultaneously with all of these data.

3.4.5. Does the effect of time since logging on diversity vary by once vs. twice logged?

A total of 70 transects from 8 compartments were sampled representing once-logged forests of ages 2-20 years after logged, while 65 transects were sampled from 8 compartments representing twice-logged forests at ages 1-15 years after experiencing the latest logging cycle. Both groups were found to have similar percentage of transects with 0 collection of fireflies: 60% of the once-logged group, and 64.62% of the twice-logged group (Appendix Table 3.2). However, the total species of fireflies collected in once-logged forests and twice-logged forests were 12 and nine species, respectively. Seven of the species occur in both groups of forest.

The effect of time since logging on firefly species richness varied by logging rotation (F = 16.81, df = 1, p = 0.0015). Species richness of firefly increased with time since logging when the forests were logged once, but decreased with time since logging when the forests were logged twice (Figure 3.5). None of the habitat characteristics explained any additional variation in this analysis (all p > 0.1).

Rarefaction and extrapolation using iNEXT enabled comparison of species richness in once and twice logged forests within the base sample size of up to 156 individuals and a base coverage of up to 93.9% (Appendix Table 3.7). For the purpose of reporting the comparison between the two groups, an estimation of species richness was made at 93% coverage as it fulfiled the criteria of reliable estimations proposed by the iNEXT programme developers. Species richness of fireflies in once-logged forests was estimated at 12.78 species and in twice-logged forests to be 7.16 species.

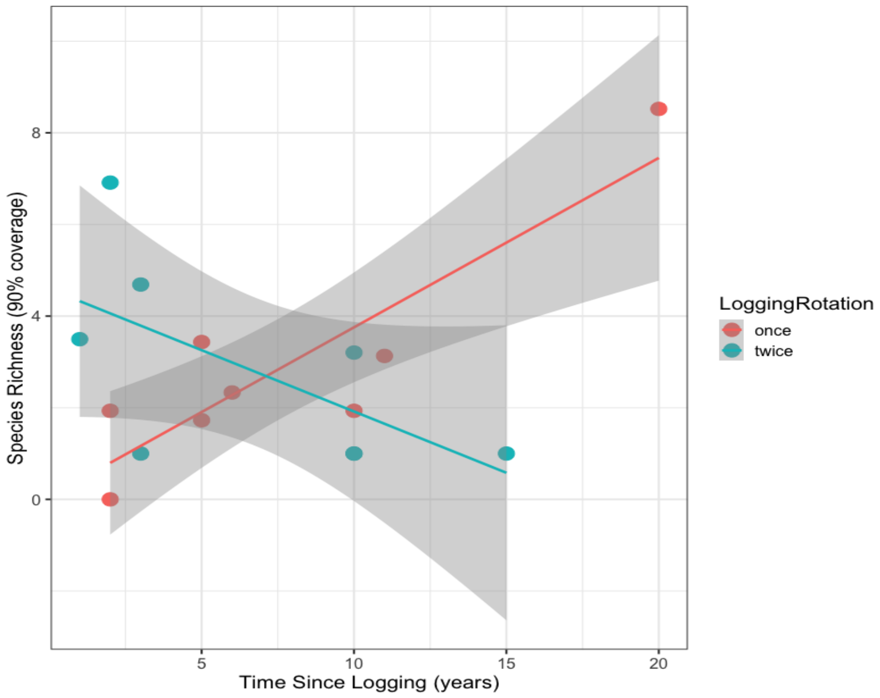

Figure 3.5: The effect of time since logging on species richness (estimated at 90% sample completeness) varied by the logging rotation (once vs. twice logged). Data are from all compartments in the <20 year old category.

3.5. Discussion

3.5.1. Species diversity of fireflies

This study was the first known attempt to systematically and extensively sample fireflies in the tropical lowland dipterocarp forests to increase our understanding of the species richness and its diversity. It was also a first look into identifying firefly species diversity within forests experiencing transitional period of succession and recovery from logging. Information on firefly species composition and distribution in lowland dipterocarp forest has benefited here from 415 man-hours of field sampling, covering 229 transects within 15 compartments of once logged forest, eight compartments of twice logged forest and three compartments of unlogged forest.

From the 16 species collected in total, three species were found to be the common species of fireflies in these forests based on their significantly higher numbers collected and frequency of occurrence by compartment. Generally, species that occured in higher abundances were also found to be widely distributed between the forests. There were two species however, that were low in abundance but found widespread, i.e. *Pyrocoelia fumigata* and *Stenocladius* sp.1.

It is known that species abundance is correlated positively with species distribution (Brown, 1984), and this is related to greater dispersal ability, increase survivability from higher chances of securing mate and adaptability to bigger range of environment niche (Gaston & Lawton, 1988; Verberk, 2011). Ecological community can be separated into two components of core species and occasional species, with the core species tend to be most abundant and biologically more adapted to the habitat, while the occasional species occurring in much lower number mainly having different habitat requirements and restrictions (Kunin & Gaston, 1993; Magurran & Henderson, 2003).

Fireflies exhibit an array of microhabitat and niche use either at species level or between life stages. Our collections consisted of the firefly adults and larvae from different microhabitats of the forest generally showed the variety of biological and ecological requirements of the fireflies. Although larvae were collected from this study, we were not able to conclusively assign them to a species as taxonomic association of the adults and the larva of fireflies are limited. Only the larvae of the diurnal fireflies were assigned to genus level. Most taxonomic identifications are based on adult males and conclusive association of females or larvae were only through *ex-situ* breeding or DNA confirmation (Ballantyne and Menayah, 2002; Fu *et al.*, 2012). The reason for this is most females and the larvae do not have distinct morphological characteristics to enable them to be taxonomically identified unless after being reliably associated with a known male of a species (Ballantyne & Lambkin, 2013; Ballantyne et al., 2015). DNA barcoding has been shown to corroborate species identification of females and larvae of the mangrove fireflies (Jusoh et al., 2014) and future research could utilise this tool to link and confirm the species of the larvae collected from current study.

iNEXT rarefaction and extrapolation using Hill number enabled us to understand and meaningfully compare species richness, Shannon diversity and Simpson diversity of an assemblage and among assemblages. The Shannon diversity estimation derived from the analysis depicts the common species of an assemblage, while the Simpson diversity reflects the dominant species. Through this statistical framework, we were able to estimate not just the species richness in a community, but also identify the estimated species that are more common and dominant. This statistical framework enabled estimation of species richness and diversity at a standard level of completeness therefore relative comparisons among community were possible. It was estimated between one and fourteen species could occur in a certain tropical lowland dipterocarp forest with the common species ranging between one and seven species. Within the common species, the dominant species could range between one and six species (reflected by the Simpson diversity). This was the first known record of firefly diversity estimation in tropical lowland dipterocarp forests.

Species richness and diversity of fireflies were found to differ between forests that remained unlogged; and that have experienced once and twice logging rotations. Besides unlogged forest showing a higher mean of firefly species, the relative evenness of species were found to be higher for unlogged forest. Jost (2010) indicated the ratio of logarithms of Hill numbers and the logarithm of species richness would express corresponding relative evenness: the closer the value to 1, the more even the species abundance of a community. Based on the ratio between values of estimated species richness and Shannon diversity of the three forest groups, evenness of species composition was highest for firefly species in unlogged forests. Species richness has been suggested to be positively correlated with evenness (Hill, 1973), although more recent studies do suggest opposing correlations (Stirling & Wilsey, 2001; Tang et al., 2010).

3.5.2. Effect of time since logging and habitat characteristics on species diversity

The effect size of each habitat characteristic on firefly species richness and the diversity estimates were analysed by identifying the partial eta-squared values of each habitat characteristics. Partial eta-squared is the ratio of variance accounted for by an effect (in this study the habitat characteristic) and this effect plus its associated error variance within an ANOVA study:

$$Partial\ \eta^2 = \frac{SS_{effect}}{SS_{effect}+SS_{error}}$$

This measure indicates how comparatively large is the effect of a habitat variable on firefly species richness and the diversity in the forest compartments. The habitat characteristics had a bigger influence on the total species richness of a community but relatively smaller effect size on Shannon and Simpson diversities. This could be translated as being, all these habitat characteristics were not highly influencing the number of common (reflected from Shannon diversity) and dominant (Simpson diversity) species of the community.

The effect size of distance to primary forest on species diversity was large. Within the forest blocks of DTC, some forest compartments were either unlogged due to their designation as high conservation value forest (HCVF) or because they do not contain economically valuable timber (Mohd Hakimi et al., 2014). The designated unlogged compartments cover a total area of 15,903 ha. These areas could provide a spill over of species into neighbouring forest compartments that have experienced logging, promoting species recovery of the logged over forest compartments (Bicknell et al., 2015; Costa et al., 2017; Patterson et al., 1998).

Contiguous forests area have been found to support higher species diversity and richness as compared to fragmented forests, even for disturbed secondary forests (Azevedo-Ramos et al., 2006). Disturbed areas located within continuous forest have also been found to recover better after disturbance than fragmented forest (Tawatao et al., 2014). Fragmented and isolated primary forests designated as forest reserves have been found to suffer from edge effects, reducing their ecological health thus affecting the species diversity they are able to support (Laurance et al., 2012; Lucey et al., 2014).

Dungun Timber Complex encompass five large forest blocks with each forest block covering an area of 2,381-51,266 ha (mean: 18,162 ha). With the exception of the two smallest forest blocks, i.e. Besul and Besul Tambahan, the rest of the forest blocks bordered with other forest blocks under direct management and purview of the Forestry Department of Peninsular Malaysia; or bordering with the National Park (Taman Negara) of Peninsular Malaysia (Borhan & Mohd Hakimi, 2014). Logged-over compartments within contiguous forest matrix which also includes unlogged compartments and bordering with large natural forest reserve, could contribute to the smaller effect size of age since logging on firefly species richness and its diversity.

The effect size of canopy closure on species richness had the second largest effect on the firefly species diversity and was found to be associated with an increase in diversity. Canopy closure regulates ambient and lower canopy temperature of the forest and filters light penetration to the forest floor (Nakamura et al., 2017). Species diversity and richness of invertebrates were reported to be affected by the percentage of canopy closure and they could either be positively or negatively correlated. Butterflies, for example were found to have decreased species richness and abundance with the increase of canopy closure, although they consisted of shade-preference or light-loving groups (Roy et al., 2012; Weerakoon et al., 2015). Ground dwelling insects including dung beetles were found to decrease in species richness when canopy closure decreased (Azevedo-Ramos et al., 2006; França et al., 2018; T Hosaka et al., 2014). These two different insects' species richness correlation with canopy closure were explained by availability of specific host plants for the butterflies; while moist and humid condition affected by shaded forest floor increased species richness for the ground dwelling beetles.

Positive correlation between firefly species richness and canopy closure could be due to the canopy closure function at filtering or reducing light penetration to the lower canopy section of the forest. Although most fireflies are nocturnal, their daily onset of light signalling is triggered by the diminishing light intensity usually occurring at twilight (Dreisig, 1975; Lall, 1993, 1994; Lloyd, 2005). Artificial skyglow caused by the alteration of the natural night lighting level from artificial lights produced by humans affects 23% of world land surfaces (Falchi et al., 2016). The light pollution measured for Malaysia was 8 times the natural night light, affecting 40% of the land area (Falchi et al., 2016). Light pollution are gaining interest due to its negative impact on the behaviour and distribution of fireflies (Firebaugh & Haynes, 2016; Thancharoen et al., 2008). Besides delaying the daily initiation of the fireflies' light signalling, their mating behaviour were found to be disturbed by artificial light causing prolonged mating ritual and delayed or unsuccessful in mate detection (Hagen et al., 2015; Ineichen & Ruttimann, 2012; Picchi et al., 2013). Canopy closure could also influence the forest microclimatic condition at the understory level where firefly of different life stages survive. A higher percentage of canopy closure could provide a conducive environment for the fireflies and their food source that largely dependent on shaded and moist conditions (Ballantyne et al., 2013; Fu, Ballantyne et al., 2012b; Kaufmann, 1965).

3.5.3. Influence of habitat characteristics to community composition

From the six habitat characteristics recorded and anticipated to have a certain degree of influence on species composition of fireflies, depth of leaf litter and number of water bodies were found to be significantly affecting the community composition of fireflies in these forests. This finding based on a multivariate analysis of abundance of all species in once and unlogged compartments, was in support of firefly's dependence on certain niche in the different stages of their lifecycles. Both habitat characteristics were directly linked to the egg, larval and pupal stages of the fireflies, functioning as breeding and food source sites.

Leaf litter provides refuge for the larval stages of the fireflies (Branham, 2010; Fu, Ballantyne et al., 2012b; Rios & Quinta, 2010), while providing the decomposed materials for sustaining their prey of snails, slugs and earthworms (Astor et al., 2015; de Oliveira et al., 2010). These aboveground refuges also provide suitable oviposition conditions for the females as the leaf litter are able to regulate and maintain moisture levels of the ground surface (Pan & Mahrt, 1987; Sayer, 2006). Fireflies with terrestrial larvae are known to oviposit their eggs on soil grounds that are damp and rich with decomposing plant materials (Nada, Kirton & Norma-Rashid, 2009; Nallakumar, 2003).

Many species of fireflies are associated with water bodies. The association is in particular during the egg and larval stage of the aquatic and semi aquatic firefly, for example *Luciola cruciata* and *Pygoluciola qinyu* (Fu & Ballantyne, 2008; Takeda et al., 2006). Although terrestrial firefly larvae do not exhibit aquatic behaviour, the habitat range of several species are in the proximity of water bodies, e.g. by rivers, in mangroves or in marshlands (Nada et al., 2012; Nak-Eiam et al., 2011b; Nallakumar, 2003).

When visualising the data, certain species abundance-environment associations were conspicuous, i.e. for *Abscondita pallescens* (Sp. 1), *Curtos costipennis* (Sp. 9), *Pygoluciola dunguna* (Sp. 13), *Diaphanes* sp. 1 (Sp. 20) and *Colophotia brevis* (Sp. 22). Our univariate analysis associated with the multivariate analysis revealed several significant associations. While the abundance of other species did not vary significantly at the $p < 0.05$ level, the value of the multivariate approach was synthesising across all effects and all species. There were also several 'marginally significant' ($0.05 < p < 0.1$)

effects. While the abundance of these species may not have any strong association with the habitat characteristics, we feel it was more likely due to the low number of individuals representing the species of firefly that caused the inability to identify conclusive associations. Ten of the sixteen species collected consisted of 1 or 2 individuals per compartment. Only the five species mentioned earlier had a collection of 3 or more individuals per compartment (mean: 5.6 individuals).

3.5.4. Does the effect of time since logging on diversity vary by once vs. twice logged?

One of the challenging patterns to explain was how firefly species richness declined as time since second logging event increased – i.e. the older the second logging compartment was, the less species it had. This was in contrast to the once logged forest of similar time since logging, which showed a recovery of firefly richness increasing from about two species to almost eight estimated species, 20 years after logging ceased. Species richness in twice logged forest were found to decrease from four species to one species for a forest that was logged 15 years before. Effect of multiple logging has been assessed for several faunal groups including ants and dung beetles. Multiple logging in a forest was found not to reduce further the species richness of dung beetles of once-logged (Edwards et al., 2011), and 80% of ant species found in unlogged forest persisted in twice-logged forests (Woodcock et al., 2011).

In this study, it was estimated the species richness of fireflies in once-logged decreased substantially after being twice-logged. Unlike ants and dung beetle that occur in high abundance, insects with low abundance such as fireflies could be more affected by multiple logging rotations to its habitat. An assessment of forest compartments in Dungun Timber Complex experiencing regrowth after the first logging cycle found that the forests comprised of comparatively low number of dipterocarp trees fulfilling the standard size allowed for logging and was anticipated to comprise of smaller trees than in the first rotation (Suhaimi & Borhan, 2010). This indirectly reflected the lower quality condition of the forests that underwent the second logging rotation. The observation made in the field by Suhaimi & Borhan (2010) was as predicted by a simulation study by Huth & Ditzer (2001) showing a logging cycle of less than 40 years produced a highly disturbed species composition and low timber yield.

Distance to primary forest could also explain the substantial difference in species richness of the once-logged and twice-logged forests. The forest compartments sampled to represent once-logged forest were located between 67 m and 10.08 km (mean: 3.43 km) from primary or unlogged forests while the twice-logged forests were located between 718 m and 9.90 km (mean: 6.04 km) from primary or unlogged forests. As mentioned in section 3.4.2., primary and unlogged forests that are contiguous with logged forest provide the spill over of species and may therefore encourage species recovery. Of the eight compartments that were twice logged, only one compartment shared a border with an unlogged compartment, while three of the once logged compartments bordered with unlogged compartment.

3.6. Summary

The forest compartments of Dungun Timber Complex were sampled to assess the effect of logging on the diversity of fireflies. Fireflies were found to persist in logged forests although their species richness were found to decrease in forests that underwent a second logging rotation, even 15 years after logging had ceased. The diversity of fireflies was largely affected by distance to primary forest and canopy closure, while their species composition within habitats was significantly influenced by depth of leaf litter and number of water bodies. Certain species abundance-environment associations were conspicuous, while others were not. We felt it was more likely that the number of individuals representing the species was too low in our set of samples, therefore future work would benefit from ensuring a higher sample collection to enable conclusive associations.

CHAPTER 4

The effects of elevation and associated habitat changes on firefly diversity in Malaysia

4.1. Abstract

Studies of the effects of elevation and associated habitat changes on biodiversity have a rich history in conservation biology and are seeing a resurgence of interest in recent decades. Mountainous regions are particularly important because they harbour endemic species and because they are relatively spared from anthropogenic effects. The relatively drastic temperature decrease as elevation increases in tropical regions has generated more research on effects of elevation especially since global warming could negatively impact the biodiversity of tropical forest mountainous species. Fireflies (Coleoptera: Lampyridae), and more so the solitary ones, represent a challenging species to work with because though they are biologically diverse, they typically occur at low densities and have rarely been studied across elevations. Many are habitat specialists and have limited dispersal abilities. We assessed firefly diversity changes on five mountains located on the main mountain range of Peninsular Malaysia which is highly representative of five major elevational forest types. Fireflies were restricted to certain elevational range of mountains and turnover of species was significant among forest types across elevations. Forest types and canopy closure were the main characteristics affecting species diversity although other characteristics of the habitat may also have influence. However because we were unable to detect strong statistical associations with habitat characteristics due to the low abundance and detectability of firefly species, our ability to reveal associations that likely do exist was limited. Firefly occurrence across elevation is restrictive and habitat loss could pose a risk to the lower elevation species, while global warming could be a threat to the high elevation species.

4.2. Introduction

Studies of the effects of elevation and associated habitat changes on biodiversity have a rich history in conservation biology and are seeing a resurgence of interest in recent decades (Guo et al., 2013; Lomolino, 2001). Mountainous regions are particularly important because they harbour endemic species as a function of their elevation profile (Bitencourt et al., 2016; Chaves et al., 2015; Macedo et al., 2016), and because they are relatively spared from expanding agriculture and development. This isolation from development could provide a refuge to numerous species and associated habitats. This is significant in light of upslope range shifts that have been recently identified to occur across tropical elevations due to global warming (Freeman & Class Freeman, 2014; Molina-Martínez et al., 2016).

The study of the effects of elevation and habitat change on diversity is sometimes focused on among taxa, e.g. comparing between birds and bats (Graham, 1990) or between birds, bats and mice (Patterson et al., 1998). The majority of the work, however, emphasised on understanding within-taxa diversity along elevation gradients, particularly of indicator taxa with established systematics and ecological understandings. For example, studies on birds (Dehling et al., 2014; Herzog et al., 2005) and non-volant small mammals (Heaney, 2001; McCain, 2004) are prevalent, as well as on abundant and taxonomically well-known insects such as ants (Bishop et al., 2014; Samson et al., 1997), butterflies (Acharya & Vijayan, 2015; Molina-Martínez et al., 2016) and dung beetles (Menendez et al., 2014; Sheldon & Tewksbury, 2014). Further evaluations and meta-analyses across compilations of studies have enabled further understanding of global species elevational patterns, e.g. for birds (McCain, 2009), bats (McCain, 2006), non-volant small mammals (McCain, 2005, 2007), ants (Szewczyk &

McCain, 2016) and geometrid moths (Beck et al., 2017); or of regional elevational patterns, e.g. for tropical region (Laurance et al., 2011).

This classic work typically addresses one of two major topics in the study of elevation and associated habitat changes. The first is focused on how diversity changes across elevation gradients and whether this can be associated with changes in habitat, which underpin the ecology and life history of a taxonomic group. For example, studies of ant species across elevation was found to have a strong correlation with elevation as well as tree basal area (Blatrix et al., 2016) and leaf litter depth (Bruhl et al., 1999); while for butterfly and dung beetle, vegetation cover was found to be strongly associated with their species diversity across elevations (Bhardwaj et al., 2012; Carneiro et al., 2014b; Chamberlain et al., 2015).

The second is focused on the shape and mechanism of the diversity-elevation relationship. The underlying hypothesis explaining the different patterns of species richness across elevational gradients are linked with variable changes as elevation increases. Recent reviews/meta-analyses of elevation patterns for species richness in many taxa around the world fall into three general patterns of increasing, decreasing or mid-elevation peak (Colwell et al., 2016; Grytnes & McCain, 2007; McCain & Grytnes, 2010). These patterns are based on hypothesised predictions based on the metabolic-theory of ecology (MTE), species-area relationships (SAR) and spatial constraint hypothesis known commonly as the mid-domain effect (Colwell & Lees, 2000; Lomolino, 2001).

Analysis of changes of diversity across elevation utilise beta-diversity analysis in order to understand how changes across spatial scale occur along elevational gradients (García-López et al., 2012; Grytnes & McCain, 2007; Tello et al., 2015). Beta diversity is an important component to understand species composition changes across spatial scale (Legendre et al., 2005; Tuomisto, 2010). Baselga (2010) proposed partitioning the Sorensen dissimilarity into two additive fractions which is β_{sim} (as a turnover component of the Sorensen dissimilarity) and β_{sne} (as a nestedness of the Sorensen dissimilarity), both of which combine to make the beta diversity pattern among various spatial or temporal scale. This additive partitioning of the beta diversity enables identification of species replacement (turnover) and species loss (nestedness) for either pairwise or multiple-site comparisons.

Unlike the less variable temperature change as latitudinal increase in the tropical regions, the relatively drastic temperature decrease as elevational increase for the region has triggered more research on effects of elevation. This is more apparent after the increase in the awareness of global warming impact towards species distributions and biodiversity (Cusack et al., 2016; Menendez et al., 2014; Zhou et al., 2013). As global temperature gradually rises, more evidence shows a shift of plants and animals upslope to escape the unconditional temperature of lower elevations (Chen et al., 2011; Freeman & Class Freeman, 2014; García-López et al., 2012; Molina-Martínez et al., 2016). Extinction of high elevation-occurring, thermal specialist species are also anticipated with the change of global climate. The detrimental effect could cause a bigger impact to species of tropical montane areas than for the temperate counterpart (Bitencourt et al., 2016; Raxworthy et al., 2008; Sheldon et al., 2018).

4.2.1. Malaysian fireflies across elevation as a case study

Fireflies (Coleoptera: Lampyridae), typically the solitary ones represent a challenging species to work with because though they are biologically diverse, they typically occur at low densities and have rarely been studied along environmental gradients including elevation. Fireflies, however, are potentially valuable because their light displays offer a compelling opportunity to develop eco-tourism in forested landscapes including for forests of higher elevations (Nada, Mohd Salleh & Khirul Faizal, 2014; Wong, 2014). Fireflies are also increasingly becoming a popular indicator species promoting environment awareness among the general public through citizen science projects (Bonney & Dickinson, 2012; Chow et al., 2014; Xing, 2012).

Most species in this group are highly specialised. They are obligate predators of snails and slugs during the larval stage (Fu & Benno Meyer-Rochow, 2013; Viviani et al., 2012), with larval habitats of either aquatic, semi-aquatic or terrestrial type (Ballantyne et al., 2016; Fu, Ballantyne et al., 2012b; Fu & Meyer-Rochow, 2012). The habitat of adults and larvae are not necessarily confined to the same microhabitats. Flying adult species are fully terrestrial, requiring herbaceous plants as their resting and mating places. Adults with flightless females are confined to the forest floors and also fully terrestrial (Fu, South et al., 2012; Jeng et al., 2011, 2001; Santos et al., 2016). Ecological theory suggests that such specialization will increase solitary fireflies' sensitivity to environmental disturbance (Firebaugh & Haynes, 2016; Kazama et al., 2007). Furthermore, solitary fireflies also appear to have low dispersal capacities (Fu, South et al., 2012; Kakehashi et al., 2014) which may limit their ability to colonise other area or adapt to the changes caused by climate change. Information on fireflies along (Macedo et al., 2017; Silveira et al., 2016; Smith, 2009) and at high elevations (Fu & Ballantyne, 2008; Jeng et al., 2011; Wattanachaiyingcharoen et al., 2016) are very limited, therefore this study would be able to provide further information to the current knowledge of firefly species diversity across elevational gradients.

Fireflies were sampled on the main mountain range of Peninsular Malaysia, the Banjaran Titiwangsa which is highly representative of five major forest types that span an elevation gradient. Most montane area (above 900 m a.s.l.) of Malaysia are covered by natural forest cover. Around 22.42% of the country's total montane area is located in Peninsular Malaysia (Kumaran et al., 2011), with the majority of montane areas of Peninsular Malaysia located along its main mountain range. This mountain range has an elevation between 243 m a.s.l. and 2,183 m a.s.l. and extends 480 km from the north to south, separating the east and west coast of the peninsular.

Changes of forest structure across elevation in tropical forest are influenced by temperature, precipitation and soil properties (Guo et al., 2013; Malhi et al., 2010; Tuomisto et al., 2014). Five floristic zones of the main mountains of Peninsular Malaysia according to elevational climatic forest formations have been identified by Whitmore (1984): lowland dipterocarp, hill dipterocarp, upperhill dipterocarp forest, oak-laurel forest, and montane ericaceous.

Lowland dipterocarp forest occur within the elevations of 0-300 m a.s.l. with around half of the trees at the emergent layer comprise of dipterocarp trees of 30-50 m tall, and the young of the emergent trees occupy the main storey of the forest. The ground layer is abundant with herbaceous plant including ferns, ginger and palms. In the lowland dipterocarp forest, lianas and large climbers are common. At higher elevation of between 330 and 830 m a.s.l., a change in the emergent and main storey are observed and this zone is the hill dipterocarp forest. Common lowland species are present at a lower number, being dominated instead, by *Shorea curtisii*, an important timber tree species. Hill dipterocarp forest is distinctively characterized by undulating and hilly terrain with moderate to steep slopes (Niiyama et al., 1999). The third forest type as the elevation increases is the upper dipterocarp forest, which could be present up to 1,200 m a.s.l. This forest is not distinctively different from hill and lowland dipterocarp, however the emergent and main storey is less distinct making the canopy more even.

As elevations increase upper dipterocarp forest transitions into oak-laurel forest (1,200-1,500 m a.s.l.) largely dominated by Fagaceae and Lauraceae. The forest stature is absent of emergent and becomes a two tree-layered forest. Shrubs could consist of tree ferns and rattans while mosses and liverworts grow at the ground layer. Montane ericaceous (> 1,500 m a.s.l.) comprise of one tree-layer structure of around 10 m in height. This forest is dominated by Ericaceae, Fagaceae and Laureaceae. The ground layer has thick humus layer and is heavily covered by mosses. In this forest orchids and rhododendron are common.

Here we focused on exploring the solitary firefly diversity within elevational forests in Malaysia. Using a combination of analyses of species partitioning beta diversity and of the relationships between species richness and diversity (via rarefaction and extrapolation of Hill numbers) and several habitat characteristics, we assessed the species richness and diversity changes along elevation gradients. We also identified whether this variation was associated with forest types, which can be tied to the natural history of the fireflies.

4.3. Methods

4.3.1. Study area

The study was conducted at the main mountain range of Peninsular Malaysia, the Banjaran Titiwangsa. This range extends across the middle of the region from the borders of Thailand-Malaysia in the north towards the southern tip of the peninsular, separating the east and the west coast. Only areas on the western slopes of the mountain range were sampled in the periods of May and July (when the western region have less rainfall) to minimise the influence of weather on the behaviour and sampling of the fireflies. Weather conditions differ between the eastern and the western slopes of the mountain range (Jamaludin et al., 2010).

Prior to fieldwork, potential transects were identified with the use of Google Earth and hiking trail coordinates retrieved from *Everytrail* website that shares GPX files of tracks used by hikers (www.everytrail.com). These potential transects comprised of road networks, nature tracks or abandoned logging roads extending towards higher altitudes. The preselected transects for the study fulfilled the criteria of: located at the western section of the mountain range; located more than 10 km latitudinally apart measured from the peak to peak distance and transect start to start point; covered at least 15 elevation bands of between 200 to 2,000 m a.s.l.; sampling were able to be conducted from the lowest accessible elevation band possible to the highest elevation band (nearest to mountain summit).

Five mountains located between 12 to 47 km latitudinally apart (latitude 3°48’ N - latitude 2° 48’ N) were sampled to represent the mountain range (Figure 4.1a). The trails from the lowest points of the mountains consisted mainly of nature trails of 1 m wide or less, going up mountain summits. The mountains sampled for the study were Gunung Nuang (189-1,459 m a.s.l.), Bukit Kutu (200-1,000 m a.s.l.), Gunung Besar Hantu (225-1,409 m a.s.l.), Gunung Berembun (264-1,057 m a.s.l.) and Gunung Liang (224 m-1,933 m a.s.l.). A total of 110, 80 m-transects sampled extended into five climatic forest formations of tropical forest as described by Whitmore (1984), i.e. lowland dipterocarp (at 0-330 m a.s.l.), hill dipterocarp (at 330-830 m a.s.l.), upper dipterocarp (830-1,350 m a.s.l.), oak-laurel (1,200-1,500m a.s.l.) and montane ericaceous (1,500-2,100m a.s.l) (Figure 4.1b).

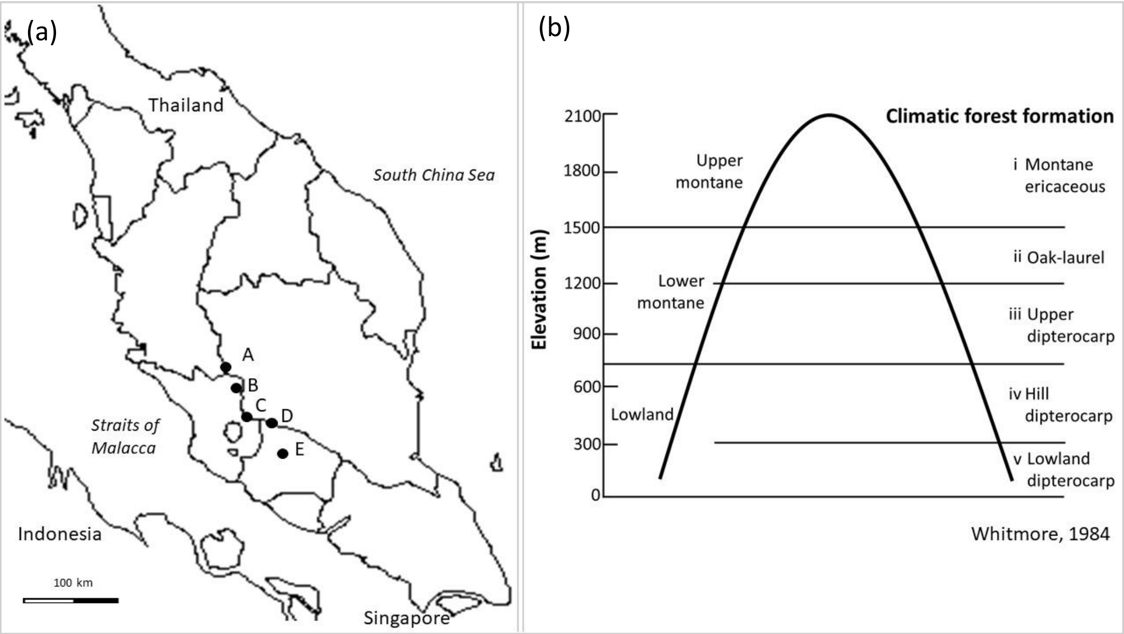

Figure 4.1: (a) Map of Peninsular Malaysia showing locations of the five mountains sampled on Banjaran Titiwangsa mountain range comprising of A) Gunung Liang, Perak; B) Bukit Kutu, Selangor; C) Gunung Nuang, Selangor; D) Gunung Besar Hantu, Negeri Sembilan and E) Gunung Berembun, Negeri Sembilan;(b) The five climatic forest formations spanning elevations of Malaysian mountains, adapted from Whitmore, 1984.

4.3.2. Firefly sampling and identification

A total of 110 transects were sampled representing the five mountains and five forest types (Appendix Table 2.1). Each sampling session consisted of day time marking of 80 m transect length and habitat assessment at 0, 20, 40 and 60 m point. The sampling was conducted at every 50 m altitude increase from the lowest possible band of 200 m a.s.l. and to the highest possible at 1,900 m a.s.l. Determination of elevation was based on altimeter reading (Suunto, altimeter watch, error reading of less than 1 m).

At each elevation band, sampling of fireflies was done along the 3m wide and 80 m length strip located on both sides of the transect. Due to varying topography of the mountains, it was not possible to standardise the sampling time at each elevation band. However, the sampling of fireflies was done for 20 to 30 minutes for each transect. The sampling of fireflies at night consisted of collecting firefly adult and larva beginning at nautical twilight which ends between 20:04 to 20:16 hours for the period between May and July 2015 (Timeanddate.com, 2015).

An active search method was used, i.e. sweep nets for adults and hand searching on the ground for larvae. Fireflies fall into two main groups – light producing adults that are active at night (mainly of the Luciolinae and Lampyrinae subfamilies) and those in which adults have reduced light organs and therefore are active during the day (Ototretinae subfamily). Both groups have light emitting larvae that are active at night and thus our sampling methods enabled both groups to be collected during a single sampling period. The fireflies were detected by their emission of light whilst in flight, on the ground or on plants. Two people (each with sweep net) sampled each transect with headlamps switched off every 3 metres for at least one minute to detect fireflies (including larvae on the ground) – if no fireflies were detected after one minute, headlamps were switched on and surveys progressed to the next stopping point. All specimens were immediately preserved in 70% ethanol.

Adult fireflies in the Luciolinae subfamily were identified to species level using firefly taxonomic identification keys (Ballantyne & Lambkin 2013; Ballantyne et al. 2013; Fu et al. 2012). Adult fireflies in the Lampyrinae subfamily and larvae of the Ototretinae subfamily were assigned to genera using Jeng et al. (1999, 2001, 2007) and Kawashima et al.(2005) taxonomic identifications and later grouped into morphospecies as species level guides are not available. The traits used to identify morphospecies are those typically used for species level identification of fireflies, i.e. the range of diameter of eye sockets, distance between the eyes, lateral length and colouration of the elytra or exoskeleton, shape and size of the light organ and the length of the antenna (Ballantyne et al., 2015; Fu, Ballantyne et al., 2012b).

4.3.3. Habitat characteristics recording

We specifically focused on four key aspects hypothesized to influence firefly distribution and abundance.

1. Canopy closure - provides light filtering and regulates forest ambient temperature and humidity (Montgomery, 2004; Montgomery & Chazdon, 2001), influencing the suitability of the habitat for different firefly species (Kaufmann, 1965; Koji et al., 2012);
2. Leaf litter depth - leaf litter provides resources for snails which are obligate prey for the predatory larvae of many firefly taxa (Rios & Quinta, 2010; Yuyong Wang et al., 2007);
3. Height of understorey plants - in many firefly taxa, adults exploit this shrub layer for shelter and mating (Dreisig, 1975; Lall, 1994; Santos et al., 2016); and
4. Number of trees with DBH >40cm - fireflies rely on visual communication via light displays as sexual attraction. It is anticipated the tree density would have an influence on suitability of habitat for fireflies.

Canopy closure was recorded using a spherical, convex densiometer and counting the number of grid cells, maximum of 24, that had a clear view of the sky. Eight readings were taken (at the four cardinal points), converted to a percentage closure using equations from Lemmon (1956). Uncompressed leaf litter thickness was measured (to the nearest cm) at the corners of a 1m quadrat located in the three metre strip parallel to the transect (16 readings per transect). The height of the understorey plants was measured using a 150 cm long ruler with fifteen alternating 10 cm white and red bands. A person stood three metres away from the pole and counted the visible sections of the pole. The value was then deducted from the total 15, to give the approximate height of the understorey plants. Readings were taken at two points with the pole remaining in one point, while the observer moved parallel to the transect line (8 readings per transect). The height of understorey plant was taken in the 3-m strip of the transect line. These three habitat characteristic readings were recorded at every 20 m point along each transect, while the number of trees with DBH > 40 cm were counted for the total length of the transect. Only trees that were < 3 m parallel to the transect on either side were counted.

4.3.4. Data analysis

4.3.4.1. Species turnover analysis

The average abundance for each species at 50 m a.s.l. intervals was calculated and graphically presented. Species turnover among forest types was analysed using multivariate generalised linear models in the mvabund package, version 3.13.1 in R (Wang et al., 2018). Multivariate generalised linear models have emerged as a more robust method of estimating species/taxonomic turnover with abundance data than distance matrix methods (permanova, CCA etc.) for several reasons. First, they use the raw abundance data, not a simplification of the data into a distance matrix. Second, the power to detect magnitude and direction of effects of covariates, such as forest type, is much less biased by the variation in abundance of species – the power of distance matrix methods (permanova) is high only for species that are highly variable in their abundance. Finally, they account appropriately for the properties of the data, which for count data are often linked to the poisson or negative binomial distribution because of the number of 0 counts and the long tail of abundances at higher values but low frequency (Wang et al., 2012).

Firefly species abundance as a function of both forest type and mountain were modelled by fitting the model: abundance ~ forest type + mountain, using the poisson family, which produced better diagnostics than a negative binomial distribution. The interactions were not fitted because there were too many missing combinations of forest type and mountain at high elevations. An ANOVA table was obtained to test the hypothesis that forest type and mountain influenced species relative abundances (e.g. turnover/beta diversity). Univariate tests identifying which species were responsible for the change were also obtained. These results were complemented by figures showing species abundances among mountains and forest types.

Despite the benefits of the multivariate generalised linear model approach, beta-diversity were partitioned into turnover and nestedness and combined with a permanova analysis to produce graphical representation of these data. The components of beta-diversity in our data were firstly estimated using the betapart package for R (Baselga & Orme, 2012). Turnover vastly exceeded nestedness (see results), therefore the resulting matrix was used as the dependent variable and a permanova analysis using the adonis2() function from the package vegan, version 2.5-2 for R (Oksanen et al., 2018, 2015) was performed. As above, the model turnover_matrix ~ forest type + mountain was fitted.

4.3.4.2. Species diversity-habitat relationships

The firefly species diversity and habitat relationships were analysed in a two-step process. First, iNEXT version 2.0.15 for R (Hsieh et al., 2016, 2018) was used to estimate species richness, Shannon diversity and Simpson diversity. The estimateD function from iNEXT was used to calculate these values for a standardised coverage of 60% for each forest type-mountain combination. In iNEXT, the maximum recommended extrapolation for species richness is suggested to be double the reference sample size. Across our 16 samples for this analysis, 60% was the maximum coverage that could be specified without influencing the predication bias for species richness. This resulted in

19 estimates of each diversity metric (3-5 estimates from among transects within 5 forest types from 5 mountains).

iNEXT has emerged as the most effective tool for estimating species diversity for the three most widely used measures, i.e. species richness (Hill number order $q = 0$), the transformed Shannon entropy (Shannon diversity, $q = 1$) and the transformed Simpson-Gini index (Simpson diversity, $q = 2$). It is an integrated sampling, rarefaction, and extrapolation methodology to reliably estimate species diversity of a set of communities based on samples of equal completeness (as measured by sample coverage) instead of equal size.

Second, these estimates were combined with the habitat characteristics data, i.e. on the mean value of canopy cover, leaf litter depth, understory height and big tree abundance estimated for each forest type (Figure 4.1b). These data were input into a linear model of richness or diversity as a function of the habitat characteristics (no interactions). The model was fitted to allow quadratic relationships among the four continuous habitat characteristics. P-values were reported based on Type II sums of squares from the Anova() function in the car package, version 3.0-0 in R (Fox, Weisberg et al., 2018) and effects sizes as Partial eta squared (Partial η^2) values from the etasq() function in the heplots package, version 1.3-5 for R (Fox, Friendly et al., 2018).

4.4. Results

4.4.1. Outcome of sampling

Between 15 and 34 transects were sampled per mountain (Appendix Table 2.1). For all mountains, the most transects were sampled in hill dipterocarp forest (ten transects per mountain), while the lowest number of transects were sampled in lowland dipterocarp forest (mean: 1.8 transects per mountain). A total of 19 species was recorded (Appendix Table 2.2), of which six were of fireflies with flightless females, while three of the complete wing species were diurnal fireflies. This study also discovered three firefly species new to science (Appendix Table 2.2). Between 3 and 12 species of fireflies were collected along the elevations of each mountain (mean: 6.4 species), with the highest species collection made in Gunung Nuang, Selangor (12 species). The highest number of collections were made for *Pygoluciola dunguna* (n = 15) followed by *Abscondita pallescens* (n = 12) and *Stenocladius* sp. 1 (n = 12). The rest of the firefly species collections were between one and eight individuals (Appendix Table 4.1).

4.4.2. Firefly elevational ranges

Fireflies were found to be distributed within certain ranges of the elevations (Figure 4.2). Several species exhibited a relatively larger elevational range. *Stenocladius* sp. 1 (Sp. 24) and *Abscondita pallescens* (Sp. 1) were present in the three lower elevational forest types, while *Curtos costipennis* (Sp. 9) were found between the elevations of 1,100 and 1,750 m a.s.l. which covered the three highest elevational forest types. There were also species that were restricted to the upper sections of the mountains, namely *Pyrocoelia* sp. 1 (Sp. 16), *Pyrocoelia fumigata* (Sp. 18), *Pyrocoelia* sp. 3 (Sp. 19) and *Drilaster* sp. (Sp. 28). There seemed to be a cut-off point at 900 m a.s.l. for the majority of the lower elevation occurring species, with 9 out of the 11 species were not found above 900 m a.s.l. (Table 4.1).

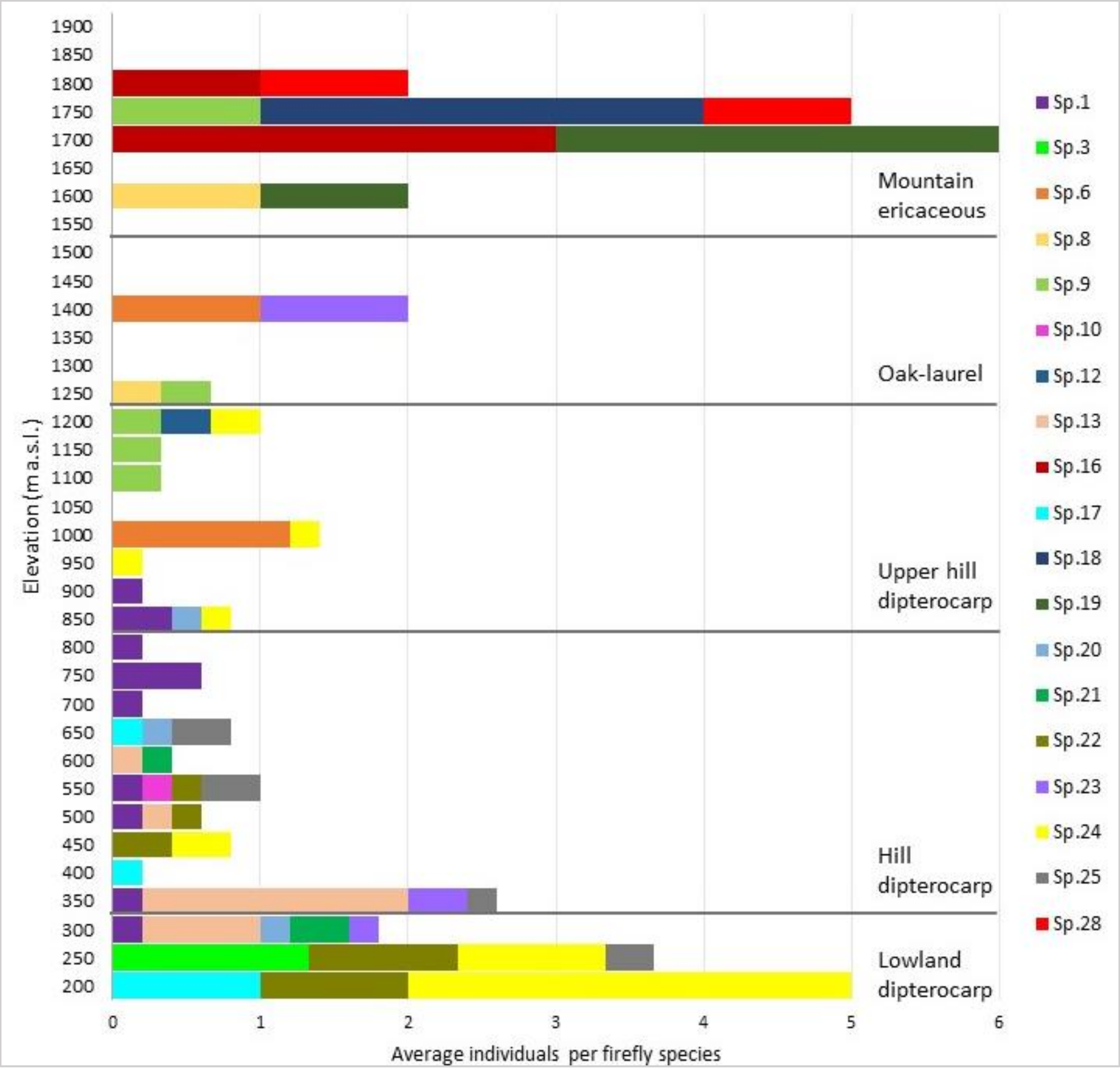

Figure 4.2: Average number individuals per firefly species according to elevation bands sampled. The average was calculated from data at each elevation among the five mountains.

Table 4.1: Firefly species grouped as (a) below or at 900 m a.s.l. and (b) 900 m a.s.l. Species written in bold occur across both groups.

(a) Firefly species ≤ 900 m a.s.l.	(b) Firefly species > 900 m a.s.l.
• *Abscondita pallescens* (Sp. 1)	• *Abscondita berembun* (Sp. 6)
• *Colophotia brevis* (Sp. 22)	• *Curtos costipennis* (Sp. 9)
• *Curtos* sp. 1 (Sp. 10)	• *Curtos obscuricolor* (Sp. 8)
• *Diaphanes* sp. 1 (Sp. 20)	• *Curtos* sp. 3 (Sp. 12)
• *Diaphanes* sp. 2 (Sp. 21)	• *Drilaster* sp. (Sp. 28)
• ***Luciola liang* (Sp. 23)**	• ***Luciola liang* (Sp. 23)**
• *Luciola pallidipes* (Sp. 3)	• *Pyrocoelia fumigata* (Sp. 18)
• *Pygoluciola dunguna* (Sp. 13)	• *Pyrocoelia* sp. 1 (Sp. 16)
• *Pyrocoelia* sp. 2 (Sp. 17)	• *Pyrocoelia* sp. 3 (Sp. 19)
• ***Stenocladius* sp. 1 (Sp. 24)**	• ***Stenocladius* sp. 1 (Sp. 24)**
• *Stenocladius* sp. 2 (Sp. 25)	

4.4.3. Species turnover (β-diversity)- Multivariate generalised linear model method

Evidence for species turnover associated with forest type but not mountain identity was detected (Table 4.2) indicating species diversity and relative abundance was changing in a consistent manner up the elevation gradient among the 5 mountains. Univariate tests indicated that species 13 (p = 0.001), species 6 (p = 0.012) and species 1 (0.025) were driving these changes.

Table 4.2: ANOVA table from the multivariate analysis of abundance (mvabund) testing the influence of mountain and forest types across elevation. Significant level at $p < 0.05$.

Term	Res.Df	Df.diff	Dev	Pr(>Dev)
(Intercept)	15			
Mountain	11	1	4179.9	0.108
Forest type	7	1	4159.3	**0.001*****

4.4.4. Species turnover (β-diversity) - Distance matrix methods

Analysis using β diversity partitioning indicated the turnover component dominated the signal of β diversity (β_{sim}, turnover = 0.89, β_{sne}, nestedness = 0.048, total = 0.94). Permanova analysis of the turnover component suggested both mountain identity and forest type were significantly associated with species turnover, though forest type captured approx. 25% more variation (SS 1.76 vs. SS 2.28, Table 4.3).

Table 4.3: PERMANOVA table from the analysis of the beta-diversity turnover component testing the influence of mountain and forest types across elevation. Significant level at $p < 0.05$.

Term	DF	SS	R^2	F	Pr(>Dev)
Mountain	4	1.7638	0.33130	2.4132	**0.02***
Forest type	4	2.2809	0.42844	3.1208	**0.005****
Residual	7	1.2790	0.24025		
Total	15	5.3237	1.00000		

4.4.5. Species diversity-habitat relationships

Figure 4.4 shows iNEXT-based estimates of species richness among the five forest types across elevational increase indicating substantial variation in predicted species richness but with large uncertainties. The relationships between iNEXT estimates of species richness and forest type and the four habitat characteristics (canopy cover, leaf litter depth, height of the herbaceous understory and number of large trees) are depicted in Figure 4.5.

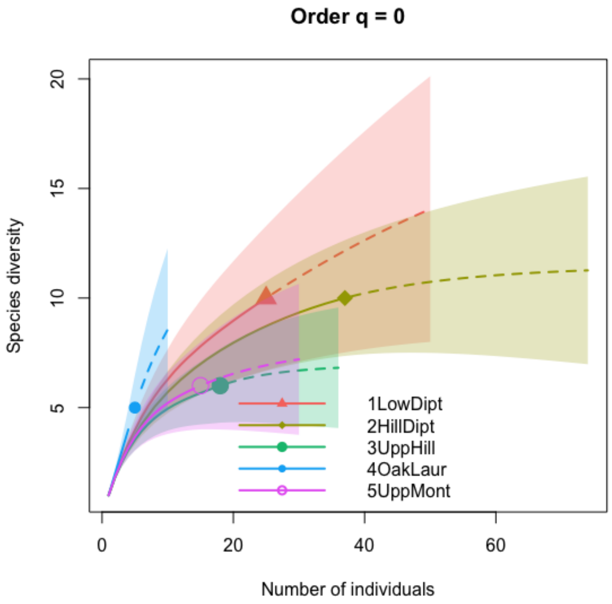

Figure 4.4: Species richness of fireflies estimated by iNEXT via extrapolation and rarefaction of Hill number (q = 0) for the five forest types across elevational gradients. Each shape is the observed species richness of fireflies in that forest type. Solid lines represent the sample-size-based rarefactions made by iNEXT. Dashed lines are the extrapolated curves produced by iNEXT up to double the value of reference sample. The 95% confidence interval (shaded regions) was obtained by a bootstrap method.

A model of log(Species Richness) was fitted to satisfy distributional and mean-variance assumptions. The polynomial model was not justified against a simpler model of only linear effects (F = 0.58, p = 0.69), i.e. polynomial model did not explain further variation than a linear only model. This linear model however did not explain variation associated with forest type or any of the habitat characteristics (all p-values > 0.5).

Variation between Shannon diversity and Simpson diversity of fireflies was also not associated with forest type or any of the habitat characteristics. However, a large effect size of forest type, a moderate effect size of canopy closure and a small effect size of leaf litter on species richness of fireflies were detected (Table 4.4, Figure 4.6).

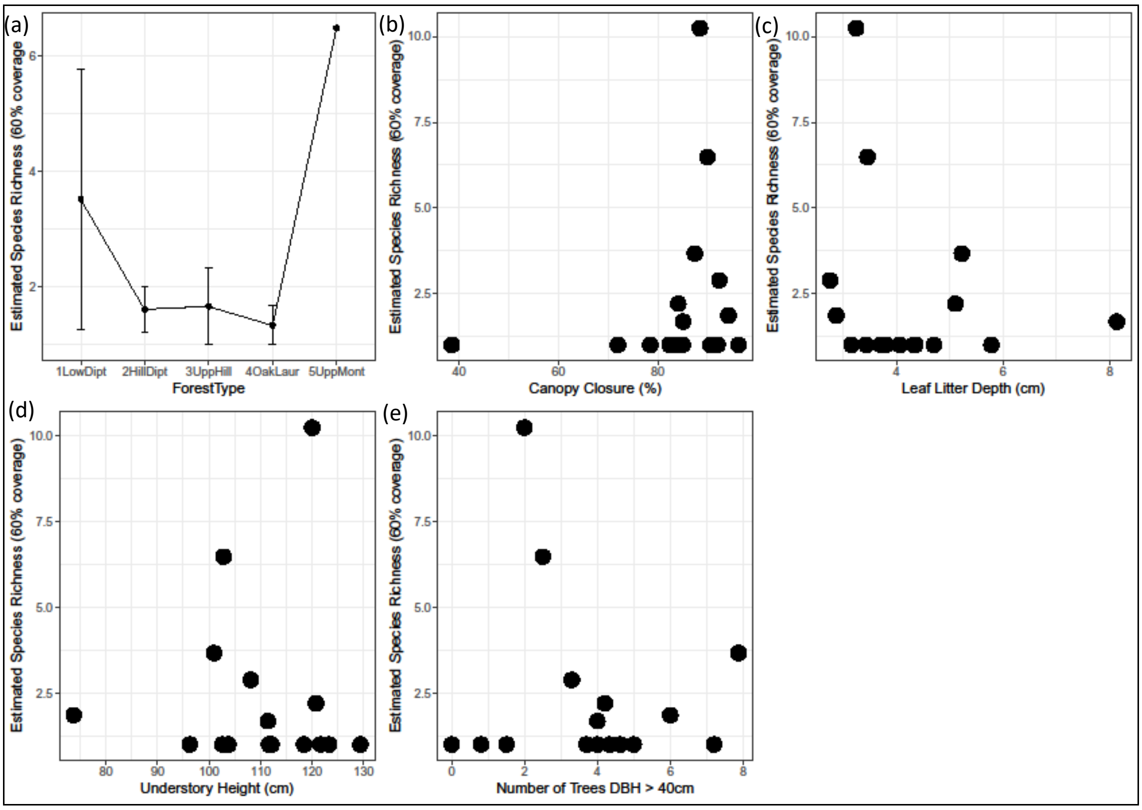

Figure 4.5: The relationships between estimated species richness and (a) forest type, (b) canopy closure, (c) leaf litter depth, (d) understorey height and (e) number of trees of DBH >40 cm. Data points are firefly species richness estimates from iNEXT at 60% coverage for each site within elevational forest type.

Table 4.4: Effect sizes and anova table derived from the linear model estimating the effect of forest type and habitat characteristics on species richness of fireflies. Effect sizes >0.3 are deemed large.

Term	Partial η2	Sum Sq	Df	F value	Pr(>F)
Forest type	**0.3253**	2.3011	4	0.8438	0.5395
Canopy closure	**0.1519**	0.8546	1	1.253	0.2998
Leaf litter depth	**0.0561**	0.2834	1	0.4157	0.5396
Understorey height	0.0154	0.0746	1	0.1095	0.7504
Number of large trees	0.0018	0.0086	1	0.0126	0.9137
Residuals	NA	4.7725	7	NA	NA

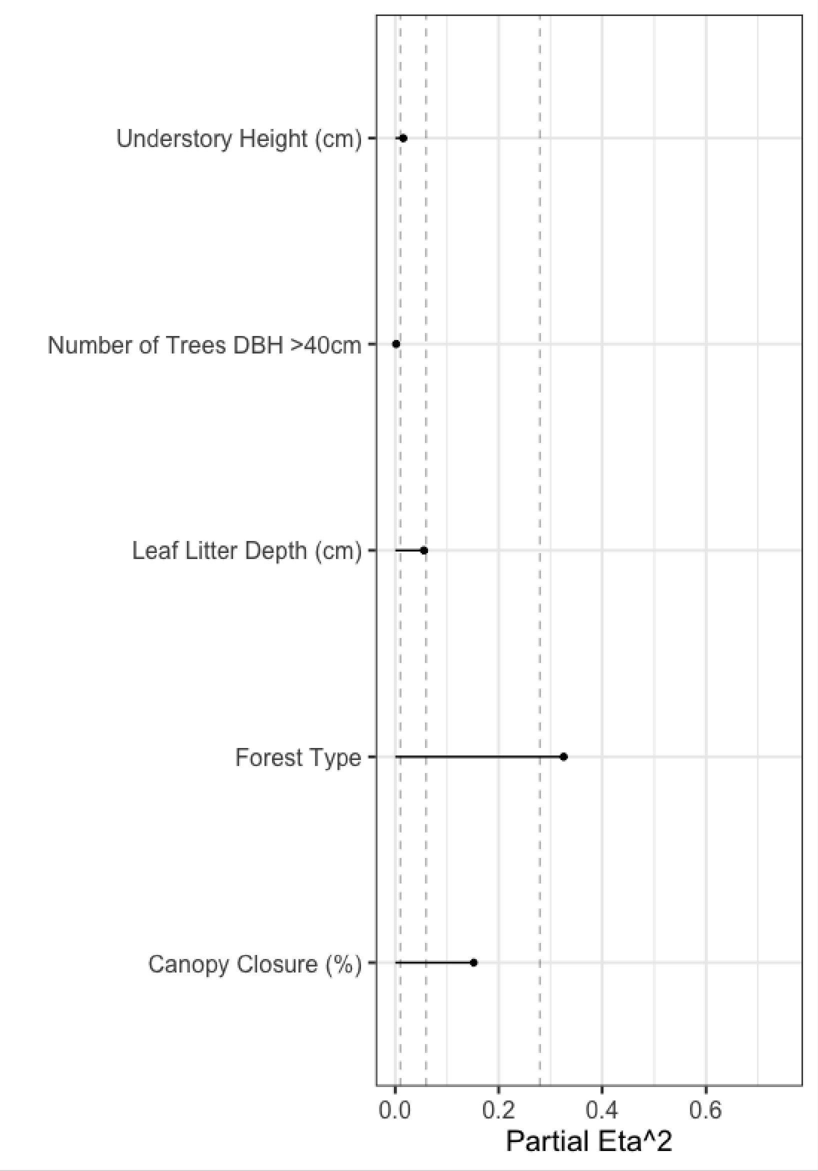

Figure 4.6: Effect size of forest types and habitat characteristics on the species richness of fireflies among elevation bands. Values > 0.3 are deemed large effect sizes.

4.5. Discussion

The relationship between biodiversity, elevation and associated changes in habitat is important because mountainous areas often harbour endemic species tied to unique environments and because they are often spared from expanding agriculture and development, making them a potential refuge. Studying biodiversity across elevation gradients also enables understanding of species distribution across different forest types in a smaller spatial scale, providing a rapid assessment of species diversity of different habitat types. This study was intiated with an aim to acquire a better understanding of an understudied taxa of the insect kingdom which is inspirationally interesting and mesmerizing to the general public as well to the scientific world. The focus was on the biodiversity of the inland forest fireflies along a well-defined elevation gradient on mountains of Peninsular Malaysia.

While the popular understanding of fireflies in Southeast Asia is of the large aggregations of nightly light displays particularly along rivers, their species occurrence is low i.e. between 2-3 species within their habitats of estuarine and riparian (Jusoh et al., 2010; Sartsanga et al., 2018; Wong & Yeap, 2012). Comparatively, aggregative fireflies are better studied because they occur in large numbers (Ohba & Wong, 2004) along rivers making them easier to sample and have economic importance via firefly watching tourism (Jamil & Suzana, 1999; Nurancha et al., 2013).

In contrast fireflies of the inland forests, also known as the solitary fireflies, are harder to detect, occur in much lower abundance, are associated with a range of aquatic and terrestrial habitats and relatively higher speciation than the aggregative fireflies. Their higher diversity is reflected in a more diverse morphology (Fu, South et al., 2012; Jeng et al., 1999, 2001; Wu et al., 2010), behaviour (Branham & Wenzel, 2003; De Cock & Matthysen, 2005) and habitat requirements (Fu, Ohba et al., 2005; Nak-Eiam et al., 2011b; Takeda et al., 2006). Their presence are associated with difficult terrains, occurring in low numbers, with limited economic potential which may have limited our understanding of their diversity. However, like any low abundant occurring taxa, their survival could easily be threatened by detrimental changes of their environment. Furthermore, their association with many forest habitats may make them a candidate indicator species for habitat loss/change and forest degradation.

The study had focused on the association of fireflies with key forest type transitions along an elevation gradient in Malaysia and several key habitat variables hypothesized to influence their distribution and abundance. Specifically, we examined patterns of β-diversity along the elevation gradient and whether firefly species richness and diversity was related to forest type and other habitat characteristics associated with the elevational transitions among these forest types.

4.5.1. Firefly elevational ranges

This study has highlighted the importance to explore the diversity and distribution of the solitary fireflies of the inland forests specifically across elevational gradients of the tropical forests. As of present only two known studies working on understanding firefly species diversity across elevations have been conducted (Macedo et al., 2017; Smith & van Belle, 1984), both of which were in Amazonia. On general inspection of the pattern of firefly species distribution of the five mountains sampled in Peninsular Malaysia (Figure 4.2), we were able to identify several preliminary understandings on the solitary firefly habitat range across elevations. Some species of fireflies were restricted to higher elevations, some at lower elevations while some species were able to adapt to larger range size across elevations.

For fireflies that occur within the lower ranges of the elevations, habitat loss could primarily be the cause of concern on their conservation as more areas typically the lowland and the hill dipterocarp forests are either being degraded from logging or; rapidly and vastly being converted into agricultural landscapes (Abdullah & Hezri, 2008; Peh et al., 2005; Saiful, 2014). An assessment by World Resource Institute identified Peninsular Malaysia experienced forest cover loss at an average of 1,609.1 km^2/year between 2001 and 2010 and the rate was not expected to decrease in near future, although forest reserves remained relatively intact (Hamid & Rahman, 2016). Aside from habitat loss from deforestation, fragmentation of natural habitat will also pose a risk to low elevation firefly species, as in order for them to be able to shift from an unconditional area, a forest corridor or continuous forest is required. The importance of habitat continuity linking the low elevation to higher elevation areas for thermal specialists have been highlighted by previous studies on amphibians, reptiles and insects (Beier & Brost, 2010; Brodie et al., 2012; Şekercioĝlu et al., 2012). The ability for fireflies to adapt to higher elevations, however, remains unknown and entails further research.

Several solitary fireflies collected from our study were also found to be confined to the highest elevation ranges. From the six species observed in the montane ericaceous forest, three were *Pyrocoelia* which has flightless females. Dispersal limitations may contribute to their restricted elevational range as well as suitability of abiotic and biotic conditions of the montane ericaceous forest for their survival. Mountain passes, described physiological barrier to thermal restrictive taxa may also explain their isolation at the highest or lowest point of mountains (Ghalambor et al., 2006; Janzen, 1967; Sheldon et al., 2018). We must be cautious here, as two of our mountains did not possess this highest realm.

The influence of temperature may also explain the restriction of certain species to certain elevational zones. Temperature plays an important function in the rate of enzyme-catalyst reactions and has been shown to modulate light flashing intervals, flash intensity and offset of flashing of the firefly lights (Dreisig, 1975; Ueda et al., 1994). The light flashes of fireflies are a by-product of a chemical reaction, inside the light organ, between luciferase with luciferin in the presence of ATP, oxygen and magnesium (Ohmiya et al., 1996). The production of firefly flashes have been found to be strongly influenced by ambient temperature therefore regulating flashing signal patterns (Iguchi, 2009, 2010; Sharma et al., 2014). Fireflies have species-specific signal patterns in order to communicate within the same species and to distinguish among species (Lewis & Cratsley, 2008; Martin et al., 2015; Ohba, 2004). As elevation increases, temperature decreases, and the different temperature experienced by the fireflies in their specific habitat could possibly restrict their elevation and habitat range.

Two main groups of fireflies present across the elevational gradients of the mountains were able to be identified where almost half of the species collected did not occur beyond 900 m a.s.l. These two groups could be described as having specialisation to upper or lower elevational zones (Table 4.1). Macedo et al. (2017) compared elevational ranges of seven families of beetles in Brazil including the fireflies (Lampyridae) and fireflies were found to be the most specialised among the groups of beetles, either being highly specialised at the lower or at the upper elevational zones. Aside from temperature, these restricted distribution across elevations could be explained by the fireflies requiring obligate prey at the larval stage and specific microhabitat requirements at different stages of their lifecycles (Ballantyne et al., 2013; Fu & Meyer-Rochow, 2012; Takeda et al., 2006; Wu et al., 2010; Yuma, 2007).

Although Whitmore (1984) was able to identify five elevational forest zones linked with changes in floristic composition and structure, the three lowest elevation forest types share many common tree species that influence the canopy structure, forest environment and its microhabitat. Ashton (2003) explained further that the ecotone of the floristic zones of the lowland and the lower montane (Figure 4.1) is gradual, happening approximately between 800-1,300 m a.s.l. However, the ecotone is more obvious between the lower montane and the upper montane which commonly comprise of warm temperate species i.e. Fagaceae (oak) and Lauraceae (laurel). The more distinct difference of floristic composition between the lower montane and the upper montane, yet a more subtle change from lowland to lower montane could explain the majority of the lower elevation fireflies not being present beyond 900 m a.s.l

4.5.2. β-diversity of fireflies between mountains and between forest types

Our results suggest that there was low turnover of species among mountains, but substantial turnover among forest types along the elevation gradient, which has form further support to our general analysis of the firefly species collected across the elevations sampled (Figure 4.2). The result indicated that the β-diversity of firefly species across elevation was strongly attributed to species replacement rather than species loss, based on the much higher turnover value, $\beta_{sim} = 0.89$. This can be interpreted as the pattern of firefly species elevational range observed from this study- some have relatively wider elevational range, while some smaller; some occur in the low sections of the mountains while some confined to the mountain tops. Three major points to discuss with respect to this result: our statistical methods, the species most responsible for this change and the pattern relative to other invertebrates.

The inference was relied on using multivariate generalised linear models of abundance (mvabund) rather than more common methods of calculating β-diversity from distance matrices followed by permutation based statistical inference. The mvabund methods for abundance data are considered more robust for several reasons as described in the methods section (Yi Wang et al., 2018, 2012). Both methods do however suggest turnover, with beta partitioning identifying turnover rather than nestedness having a greater influence on the firefly β-diversity among forest types. Although β-diversity approach also indicated significant turnover of species among mountains, mountain identity was relatively less significant than forest type in the permanova approach. Ultimately, both approaches to determine the β-diversity of fireflies pointed to a strong effect of forest type along the elevation gradient and a weaker equivocal effect of mountain identity. This implied that the firefly β-diversity of the Banjaran Titiwangsa mountain range was more influenced by the elevational gradients rather than the latitudinal gradients.

There were relatively few species responsible for the turnover. The mvabund models identified *Abscondita pallescens* (Sp. 1), *Abscondita berembun* (Sp. 6) and *Pygoluciola dunguna* (Sp. 13) having significant influences to the patterns. Among the species of fireflies collected, *Abscondita pallescens* (n = 12), was the most widely distributed across elevations (200-1,200 m a.s.l.), occurring in four of the mountains and three of the forest types. *Abscondita berembun* is a new species to science and was only collected at the highest sections of two mountains (elevation between 1,750-1,800 m a.s.l.). *Pygoluciola dunguna*, also a new species to science was the most collected from this study (n = 15) and occured in the lowland and hill dipterocarp forest at elevations of 300-600 m a.s.l.

Abscondita is a new genus from Southeast Asia, described in 2013 (Ballantyne et al., 2013) with information of the biology and behaviour of this genus only described from two species, i.e. *Abs. chinensis* and *Abs. terminalis*. Both species have been recorded from mountains in China, although they were also found in other types of habitat e.g. grasslands. Until recently *Pygouciola* was thought to be a rare genus found only in Malaysia (Ballantyne & Lambkin, 2001, 2006). Growing firefly collections by numerous researchers have identified a total of eight species from this genus, all confined to the Southeast Asian region (Ballantyne et al., 2015). Details on habitat, behaviour and distribution of this genus can be referenced to only one species, i.e. of *Pygoluciola dunguna* (Nada & Ballantyne, 2018) which identified its habitat to be confined between the two lowest elevational forests, i.e. lowland and hill dipterocarp forests.

Our results were in line with other studies of invertebrates which often showed different groups within taxa having different elevational range and which occur at habitats with different elevation heights. For example, studies of ant species and elevation in Mediterranean mountain were found to have a strong correlation with elevation, and classified into three distinct groups: generalist spanning all elevations; cold tolerant restricted to high-elevations; and low elevation specialists (Blatrix et al., 2016). Almost half of the butterfly species in the East Himalaya were confined to low elevations of below 500 m a.s.l., 25% were restricted to specific elevation site, and one generalist species, spanned an elevation range of more than 3,500 m (Acharya & Vijayan, 2015). Dung beetles of Costa Rica in contrast, revealed high levels of specialism with species specific, narrow elevational ranges (García-López et al., 2012). This comparison suggests that while fireflies are challenging to study, they are largely behaving as other invertebrates with evidence of generalist, broad specialist to high or low altitudes and instances of high specialisation.

4.5.3. Firefly species diversity and habitat relationships

In contrast to many other studies of invertebrates across elevations (Bhardwaj et al., 2012; Blatrix et al., 2016; Carneiro et al., 2014b; Chamberlain et al., 2015), strong statistical associations with habitat characteristics that were hypothesized to be important to fireflies, were not detected. However, substantial effect sizes of forest type and canopy closure suggested, as noted above, that these factors are important and that the power to detect significant relationships were likely lacking. The low abundance and detectability of the firefly species were probably limiting the ability to reveal associations that likely existed (i.e. large effect sizes and large p-values suggest a sample size issue). Several explanations could support this observation.

The data distribution for several habitat characteristics was likely influencing the ability to make strong inference. There were few locations where canopy closure and understorey height were low, and where leaf litter depth was high (Figure 4.5). Substantial replication of the high elevation forest types was not available (note the absent of standard error bar in Figure 4.4a). There are more mountains to survey for this mountain range and future work to better resolve the potential patterns here was justified by our large effect sizes. The challenge is thus in developing a sampling strategy with enough people to build as large a profile of these species in as many locations as possible.

Based on the firefly biology, we expected canopy closure to influence diversity because it regulates ambient and lower canopy temperature of the forest and filters light penetration to the forest floor (Nakamura et al., 2017). Ground dwelling insects including dung beetles were found to decrease in species richness when canopy closure decreases (Azevedo-Ramos et al., 2006; França et al., 2018; T Hosaka et al., 2014). With respect to fireflies, canopy closure could influence the forest microclimatic condition at the understory level where firefly at different life stages survive, and with increasing canopy closure, it could provide a conducive environment for the fireflies and their food source that largely depend on shaded and moist conditions (Ballantyne et al., 2013; Fu, Ballantyne et al., 2012b; Kaufmann, 1965).

4.6. Summary

Fireflies in five forest types along elevational gradients among five mountains were sampled in order to assess whether their diversity and community composition varied, linked to changes of forest and habitat characteristics important to fireflies as elevation increases. There was strong evidence for change in the firefly community, and strong effect sizes of forest type and canopy closure on firefly abundance and distribution along the elevation gradients. The data suggested that fireflies are a challenging and interesting taxon to work with in Malaysian tropical forests, but that a doubling of person-power and mountains is likely necessary to reveal patterns in this low abundance and difficult to detect group.

CHAPTER 5

A new species of *Pygoluciola* Wittmer with unusual abdominal configuration, from lowland dipterocarp forest in Peninsular Malaysia (Coleoptera: Lampyridae: Luciolinae)

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CHAPTER 5

A new species of *Pygoluciola* Wittmer with unusual abdominal configuration, from lowland dipterocarp forest in Peninsular Malaysia (Coleoptera: Lampyridae: Luciolinae)

5.1. Abstract

A new species of firefly (Coleoptera: Lampyridae) *Pygoluciola dunguna* Nada **sp. nov**. is described from males and reliably associated females, collected mainly from lowland dipterocarp forests of Peninsular Malaysia at elevations below 300 m a.s.l. This species is found to be terrestrial, flying at low heights between 10−15 m above ground in between the herbaceous plants. Males are intermediate between the two types of *Pygoluciola* Wittmer known until now. A list of species, and a key to males and known females of *Pygoluciola* is given. The female bursa has paired elongate hook like bursa plates.

5.2. Introduction

An elaborate field sampling study to collect information on the diversity of the inland fireflies of the tropical forests (logged and unlogged) in Malaysia was conducted by Nada to better understand the distribution and abundance of fireflies (Coleoptera: Lampyridae). Although having charismatic appeal to the public and being recognised as a tourism attraction (Jamil & Suzana, 1999; Lemelin, 2013; Mohd Shahwahid et al., 2013; Nurancha et al., 2013) and nature conservation tool (Faust, 2004; Lloyd, 1997; Mendonca et al., 2012; Toshio et al., 2005), much is still not known about fireflies. The negative impact of human to their habitats is recognised and numerous types of pollution including light pollution have been described as possibly influencing the survival of the firefly population around the world (Firebaugh & Haynes, 2016; Katoh et al., 2009; Picchi et al., 2013; Takeda et al., 2006).

Logged over forests are known to impact the diversity of organisms (T Hosaka et al., 2014; Pavlacky et al., 2015; Yamada et al., 2013). Among the disturbance to tropical forests from logging activities are alteration of (a) microclimate, (b) forest structure and (c) surface water drainage (Hawthorne et al., 2011). The post logging conditions of forests could have the same negative effects on the firefly diversity and distribution. Fireflies are sensitive to changes of the environment and have been shown to decline in population size where breeding and mating areas are disturbed (Hagen & Viviani, 2009; Khoo et al., 2012; Lloyd, 2005). Many are known to be soil-dwelling in their larval stage and are less mobile (Jeng et al., 1999; Kakehashi et al., 2014; Yuyong Wang et al., 2007) and are therefore, especially susceptible to habitat disturbance. During the course of this investigation we collected male and female specimens which we determined to be a new species of *Pygoluciola* Wittmer. Not only is this a new record of the genus for Peninsular Malaysia but the new species is unusual among *Pygoluciola* for several reasons. What is most unusual is that it seems to be an intermediate form between the two morphological types of *Pygoluciola* so far described.

Wittmer (1939) described the genus *Pygoluciola* from *Pygoluciola stylifer* Wittmer, having terminal abdomen modifications where both the median posterior areas of abdominal ventrite 7 and tergite 8 are prolonged. These areas may incline, ventrite 7 dorsally and tergite 8 ventrally, and in dried pinned specimens they may envelop each other. *Pygoluciola* Wittmer was thought to be a rare genus as it was previously ill represented in collections (Ballantyne, 2008; Ballantyne & Lambkin, 2001, 2006). *Pygoluciola* was submerged under the genus *Luciola* by McDermott (1966) and treated as a subgenus by Ballantyne (1968) and Ballantyne & Lambkin, (2000, 2001), until the phylogenetic analysis of Ballantyne & Lambkin (2006), using morphological characters, reassigned it to generic status. Ballantyne (1968), Ballantyne & Lambkin (2001, 2006), and Ballantyne (2008) described five more species, all with the distinctive terminal abdomen morphology described above. The distinctiveness of *Pygoluciola* first as a subgenus and now as a genus, has been confirmed in nine morphological phylogenetic analyses (Ballantyne & Lambkin, 2000, 2001, 2006, 2009, 2013, Ballantyne et al., 2015, 2016; Fu et al., 2010; Fu, Ballantyne et al., 2012a).

Fu & Ballantyne (2008) first realised that *Pygoluciola* could exist in a second form where the pronounced abdominal modifications described above did not exist. Species having this form are only recognisable on dissection, where the typical *Pygoluciola* patterns of genitalia are seen:

The aedeagus has lateral lobes considerably longer than the median lobe and is membranous in the apical half; the basal portion of the lateral lobes are well sclerotised and not fused along all dorsal length; the aedeagal sheath is symmetrical, with narrow elongated anterior portion of sheath sternite expanding in its posterior area and often terminated by paired lobes; lateral arms of tergite of sheath visible beside the sheath sternite. Fu & Ballantyne (2008) described a distinctively coloured species from China where the pronounced abdominal modification does not exist, as *P. qingyu.*

The first form, as described by Wittmer (1939), is the rarer form, and consists of six species (Ballantyne & Lambkin 2013: 108) which are easily recognised by the modifications to the terminal abdomen in males. They are ill represented in collections. The second form is without the pronounced prolongations of ventrite 7 and tergite 8, and is much more widespread, although more difficult to recognise to generic level. Nak-Eiam (2015) in Thailand has discovered several species (presently undescribed) with the same genitalic characters. Wattanachaiyingcharoen & Nak-eiam (2012) distinguished mainland (Asian) species from island species (Borneo and Mindanao) and indicated that the pronounced terminal abdomen modifications seemed to be characteristic of the island species. They felt the long geographic separation of the mainland from the islands mentioned may have led to the separation of the different forms of this genus. Fu (2014: 65, 67, 68) identified three possible *Pygoluciola* sp. from China, generally conforming in external morphology to *P. qingyu*, for which COI genes are being investigated, and which are yet to be described.

The discovery of yet another form of *Pygoluciola*, seemingly intermediate between the two forms described above in which the median area of abdominal ventrite 7 (the terminal ventrite) is prolonged but not inclined dorsally, and the tergite 8 is neither prolonged nor downturned, was unexpected. It is this species that we describe here from males and reliably associated females as *Pygoluciola dunguna* Nada **sp. nov**. Distribution, abundance and habitat characteristics of *Pygoluciola dunguna* **sp. nov**. in natural and recovering logged-over forest are described herein from the tropical lowland dipterocarp forest.

5.3. Methods

5.3.1. Study area

The study of the firefly was divided into two focal study areas (Figure 5.1). In 2015, the main mountain range of Peninsular Malaysia, the Banjaran Titiwangsa, was sampled. This range extends across the middle of the region from the borders of Thailand and Malaysia in the north towards the southern tip of the peninsula, separating the east and the west coast. It has elevations between 243 m a.s.l. (above sea level) and 2,183 m a.s.l., extending 480 km from the north to south. Five mountains located on the western slopes of Banjaran Titiwangsa were sampled between May and July 2015. The sampling sessions were conducted during the Southwest monsoon when the whole country experiences a stable weather condition (Jamaludin et al., 2010). These mountains are spread along the mountain range between 12 km to 47 km apart (latitude 3°48′ N − latitude 2° 48′ N). A total of 110 transects were sampled representing elevational gradients of between 200 and 1,900 m a.s.l.

The logged and unlogged (primary) lowland dipterocarp forests in the Dungun Timber Complex (DTC), Terengganu, Malaysia were sampled the following year (2016). This forest complex covers over 108,000 ha of forest reserves being managed for logging purposes (Figure 5.1). The logging system follows the tenets of the Malaysian Selective Management System (SMS). Here, the logging is in its second rotation beginning in 2008 (Mohd Hakimi et al., 2014). The first rotation ran between 1982 and 2007. Prior to this, the Malayan Uniform System (MUS), which emphasizes only sustained-yield timber production, was adopted. The current system however attempts to ensure sustainability of multiple resources of the forest and acknowledges the importance of sustaining other goods and services it provides. Seven forest reserves, i.e. Besul, Besul Tambahan, Hulu Terengganu Tambahan, Jengai, Jerangau, Pasir Raja Barat and Pasir Raja Selatan covering more than 1,080 km^2 were sampled from 229 transects between May and September 2016. The weather in the area is influenced mostly by the Northeast monsoon, where unusually high downpour is expected between October and February (70 mm/hour). The driest months usually occur from February to June (109mm/ month).

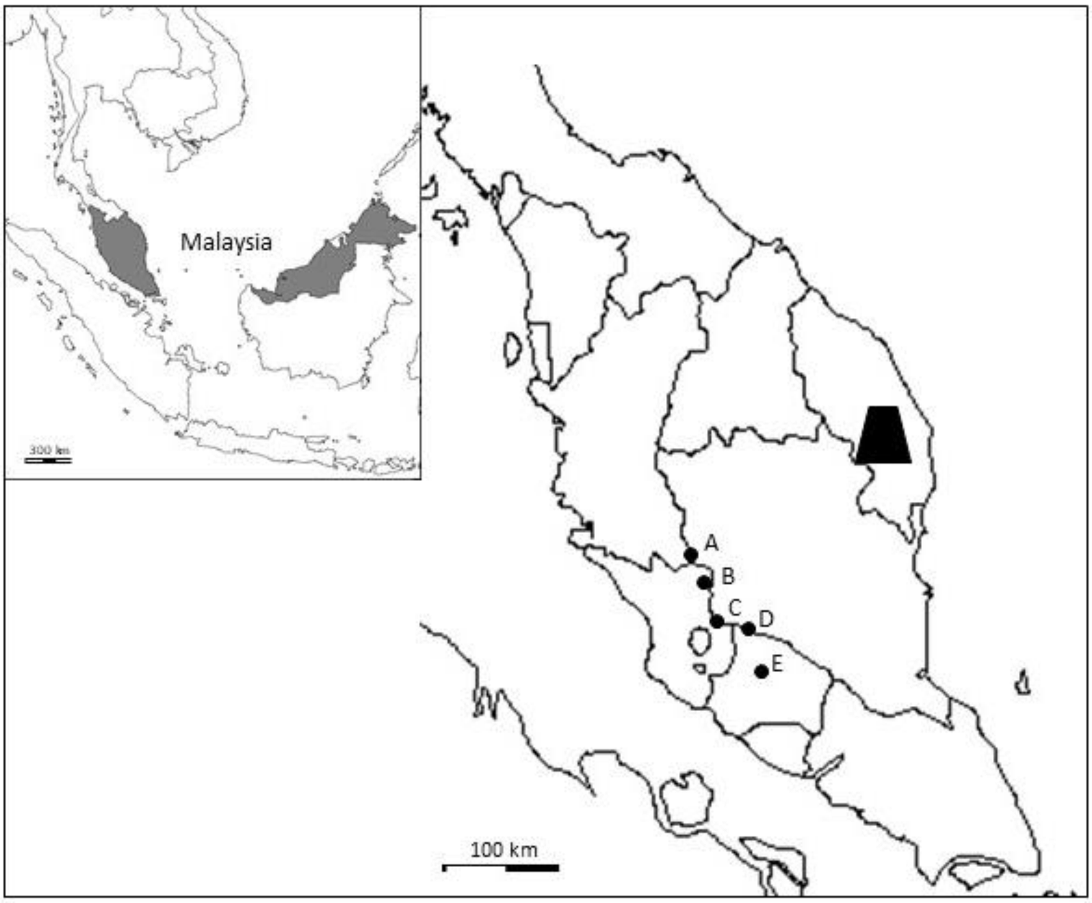


Figure 5.1: The collection of fireflies were made in two focal study areas representing gradients of elevations in the main mountain range of Peninsular Malaysia (Solid dots) and unlogged and gradients of age after-logged lowland dipterocarp forests in Dungun Timber Complex, Terengganu (Solid trapezoid). A to E: A. Gunung Liang, Perak; B. Bukit Kutu, Selangor; C. Gunung Nuang, Selangor; D. Gunung Besar Hantu, Negeri Sembilan and E. Gunung Berembun, Negeri Sembilan. Inset: Map of Malaysia in Southeast Asia.

5.3.2. Field sampling

For both sampling seasons, collection of fireflies were conducted while walking along a length of transect. Fireflies across elevation were generally sampled through nature trails of 1 m wide or less, at every 50 m elevation increase from the lowest possible band of 200 m a.s.l. to the highest possible at 1,900 m a.s.l. Each transect was 80 m in length. The lowland dipterocarp forests of Dungun were sampled along 100 m transects that were cut through the forest comprising unlogged forest (as of 2016) and ages after-logged of between 0−5, 6−15, 16−25 and more than 26 years. Forests representing 0−5 and 6−15 years post logging were subdivided into forest of first and second rotation of the timber felling. For each compartment, an entry point to the forest compartment was identified and from 100 m inwards as the starting point of the first transect. The starting position of subsequent transects in the forest depended largely on accessibility but were always 100 m from compartment boundaries, roads and other transects.

Collection of adults was made mostly using sweep nets and the larvae were collected using soft insect forceps. On average, five transects were sampled per night. The sampling of fireflies began at nautical twilight and ended approximately three hours later, depending on the difficulty of movement on the terrain. All specimens were directly collected into, and are preserved in, 70% ethanol.

5.3.3. Taxonomic description

The most recent phylogenetic analysis of the Luciolinae including *Pygoluciola*, and description of characters used, appear in Ballantyne et al. (2016). A key to genera of Luciolinae using males is in Ballantyne & Lambkin (2013: 35). Localities in Malaysia are listed first by state, then district, then location. Geographical coordinates were obtained by GPS device (GPS 64MAP device, accuracy of up to 3 m). We refer to figures in this document as Figure, and figures in already published work as fig. Abbreviations for taxonomic characters are given in Appendix Table 5.1(a), and the location of specimen depositories are listed in Appendix Table 5.1(b).

5.4. Taxonomy

5.4.1. *Pygoluciola* Wittmer, 1939

Pygoluciola Wittmer, 1939: 21. Ballantyne 2008: 1. Ballantyne & Lambkin 2006: 21; 2009: 107; 2013: 108. Ballantyne Lambkin Boontop et al. 2015: 8. Ballantyne Lambkin Luan et al. 2016: 204. Fu & Ballantyne 2008: 1. (Fu Ballantyne & Lambkin 2010: 2; 2012: 6. Wattanachaiyingcharoen & Nak-Eiam 2012: 24.

Luciola subgenus *Pygoluciola* (Wittmer). McDermott, 1966: 115; Ballantyne, 1968: 119; 1987: 173. Ballantyne & Lambkin, 2000: 82; 2001: 361; Ballantyne & McLean, 1970: 233.

Type species. *Pygoluciola stylifer* Wittmer, 1939, by monotypy (LEIDEN).

5.4.1.1. Diagnosis

It is not always possible to diagnose to genus all species of *Pygoluciola* using external morphology only. However all *Pygoluciola* have a similar distinctive, and easily recognised, genitalic pattern. The aedeagal sheath has an elongate narrow sternite which extends well beyond the lateral tergite articulations and may bear paired lobes at its expanded apex. The aedeagal LL are divisible into two sections, a basal well sclerotized portion with an asymmetrical anterior margin, a short wide median dorsal separation, and a membranous apical portion which is elongated, usually reaching well beyond the rounded apex of the ML. LO in V7 are always entire. Based on external morphology, *Pygoluciola* exists in at least three different forms: 1. The form described originally by Wittmer (1939) has V7 with a median posterior prolongation which often curves dorsally and may be engulfed by a similar elongate prolongation of the midposterior margin of T8, which curves ventrally; 2. In *P. dunguna* **sp. nov.** the median posterior margin of V7 is prolonged and inclines slightly upward where the tip of the MPP abuts against the underside of the narrow T8 (Figures 5.3, 5.10, 5.12, 5.15); 3. In both *P. cowleyi* (Blackburn) and *P. qingyu* (Fu et Ballantyne) there is no MPP and the posterior margin of V7 is evenly rounded; the posterior margin of T8 in *P. qingyu* is very narrowly downturned (at right angles to the longitudinal axis of the body) but not narrowed. LOs in V7 are often retracted from the lateral and posterior margins and these lateral margins may be uprolled. T8 is always narrower than T7, often with parallel sides, elongate slender anterolateral prolongations, and entire posterior margin; dorsoventral muscles joining the lateral margins of T7 to the ventrite below create depressed areas at the sides of T7. Known females are macropterous and bursa plates appear to be hooked with a single point of attachment to the inside walls of the bursa and two or three extensions of irregular length, which incline in an anterior, posterior and inner direction. Larvae associated by breeding for *P. qingyu* are terrestrial with strong well sclerotized dorsal plates, and mandibles with two inner teeth. Table 5.1 lists the species of *Pygoluciola* Wittmer.

Table 5.1: List of species of *Pygoluciola* Wittmer.

Species	Australia	Peninsular Malaysia	Island of Borneo	China	Philippines	Location of types	Females	Larvae	References
cowleyi (Blackburn 1897)	√					NHML			6
dunguna Nada **sp. nov.**		√				FRIM	√		
guigliae (Ballantyne 1968)			√			BPBM	√		1 3
hamulata (Olivier 1885)			√		√	CMG			1 3
kinabalua (Ballantyne & Lambkin 2001)			√			NHML	√		2 3
qingyu Fu & Ballantyne 2008				√		BEIJING	√	√	5
satoi (Ballantyne 2008)					√	ZRC	√		4
stylifer Wittmer 1939			√			LEIDEN			3
wittmeri (Ballantyne 1968)			√			BPBM	√		1 3

*1 = Ballantyne (1968); 2 = Ballantyne & Lambkin (2001); 3 = Ballantyne & Lambkin (2006); 4 = Ballantyne (2008); 5 = Fu & Ballantyne (2008); 6 = Ballantyne & Lambkin (2013).

5.4.1.2. Key to species of *Pygoluciola* using males

Modified and expanded from Ballantyne (2008)

1. Median posterior margin of V7 and T8 prolonged and often curving, V7 dorsally and T8 ventrally and partially engulfing each other. 2

\- Median posterior margin of V7 and T8 not prolonged; if V7 prolonged then not curving strongly dorsally and not engulfed by T8; posterior margin of T8 may be slightly downturned but not narrowed. 7

2. All tibiae curved; lateral margins of elytra tapering posteriorly (Ballantyne & Lambkin, 2006, fig 6) 3

\- No tibiae curved; lateral margins of elytra usually sub-parallel-sided 4

3. Apex of median posterior projection of tergite 8 no wider than rest and rounded, not emarginate; lateral margins of pronotum slightly sinuate (Ballantyne & Lambkin, 2006 figs 1, 19, 21). . . . .*guigliae* (Ballantyne)

\- Apex of median posterior projection of tergite 8 wider than rest; median emarginate; lateral margins of pronotum not slightly sinuate (Ballantyne & Lambkin, 2006 figs 4, 25) . . . . *stylifer* Wittmer

4. Median posterior projection of abdominal V 7 bifurcate at apex (Ballantyne & Lambkin, 2006 figs 18, 26). 5

\- Median posterior projection of abdominal V 7 not bifurcate at apex 6

5. Apex of median posterior projection of abdominal V 7 deeply emarginate, laterally ensheathing the downturned apex of tergite 8 and projecting laterally beside it (Ballantyne & Lambkin, 2006 figs 18, 26; Chey 2008 fig 2) . . . . *wittmeri* (Ballantyne)

- Apex of median posterior projection of abdominal V 7 shallowly emarginate, not laterally ensheathing the downturned apex of tergite 8 and not projecting beside it (Ballantyne & Lambkin, 2001 figs 5, 10) . . . . *kinabalua* (Ballantyne)

6. MPP of V7 elongate slender, ventral surface shallowly depressed along its length, and bearing on its median dorsal surface two slender teeth; posterior apex of MPP not differentiated; lateral margins of T8 downturned . . . . *satoi* Ballantyne

- MPP of V7 shorter, about as wide as long, ventral surface not shallowly depressed along its length, and not bearing dorsal teeth; posterior apex (face) of MPP differentiated and shallowly depressed; lateral margins T 8 not downturned . . . .*hamulata* (Olivier)

7. MPP of V7 defined, longer than wide and either horizontal or inclined slightly upwards along its length and grooved along its ventral surface (Figures 5.3, 6, 10, 12, 14); T8 much narrower than preceding tergite and apically pointed (Figure 5.15) . . . . *dunguna* Nada **sp. nov.**

- MPP not defined, posterior margin of V7 rounded; T8 not much narrower than preceding tergite and not apically pointed 8

8. Australian species; pronotum with wide median black band reaching to anterior and posterior margins; eyes large, subcontiguous ventrally, with well-defined posterolateral eye emargination; elytra brown with pale lateral margins . . . . *cowleyi* (Blackburn)

- Chinese species; pronotum pale whitish cream with restricted median brown spots; eyes not subcontiguous ventrally nor with well-defined eye emargination; elytra black . . . . *qingyu* Fu et Ballantyne

5.4.1.3. Key to species of *Pygoluciola* using females

Extended from Ballantyne & Lambkin (2006)

1. All tibiae curved . . . . *guigliae* (Ballantyne)

\- No tibiae curved 2

2. Posterior margin of V7 deeply emarginate; bearing a small ridge anterior to median area of deepest emargination (possibility this ridge is an artefact having been seen only on dried pinned specimens); V8 with anteromedian prolongation not any more sclerotised than remainder of V8; T7 with anteromedian area rounded and elevated, lateral areas not flattened (Ballantyne & Lambkin 2001 figs 16, 17) . . . . *kinabalua* (Ballantyne)

\- Posterior margin of V7 without an anteromedian ridge; V8 with anteromedian prolongation well sclerotised and visibly separated from remainder of V7; T7 without a rounded and elevated anteromedian area, with lateral areas flattened 3

3. Posterolateral areas of V7 irregularly expanded with aggregation of fat body beneath (Ballantyne & Lambkin 2006 fig 7). . . . . *satoi* Ballantyne

\- Posterolateral areas of V7 not expanded 4

4. Ventral surface yellow except for white LOs in V6, and narrow black line across posterior margin of V5 (Figures 5.25–27, 5.29−33); bursa plates in form of two very elongate slender projections one directed anteriorly and one posteriorly (Figures 5.34−37) . . . . *dunguna* **sp. nov.**

\- Ventral surface brown except for white LOs in V6, without narrow black line across posterior margin of V5; bursa plates in form of two anteriorly directed hooks. . . . . *wittmeri* (Ballantyne)

5.4.2. *Pygoluciola dunguna* Nada **sp. nov.**

5.4.2.1. Type and Paratype

Type. Holotype male. MALAYSIA. *Terengganu*: Dungun, Jengai Forest Reserve, Compartment 40, lat. 4.610939, long. 103.158919 19.vii.2016, B. Nada. (FRIM).

Paratypes. MALAYSIA. *Perak*: Tanjung Malim, Gunung Liang, 3.80205 N, 101.590969 E, 350 m a.s.l., 21.vi.2015, B. Nada, female (GL350) (FRIM). *Selangor*: Gombak x.4.1965, J. Buck, male (ANIC); 30.i.2015, W. Jusoh & Thary, male (MZUM). Kepong, Forest Research Institute Malaysia, 3.233139 N, 101.630403 E, 14.vi.2011, Rover Track,171 m a.s.l., O. Khirul-Faizal, male (ADULT8); 27.vi.2011, Canopy Walkway Trail, C.N. Nafaruding, male (ADULTCNPY2); 6.vii.2011, Waterfall Trail, 139 m a.s.l., M.S. Salman, male (ADULTWFALL4) (FRIM). Kuala Kubu Bharu, Bukit Kutu, 3.55395 N, 101.734211 E, 26.v.2015, 400 m a.s.l. and 600 m a.s.l., B. Nada, male, female (BK400) (BK600) (FRIM). *Terengganu*: Dungun, Besul Forest Reserve, Compartment 10, l4.693225 N, 103.167175 E, 10.v.2016, S. Muhammad-Jafni, 2 males, female (B10); Compartment 19, lat.4.63415, long. 103.200553, 8.viii.2016, Z.A. Saiful-Azhari, 4 males, 3 females (B19) (FRIM). Jengai Forest Reserve, Compartment 52, 4.548261 N, 102.979878 E, 30.vi.2016, M.S. Asraf, 2 males (JI52); Compartment 40, 4.610939 N, 103.158919 E, 19.vii.2016, R.S. Raja-Ahmad-Bazli, female (JI40) (FRIM). Jerangau Forest Reserve, Compartment 100, 4.8699 N, 103.046725 E, 20.vii.2016, M.S. Asraf, female (JU100); Compartment 99, 4.862742 N, 103.048636 E, 17.viii.2016, S. Mohd-Fadhlullah, 4 males, female (JU99) (FRIM). Pasir Raja Barat Forest Reserve, Compartment 87, 4.858047 N, 103.009394 E, 2.viii.2016, S. Muhammad-Jafni, 6 males, 2 females, 22.viii.2016, Z.A. Saiful-Azhari, 1 female (PB87) (FRIM). Hulu Terengganu Tambahan Forest Reserve, Compartment 27, 4.984031 N, 102.932167 E, 30.viii.2016, Z.A. Saiful-

Azhari, 4 males, female (UTT27) (FRIM). All but two specimens (in ANIC and MZUM) are preserved in 70% ethanol. Table 5.2 lists the areas of collections.

5.4.2.2. Diagnosis

Dorsally pale yellowish brown with diffuse pale brown pronotal markings; ventral abdomen yellow except for white LO in V6, 7, with narrow black posterior margin of V5; 9.1−10.6 mm long. The only species of *Pygoluciola* having a broad apically truncate MPP which inclines without any bend slightly upwards to engage against the under surface of the very narrow T8, and a yellow ventral abdomen with narrow black posterior margin of V5. Female macropterous and observed in flight; bursa plates in form of two elongated slender hooks which incline anteriorly and posteriorly.

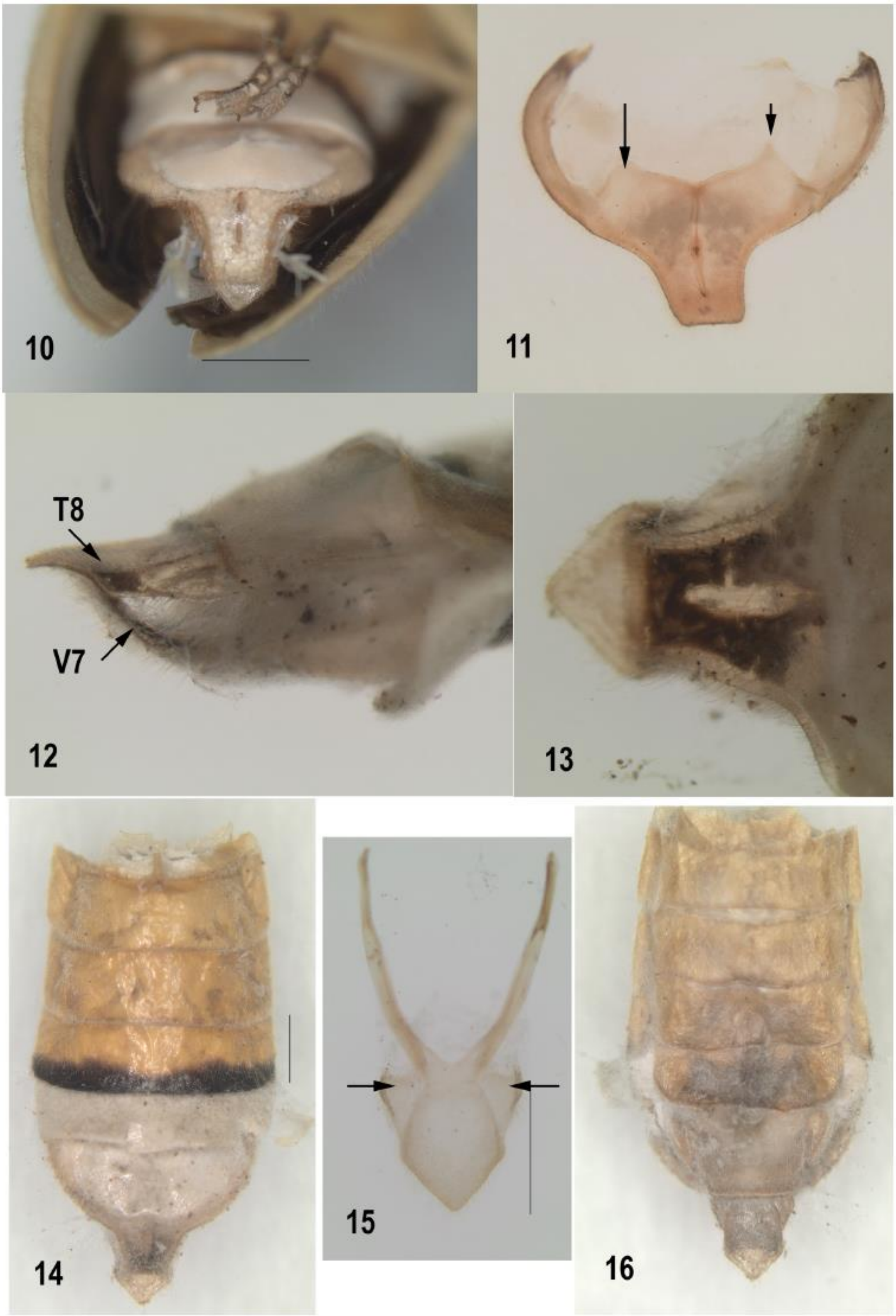
5.4.2.3. Description of male

Length: 9.1–10.6 mm long. Colour (Figures 5.2−9, 5.14, 5.16−18, 5.25–26): creamy yellow semi-transparent pronotum with single median, and paired reddish markings along the posterior margin, all of which often coincide with retraction of fat body beneath the cuticle (Figures 5.2, 5.4, 5.6−9); retraction of fat body along anterior margin of pronotum in ethanol preserved specimens allows black head to be visible from beneath and gives the erroneous impression of a dark marking along the pronotum (e.g. Figure 5.9); MN and MS brown; elytra semi-transparent, very light brown with lateral margins slightly paler (underlying body outline confuses interpretation of elytral colour especially in ethanol preserved specimens where the elytral punctures are dark brown at their bases) (Figures 5.2, 5.6); one of the two pinned Gombak males (Figure 5.4) pale creamy yellow dorsally, pronotum with faint traces of median ginger brown markings (single median mark and paired areas along posterior margin); head antennae and palpi black (Figures 5.17–18); venter of thorax pale yellow (Figures 5.3, 5.6); legs 1, 2 pale brown with black tibiae and tarsi; legs 3 light brown with slightly darker tibiae and black tarsi (BK 600 single male with brown tints in middle area of coxae; B19 (1) II has tibiae 3 pale yellow); abdominal ventrites yellow with posterior margin of V5 narrowly black (Figures 5.3, 5.6, 5.14, 5.25–26); LO in V7 white, retracted from sides and posterior margin, with white areas at side and area behind LO semi-transparent with white fat body visible beneath cuticle (Figures 5.3, 5.6, 5.10, 5.14), and narrow longitudinal median line on MPP which is brown in the MZUM specimen (Figure 5.6); abdominal tergites pale yellowish, semi-transparent, T6 slightly darker than rest, T7, 8 slightly paler than preceding tergites (Figure 5.16 shows one of two pinned males).

Pronotum (Figures 5.2, 5.4, 5.5, 5.7−9): width subequal to humeral width; median anterior margin broadly rounded and barely produced in front of the broadly rounded anterolateral corners; lateral margins strongly divergent along anterior 2/3 and posterolateral corners rounded and not projecting beyond median posterior margin; surface along posterior margin coinciding with the brown markings may appear elevated (only clearly visible in pinned specimens Figures 5.7–8). Elytron (Figures 5.2, 5.4–5): slightly convex sided; interstitial lines not well defined. Head: (Figures 5.3, 5.6, 5.17–18, 5.25–26) GHW 7 x SIW; ASD < ASW. Mouthparts: apical labial palpomere laterally flattened of the form of a broad triangle with inner edge dentate (up to 7 teeth). Antennae (Figures 5.17–18): length > 2 x GHW but not attaining 3 x GHW; scape clavate, all other segments elongate slender about 7 x as long as wide. Abdomen (Figures 5.3, 5.6, 5.10−16): posterior margin of V7 with elongate apically truncate MPP which curves gently upwards with the apex engaging against the underside of T8 (Figure 5.12); dorsally reflexed margins of V7 well defined and anterior margin to either side of MPP produced into short rounded pieces (arrowed in Figure 5.11); reflexed margin in two parts on dorsal surface of MPP where the narrow margin between left and right side is visible from beneath as a line in the middle of the MPP (Figures 5.10–11, 5.13); much darker markings observed in pinned male (Figure 5.13) may be due to age and appear to be accumulated material. T8 with narrow triangular posterior margin, lateral wing like projections and elongate slender anterolateral prolongations that diverge (Figure 5.15).

Aedeagal sheath (Figures 5.22−24): basal ¾ of sheath sternite with narrow sclerotized margins which expand in apical ¼ where they are terminated by a slightly curved, transverse narrow strip of cuticle; to the sides of the apical ¼ (coinciding with the area of expansion of the median strip) there are wider more membranous portions (Figure 5.22); tip of sternite terminates in paired narrowed hairy membranous lobes arising at the sides of the transverse strip, and are not clearly visible in Figure 5.22; anterior margin of tergite shallowly emarginated. Aedeagus (Figures 5.19−21): 2.5 x as long as wide and evenly wide along its entire length; basal piece well defined and in two well cuticularised narrow parts; membranous apical section of LL having short apically acute hair bearing lobe at the outer margin just before origin of the more membranous portion (arrowed in Figures 5.19, 5.21); with dense line of long hairs originating at this lobe and continuing inside their lateral margins (Figure 5.21); membranous portion of LL as wide at base as at apex with both lobes having apices irregularly inclined ventrally (assumed to be an artefact of preparation) (Figures 5.19−21); ML tapering to a rounded narrow apex, much shorter than LL and extending a little beyond the posterior margin of the darker basal portion of the LL which is widely separated for slightly more than half its length in middorsal line; anterior margin of basal portion of LL asymmetrical, being produced on its left side and margin rounded (Figure 5.20).

Figures 5.2-9: *Pygoluciola dunguna* male. (2, 3 J152[1];4, 6 Gombak pinned male ANIC; 5, 6 Gombak pinned male MZUM; 9 B19[2]. 2−6 habitus, 2, 4, 5 dorsal, 3, 6 ventral; 7−9 pronota dorsal.



Figures 5.10-16: (10 Gombak pinned male ANIC; 11−16 Gombak pinned male MZUM). 10 terminal abdomen from behind, ventral surface uppermost; 11 dorsal surface V7 (rounded projections of reflexed dorsal margin arrowed); 12 right lateral terminal abdomen; 13 dorsal surface MPP only; 14, 16 whole abdomen ventral (14) and dorsal; 15 T8 with lateral ‘wings’ arrowed. Scale line is 1 mm.

Figures 5.17-18: Head, antennae and mouthparts, dorsal (17) and left lateral. Scale line is 1 mm.

5.4.2.4. Description of female

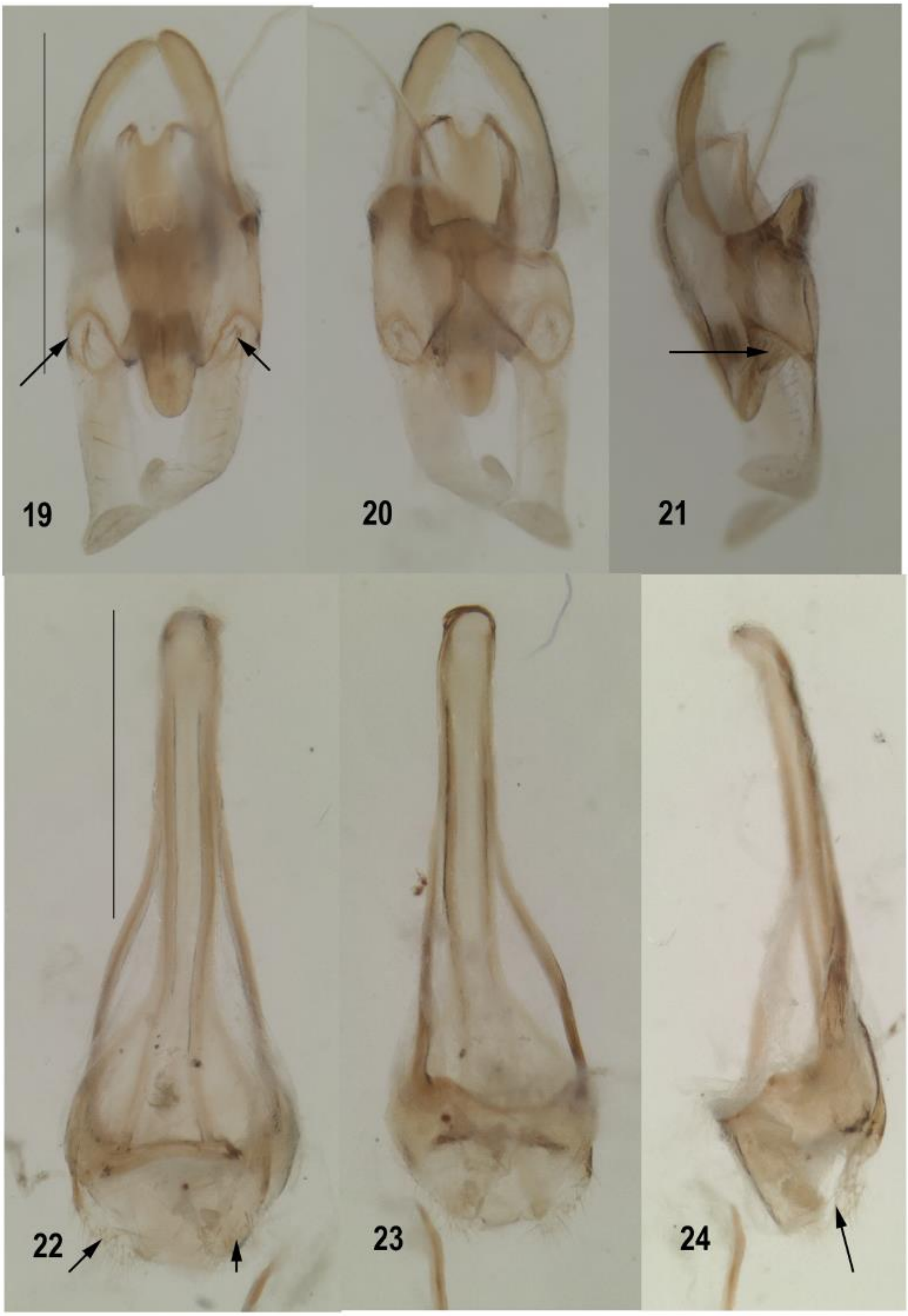
Length: 9.2−10.3 mm long. Macropterous and taken in flight. Coloured as for male except for white LO in V6 only and V7, 8 pale coloured; V7 may have narrow darker marking in anteromedian area and the darker anterior apodeme of V8 may be visible through the transparent cuticle (e.g. Figures 5.27, 5.30, 5.33). Abdomen: LO occupying all of V6 only. Reproductive system differs little from what has been described elsewhere. An elongate vagina leads into a muscular bursa which may or may not be expanded (Figures 5.36–37 show muscular striations). Just behind the bursa is the median oviduct (no median oviduct plates were detected). The bursa bears at its anterior end a thinner walled digesting gland, and towards its posterior end a stalked spermatheca which has an expanded base (Figures 5.35–36). In some cases these may attain similar size (possibly due to immersion in water during dissection) and it may be difficult to determine which is which e.g. Ballantyne & Lambkin (2006 fig 37) indicated the spermatheca and digesting gland of essentially equal size. In this species a large spermatheca was observed but whether this was due to immersion in water or not is not clear. There are two long slender needle shaped bursa hooks projecting either forwards or backwards and lying free in the bursa cavity, with the point of attachment to the bursa wall at their junction (Figures 5.34−37). Both curve slightly inwards at their apices but their exact method of functioning within the bursa, and how it relates to a spermatophore, is not entirely clear. The posterior ‘plates’ may ensure the spermatophore is held within the bursa.

Table 5.2: Collection areas for *Pygoluciola dunguna* **sp. nov.**

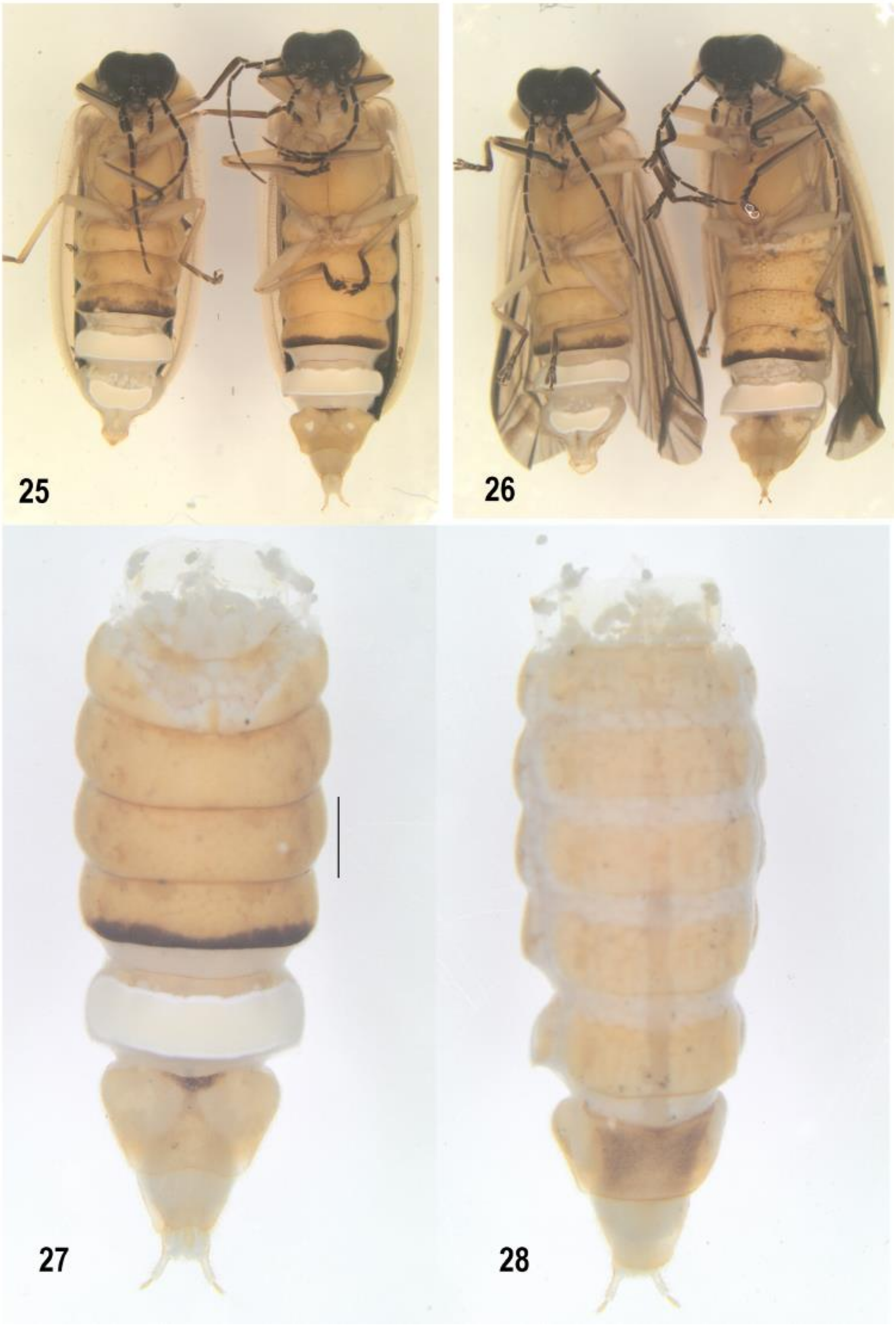
Location (Compartment number)	Forest ID.	Number of collections
Bukit Kutu	BK400	1
Bukit Kutu	BK600	1
Gunung Liang	GL350	1
Besul (10)	B10	3
Besul (19)	B19	7
Hulu Terengganu Tambahan (27)	UTT27	5
Jengai (40)	JI40	2
Jengai (52)	JI52	2
Jerangau (99)	JU99	5
Jerangau (100)	JU100	1
Pasir Raja Barat (87)	PB87	9

5.4.2.5. Ecological information

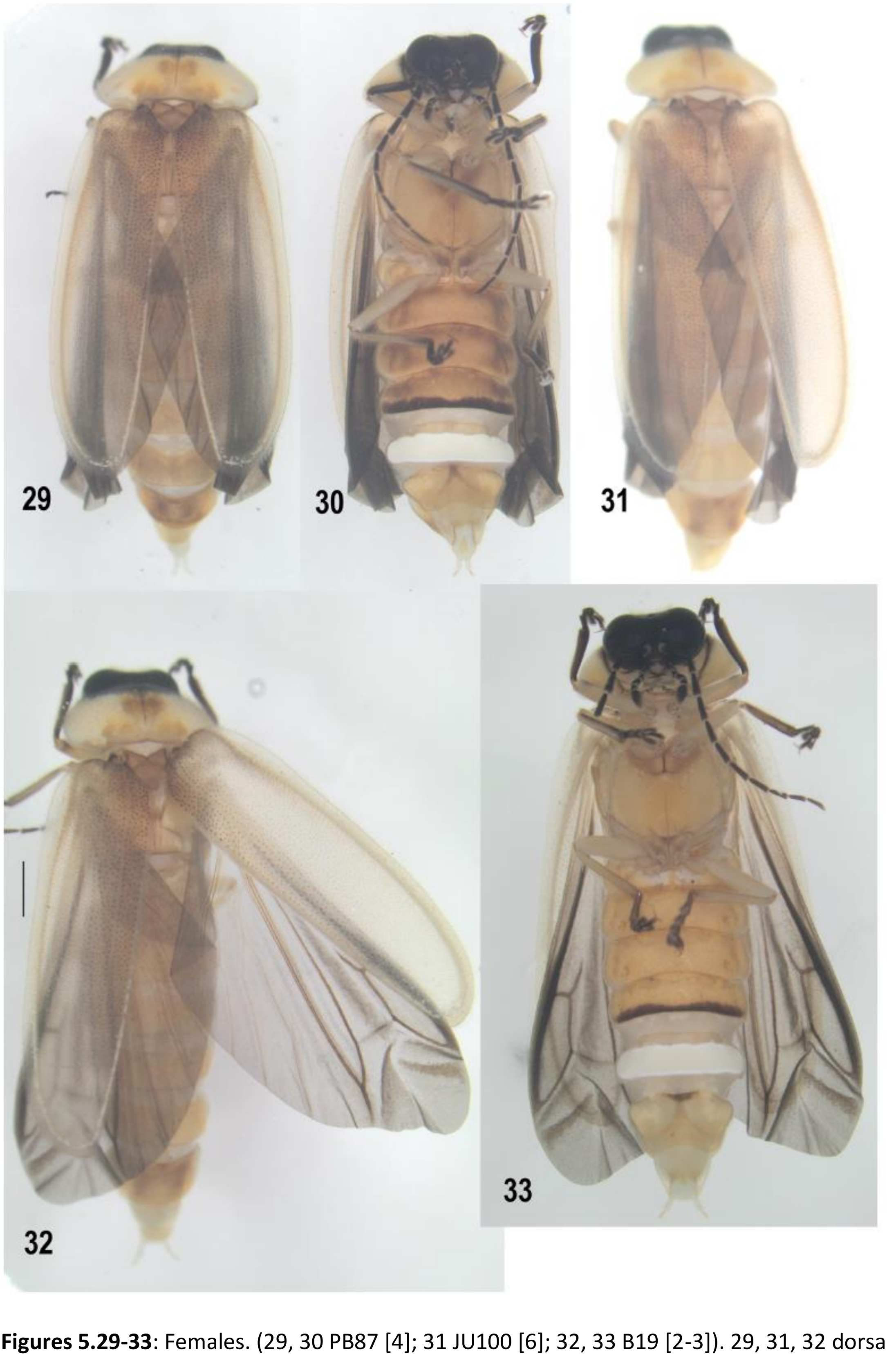
Pygoluciola dunguna **sp. nov.** is present in forested areas where shallow streams flow. The streams were less than 30 cm deep and 3−10 m wide. All the streams have small rocks and sandy edges. They were found mainly flying among the undergrowth of the forest, 10−15 meters above ground. On frequent occasions, the females were collected apparently resting on herbaceous plants. Pairs of *P. dunguna* **sp. nov.** were also collected while mating on stems or leaves of undergrowth.



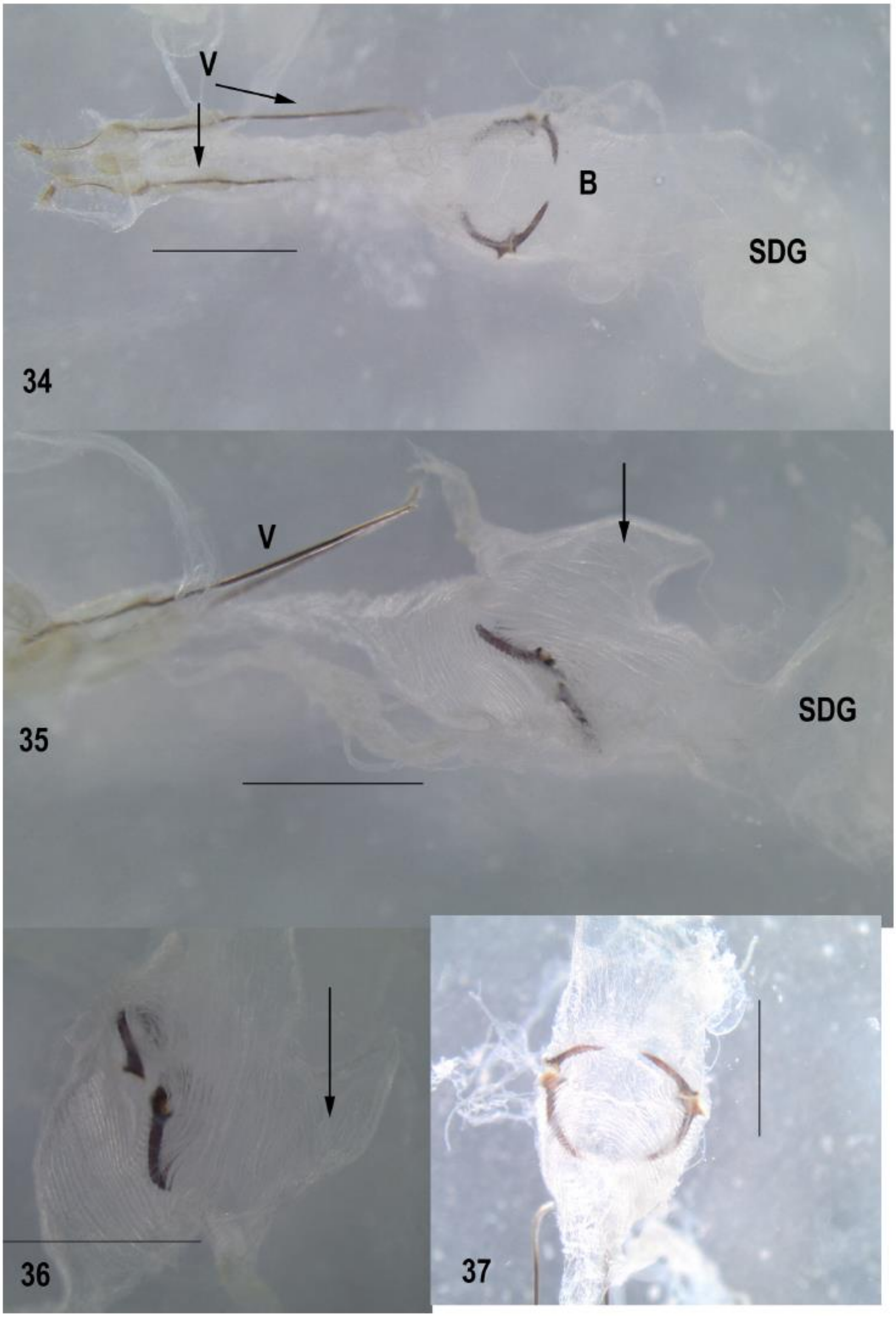
Figures 5.19–24: 19−21 Aedeagus 19 ventral; 20 dorsal; 21 left lateral (hairy lobes on LL arrowed). 22−24 aedeagal sheath 22 ventral (position of bulbous apical lobes arrowed); 23 dorsal; 24 right lateral, hairy lobes arrowed. Scale lines are 1 mm.



Figures 5.25–28: Ventral aspect, mating pairs, male to left (25 JI40 [8], 26 B10 [gap 5-6]). 27, 28 dissected abdomen, anterior end to top of page (B19 [2-3]) 27 ventral; 28 dorsal. Scale line is 1 mm.



Figures 5.29-33: Females. (29, 30 PB87 [4]; 31 JU100 [6]; 32, 33 B19 [2-3]). 29, 31, 32 dorsal; 30 33 ventral. Scale line is 1 mm.



Figures 5.34−37: Female reproductive system (B19 [2-3[). 34 system without ovaries, ovipositor to left and digesting gland to right, from above; 35 as for 34 from side expanded base of spermatheca arrowed; 36 detail bursa and expanded base of spermatheca (arrowed); 37 bursa in area of bursa hooks from above. Figure legend: B = bursa; SDG = spermatophore digesting gland; V = valvifers of the ovipositor. Scale lines are 1 mm.

5.5. Discussion

From both focal study areas, it can be concluded that *P. dunguna* **sp. nov**. has a distribution within elevations of 90 m–630 m a.s.l. Sampling of fireflies from 650 m a.s.l. to 1,900 m a.s.l. did not produce any *P. dunguna* **sp. nov.** The altitudinal range of this species lies between two types of tropical forest formations, i.e. the lowland dipterocarp forest (0−330 m a.s.l.) and hill dipterocarp forest (330−800 m a.s.l.) (Whitmore, 1984). In the lowland dipterocarp forest, they were found in unlogged as well as in forests of different age after logging (Table 5.3). This might not indicate their adaptiveness to changes of their natural habitat caused by logging. However adults were found from 0–700 m from shallow streams, which could possibly indicate a priority for the presence of flowing water bodies as breeding areas albeit within a pristine or disturbed forests.

Table 5.3: Localities of *Pygoluciola dunguna* **sp. nov.** showing habitat types.

Location (Compartment number)	Elevation (m a.s.l.)	Forest type
Bukit Kutu	400	Hill dipterocarp forest
Bukit Kutu	600	Hill dipterocarp forest
Gunung Liang	350	Hill dipterocarp forest
Hulu Terengganu Tambahan (27)	630	Hill dipterocarp forest
Jerangau (100)	100	Lowland dipterocarp forest
Besul (19)	70	>26 years after logging
Jerangau (99)	100	>26 years after logging
Jengai (52)	100	16−25 years after logging
Besul (10)	320	0−5 years after logging (second rotation)
Jengai (40)	90	0−5 years after logging (second rotation)
Pasir Raja Barat (87)	160	0−5 years after logging (second rotation)

During the field sampling, firefly larvae were collected in these shallow streams (Figure 5.40). All these larvae (n = 55) were collected at 0 to 200 m from where the *P. dunguna* **sp. nov.** were found suggesting a possible association. Only through laboratory rearing (Ballantyne & Menayah, 2002) or DNA identification (Jusoh et al., 2014) would we be able to associate these two life stages reliably.

Figure 5.40: One of the larvae found crawling on the surface of sandy edges of shallow stream suggesting riparian rather than aquatic behaviour. They were found abundant in areas where *P. dunguna* **sp. nov.** adults were collected.

Within the Luciolinae few females have thus far been investigated as previous treatments dealt with dried pinned specimens, and few collections provide reliably associated females as in the current study. This species is investigated from freshly collected specimens. All females of *Pygoluciola* thus far investigated have paired hooks in the bursa. The configuration of bursa plates in this species differs somewhat from that seen in other species. There are two long slender needle shapes projecting either forward or backward and lying free in the bursa cavity, with the point of attachment to the bursa wall at their junction. Both curve slightly inwards at their apices but their exact method of functioning within the bursa, and how it relates to a spermatophore, is not entirely clear. The posterior 'plates' may ensure the spermatophore is held within the bursa. In *P. qingyu* the bursa has three slightly hooked, short and thick arms, one pointing forward, the longest backwards, and the shortest inwards, with attachment to the bursa wall at the junction of all three (Fu *et al.* 2008: 27, fig 22). *P. guigliae* has anteriorly directed hooks with one point of articulation only (Ballantyne and Lambkin, 2006 fig 37). In the abdomen of dried pinned specimens of *P. satoi* the only part of the reproductive system visible were paired, anteriorly directed bursa hooks (Ballantyne, 2008 fig 7).

Certain modification of the terminal abdomen in dried pinned female specimens of some *Pygoluciola* may be a consequence of dehydration and not reflect the situation in living specimens. Muscles attach onto the internal apodeme which arises from the anterior margin of V8 and extends anteriorly beneath the light organ in V6. Other sets of muscles attach onto the two elongate valvifers of the ovipositor, and all attach, at least in part, to the sides of the vagina, and their contractions help expand the vagina during egg laying.

In dried pinned specimens of *P. kinabalua*, this can result in an apparent 'hole' in the median area at the base of V7 (Ballantyne & Lambkin 2001 figs 16, 17). However dehydration does not necessarily explain other female modifications seen in this species. The posterior margin of V7 is deeply emarginated and there is a transverse ridge just anterior to the emargination. Additionally the anterolateral margins of V7 are produced and appear slightly hooked. *P. kinabalua* pinned females also have a distinct 'mound' on the dorsal surface of T7 which may be caused by a bursa with one, or more, spermatophores (Ballantyne and Lambkin, 2001 figs 18, 19).

Ballantyne & Lambkin (2001) suggested the possibility that the extreme abdominal modifications seen in *Pygoluciola* where tergite 8 and ventrite 7 are prolonged and may curve around each other, plus some of the modifications of females discussed above, might suggest the presence of a copulation clamp. Subsequently this was dismissed as more information became available about the functioning of a copulation clamp in two species of *Pteroptyx*, as well as internal female reproductive anatomy. A clamp in both *Pteroptyx valida* and *Pt. maipo* involves deflexed elytral apices of the male pressing down on the flattened and expanded dorsal surface of the MPP of ventrite 7 (Ballantyne et al., 2011). Ballantyne (1987) indicated that many of the modifications seen at the end of the abdomen in Luciolinae males could be explained as increased surface area for muscle attachment, and were not of copulatory significance but a consequence of the need for surface areas for longitudinal muscle attachment probably brought about by the loss of V8.

5.6. Summary

A new species of firefly, *Pygoluciola dunguna* **sp. nov.** was described from specimens collected during an elaborate field sampling made in logged and unlogged forests of Peninsular Malaysia. Not only is this a new record of the genus for Peninsular Malaysia but the species is unusual among *Pygoluciola*. It seemed to be an intermediate form between the two morphological types of *Pygoluciola* so far described and the configuration of the bursa plates in this species differ from that seen in other species. Within the Luciolinae few females have thus far been investigated as previous treatments dealt mainly with dried pinned specimens, and few collections provided reliably associated females as in the current study. This new species was found to be restricted to the elevations of under 650 m a.s.l. and could have a priority for the presence of flowing water bodies. During the field sampling, a type of firefly larva ($n = 55$) was collected in shallow streams located within proximity of adults of *P. dunguna* **sp. nov.** suggesting a possible association. Future DNA identification or laboratory rearing would enable reliable associations between the two life stages.

CHAPTER 6

Discussion and Summary

6.1. Introduction

In spite of the continuing interest in the drivers behind the high species diversity observed in the tropical forests, many species groups, and in particular the invertebrates (Ballesteros-Mejia et al., 2013; Dunn, 2005; McKinney, 1999), are still poorly studied (Ballesteros-Mejia et al., 2013; Jetz et al., 2012; Magurran, 2017). Obtaining knowledge and understanding of species diversity of invertebrates is vital because of their role in numerous ecosystem services such as pollination and as food for numerous larger taxa. Invertebrate biodiversity research is important in light of their functions and continued threats from climate change and anthropogenic modification (Abdullah & Hezri, 2008; Achard et al., 2002; Kuussaari et al., 2009; Lawrence & Vandecar, 2015; Wright, 2005).

In this thesis new methods for estimating species richness and diversity was applied to assess whether logging history and elevation influence several habitat factors driving variation in firefly biodiversity. The solitary fireflies of the Malaysian lowland tropical forests was the focus of this study. On contrary to the aggregative fireflies, this group typically present in low abundance across many habitat types but has potentially high diversity.

Fireflies have diverse ecological requirements to complete their lifecycle. Key features of the landscape important to them include leaf litter and water for egg laying and larval growth and foraging, and understory and copy structure for foraging and courtship by adults. They are either aquatic, semi-aquatic or terrestrial as larvae. As adults, they are dependent on availability of trees and plants for displaying their light communications, while some would move around in flight, displaying their lights in order to attract mates. Flightless females and terrestrial larvae occur on forest floor where leaf litter, undergrowth and crevices of the ground are their refuge areas. The larvae prey on snails, slugs and earthworms; while the females with terrestrial larvae oviposit their eggs within these areas.

This study has managed to identify the influence of habitat features that are closely associated with firefly and estimated the effect size of these variables on the firefly species richness and the firefly community composition. Canopy closure, leaf litter depth and understorey height were measured in both the logged forest and elevational forest studies. Number of water bodies and proximity to unlogged/primary forest were recorded in the logged forest study, while the number of trees with DBH of more than 40 cm was recorded in the firefly in elevational forest study.

Logging has been and continues to be a significant modifier of the Malaysian tropical forest landscape. Over the past 100 years, logging has changed from clear felling to more sustainable selective logging approaches and even second rounds of logging on some compartments. The result is a patchwork of logging history ranging from primary, untouched forests to recently logged forests through to forests logged decades ago. Such variation in logging history leaves a signature on the habitat with various stages of secondary forest regeneration and associated patterns of leaf litter, water access and forest structure. In this thesis, focus was specifically made in assessing how time since last logging and associated habitat characteristics influenced solitary firefly diversity.

Furthermore, the history of logging and agricultural expansion over the past few decades means that mountain areas, with potentially difficult access for forestry, can often be refuges for certain types of forests. Intrinsic variation in forest types associated with elevation and climate result in distinctive forest types with unique habitat characteristics. The study of species diversity along elevation gradients has a long history in conservation ecology. In this thesis, specific assessment was made on how habitat characteristics that change with forest types along the elevation gradient influenced solitary firefly species diversity.

In the following sections the outcome of the research conducted was reviewed. Firstly, the accuracy and precision of iNEXT (Hsieh et al., 2016), a new statistical framework for analysing species diversity, applied to fireflies, a low abundance taxon was reviewed. A review was made for the assessment of habitat characteristics on firefly diversity in both the logging history and elevation study. Specific evidence about forest age (time since logging) and elevation per se on firefly species diversity were also reviewed. Limitations of current study was also discussed. Finally, the prospect for finding new species of fireflies, extending from this work was suggested.

6.2. Reliable estimation of species richness and diversity of fireflies

iNEXT is a newly developed statistical framework for estimating species richness and species diversity. It advances current methods by integrating Hill numbers with rarefaction/extrapolation and standardisation based on sampling completeness. This framework has been used to estimate species diversity for large samples of highly abundant and diverse groups. As part of this work, I aimed to identify if this statistical framework is able to perform equally well for low abundance taxa including the tropical forest fireflies.

The performance of a species diversity estimator can be assessed by its accuracy and precision. In order to do this, data of fireflies were collected from two major forest types representing the inland tropical forest of Peninsular Malaysia: among 274 transects within five types of climatic forest formation across elevations (lowland dipterocarp; hill dipterocarp; upperhill dipterocarp; oak laurel and montane ericaceous); and within five categories of forest in lowland dipterocarp logging concession (unlogged and 0-5; 6-15; 16-25; and >25 years after logging).

The accuracy of the iNEXT method was assessed using cross-validation, also known as a leave-one-out approach. The absolute value of the difference between the estimated species richness/diversity projected by iNEXT and the observed species richness of fireflies from the left out transect was taken as a measure of accuracy, known as the mean absolute error (MAE). The precision of iNEXT estimations were measured based on the standard error (SE) values generated by iNEXT calculations at the asymptotic sections of the sample-size-based rarefaction/extrapolation curves. The MAE and SE values were scaled for the purpose of comparing the estimates of the firefly species diversity across different forest types.

The results showed that iNEXT was able to accurately predict species richness evidenced by a small range of the MAE values (Figure 2.3, page 33). The precision of estimations were, however, low, especially in estimating species richness of the fireflies (Figure 2.4, page 35). Importantly, the accuracy and precision of iNEXT species richness/diversity estimates did not vary appreciably across elevation bands representing different forest types or among different age classes of forests after logging. These findings suggest that iNEXT can be a reliable estimator of species richness and species diversity for low abundance, low diversity taxa.

6.3. Habitat characteristics affecting the firefly community composition and diversity

Fireflies have diverse ecological requirements to complete their lifecycle. They are known to be aquatic, semi-aquatic or terrestrial as larvae. As adults they are dependent on availability of trees and plants for displaying their light communications, while some would move around in flight, displaying their lights in order to attract mates. Flightless females and terrestrial larvae occur on forest floor where leaf litter, undergrowth and crevices of the ground are their refuge areas. The larvae prey on snails, slugs and earthworms; while the females with terrestrial larvae oviposit their eggs within these areas.

Firefly species diversity in forest compartments of differing ages after logged were estimated using iNEXT analysis framework. These estimations were analysed as a function of time since logging and habitat characteristics. The analysis combined the use of statistical significance testing and evaluation of effect sizes to estimate the importance of various habitat characteristics on firefly species diversity and richness. In order to estimate the influence of the habitat characteristics on firefly community composition, a multivariate analysis of abundance using a model-based approach was implemented. This approach is advantageous in comparison to the more commonly used distance-based approaches (e.g. beta diversity methods) as it models abundance explicitly and enables statistical inference about how multiple habitat characteristics can combine to influence community structure (Yi Wang et al., 2012).

Canopy closure and leaf litter depth were found to have large effect size on firefly species richness in both logged forests and in forest across elevations (Figure 3.3, page 59 and Figure 4.6, page 92). Distance to primary forest was found to have the largest effect size on firefly species richness and species diversity for forests that were previously logged (Figure 3.3, page 59). The effects of distance to primary forests, canopy closure and leaf litter depth were significant on firefly species richness in logged forests (Appendix Table 3.5, page 182). However, the effect sizes of canopy closure and leaf litter depth on species richness of the fireflies were not statistically significant in the forests across elevations (Table 4.4, page 92). The low abundance and detectability of the firefly species were likely the reasons for the limitations of the analysis to reveal associations that likely existed, i.e. large effect sizes with large p-values suggest a sample size issue.

The firefly community composition in logged forests was found to be significantly influenced by leaf litter depth and the number of water bodies (Table 3.2, page 60). Changes in firefly species abundance were most noticeable for the firefly species of *Curtos costipennis*, *Pygoluciola dunguna*, *Diaphanes* sp.1 and *Colophotia brevis*. I was unable to detect any influence of the habitat characteristics on firefly community composition in the elevational forests. This is probably due to the uneven distribution of several habitat characteristics, namely canopy closure, understorey height and leaf litter depth. Only a few locations sampled along the mountains had low percentages of canopy closure and low understorey height, and high leaf litter depth (Figure 4.5, page 91). Future work in other mountains on the Banjaran Titiwangsa mountain range would better resolve the patterns of associations between the fireflies and the habitat characteristics.

The firefly community composition in logged forests was found to be significantly influenced by leaf litter depth and the number of water bodies (Table 3.2, page 60). Changes in firefly species abundance were most noticeable for the firefly species of *Curtos costipennis*, *Pygoluciola dunguna*, *Diaphanes* sp.1 and *Colophotia brevis*. The influence of the recorded habitat characteristics on firefly community composition in the elevational forests was unable to be detected probably due to the data distribution of several habitat characteristics namely canopy closure, understorey height and leaf litter depth. Only a few locations sampled along the mountains had low percentages of canopy closure and low understorey height, and high leaf litter depth (Figure 4.5, page 91). Future work in other mountains on the Banjaran Titiwangsa mountain range would better resolve the patterns of associations between the fireflies and the habitat characteristics.

6.4. Logging effects on firefly diversity

Forest conversions to agricultural land and human settlements place pressures on remaining forested land to supply the growing demand for timber (Abdullah & Hezri, 2008; Phalan et al., 2013; Sist et al., 2014). Peninsular Malaysia experienced forest cover loss at an average of 1,609.1 km^2/ year between 2001 and 2010 and the rate is not expected to decrease in near future, although forest reserves remained relatively intact (Hamid & Rahman, 2016). Consequently, a large proportion of the forest concessions for timber production are being subjected to multiple logging cycles (Blaser et al., 2011), exerting additional pressures. The indirect effects of logging frequently have substantial adverse impacts on biodiversity. These indirect effects, i.e. soil compaction and erosion, increase of temperature and reduced humidity, and increase of canopy openness can be more influential than the direct effects of tree removal (Delgado et al., 2007; F. A. Edwards et al., 2017; Vinson et al., 2015).

Previous studies have shown that logged tropical forests are able to support substantial amount of biodiversity (Clarke et al., 2005; Dunn, 2004; D. P. Edwards, Tobias et al., 2014) and protection of these areas would achieve conservation goals (D. P. Edwards et al., 2011; Ewers et al., 2015). However these studies had relied on assessment of taxonomic groups that are considerably easy to study, occur in high abundance and taxonomically well described, e.g. birds (Hamer et al., 2015; Rajpar &

Zakaria, 2014a; Yap et al., 2007), butterflies (Hamer et al., 2003; Nyafwono et al., 2014) and dung beetles (Bourg et al., 2016; França et al., 2017; T Hosaka et al., 2014).

Despite possible sensitivity of fireflies to habitat changes, inland tropical forest fireflies have not been assessed for their response to habitat changes caused by logging. The analysis encompassed identifying the species diversity of firefly in forests of varying ages after logging and how forests that experienced a second cycle of logging affects the species richness of the fireflies. Firefly species diversity in forest compartments of differing ages after logged were estimated using iNEXT analysis framework. These estimations were later analysed as a function of time since logging.

As above, the significance testing and evaluation of effect sizes were conducted. The effect of once vs. twice logging on species diversity of fireflies was analysed using an analysis of covariance (ANCOVA). Due to constrained sample size, each habitat characteristics (canopy closure, leaf litter depth, understorey height, number of water bodies and proximity to primary forest) was only added individually to the baseline model, to assess whether it explained additional variations.

Time since logging was found to have a small to medium effect size on species diversity (Figure 3.3, page 59) and these relationships were not found to be statistically significant (Table 3.2, page 60). However the effect of time since logging on firefly species richness varied significantly by number of logging rotations. Species richness of firefly increased with time for once-logged forests, but decreased with time for twice-logged forests (Figure 3.5, page 62). None of the habitat characteristics explained additional variation in this analysis (all p-values were > 0.1). The unexpected interesting phenomenon requires further investigations.

6.5. Fireflies across elevations

Studies of biodiversity along elevations enable the identification of diversity changes associated with changes in habitat as elevation increases. The main variables that alter along elevation gradients are temperature, precipitation and availability of space (Körner, 2007). The analysis of change in diversity across elevation utilise beta-diversity analysis to understand how species composition shifts across spatial scale (Legendre et al., 2005; Tuomisto, 2010). Partitioning the beta-diversity into two additive fractions enables the identification of whether the diversity shifts are associated with species replacement (turnover) or species loss (nestedness) (Baselga, 2010).

Study of diversity across elevational gradients also allows rapid assessment of diversity across varying habitats and this approach is particularly important for understudied taxa with minimal data on species richness and distribution. This is especially true for taxa within the tropical regions that are fast experiencing anthropogenic modifications (Bhardwaj et al., 2012; Veijalainen et al., 2014). Tropical forests at higher elevations tend to be ecologically and evolutionarily different from lowland forests; with large percentage of highly endemic species occurring along elevational gradients of montane environments (Myers et al., 2000). These areas are even more poorly researched than the understudied tropical forests (Malhi et al., 2010).

Understanding species turnover across elevations helps to predict the outcome of climate change towards these groups. Climate change is expected to decrease the biodiversity of species in the tropics, with a high chance of significant species turnover (Cusack et al., 2016). The tropical forest species at higher elevations could face a bigger threat than their counterparts in the temperate regions due to their predicted narrower tolerance and more restricted distributions (Ghalambor et al., 2006; Sheldon et al., 2018).

The solitary fireflies typically occur in low densities and have rarely been studied along environmental gradients including along elevations. Most species of fireflies are highly specialised requiring different microhabitats for their breeding, mating and immature stages. Their dispersal abilities are limited especially for species with flightless females (Fu, South et al., 2012; Jeng et al., 2011; Santos et al., 2016) or for species with aquatic larvae (Ballantyne et al., 2016; Fu, Wang et al., 2005). Fireflies have species-specific light signal patterns (Lewis & Cratsley, 2008; Ohba, 2004) and their light productions have been found to be strongly influenced by ambient temperature, that regulates their flashing signal patterns (Iguchi, 2009, 2010; Sharma et al., 2014). Due to their restricted dispersal abilities and specialised behaviour and habitat, fireflies along elevations could be susceptible to habitat alterations caused by habitat loss and climate change. This study focussed on identifying the biodiversity of the solitary fireflies in different forest types across tropical elevations by combining the analyses of species beta diversity partitioning and multivariate generalised linear model approach.

Five mountains were sampled to represent the main mountain range of Peninsular Malaysia, the Banjaran Titiwangsa (Figure 4.1a, page 81). A total of 110 transects of 80 m in length were sampled extending into five climatic forest formations of the tropical forest (Figure 4.1b, page 81).

The average abundance for each species at 50 m a.s.l. intervals was graphically presented to identify the elevational ranges of the solitary fireflies. As above, a combination of significance testing, effect size evaluation and model-based analysis of community composition were implemented. This was complemented by a formal analysis using modern distance based methods for partitioning beta diversity into two additive fractions to identify turnover and nestedness.

In contrast to the absence of effect of time since logging *per se* on firefly communities, firefly community composition varied significantly with forest type but not with mountain identity (Table 4.2, page 89). The partitioning of the beta diversity suggested the changes of firefly species across elevations were influenced by species replacement rather than species loss (β_{sim}, turnover = 0.89, β_{sne}, nestedness = 0.048, total = 0.94). Solitary fireflies of the tropical forest were found to be restricted to certain elevational ranges and were able to be categorised as i) having a relatively large elevational range, ii) restricted to the upper sections of the mountains or iii) restricted to the lower sections of the mountains (Figure 4.2 and Table 4.1, page 101).

6.6. Improvement to firefly species records and discovery of new species

This study has increased our understanding on the firefly diversity and distribution in tropical forests by targeting to sample fireflies in as many different forest types representing the forest landscapes of Malaysia specifically and the tropical regions, in general. Based on the two fieldworks sessions conducted within the span of two years, 13 species from five genera in Luciolinae, 7 species from two genera in Lampyrinae and 3 species from two genera in Ototretinae subfamilies were recorded. Prior to this work, 19 firefly species were confirmed to occur in Peninsular Malaysia consisting 7 aggregative and 12 solitary species (Jusoh, 2015). The information has now increased to another 17 new species for Peninsular Malaysia, of which 5 are new to science.

Upon further examination of the firefly species collections made from the post-logging and from the elevation studies, eleven firefly species were identified to occur in both studies, i.e. in lowland dipterocarp forests within the Dungun Timber Complex (DTC) and among the five mountains sampled along the Banjaran Titiwangsa mountain range. Seven out of these eleven species showed consistent pattern of being present below 900 m a.s.l. Two species, i.e. *Luciola liang* and *Stenocladius* sp. 1 were found in the lowland dipterocarp forests of the DTC, as well as across elevations of our mountains. Their elevational range were wider, ranging between 300-1,400 m a.s.l and between 200-1,200 m a.s.l., respectively. A contrasting observation was made, however for two species, i.e. the *Curtos costipennis* and *Curtos obscuricolor* as they were only found above 900 m a.s.l. in the elevation study; but were found in the lowland dipterocarp forests of the DTC (elevations below 300 m a.s.l.). Therefore further research is needed to decipher the habitat requirements and differences observed for these species.

One of the five new species of fireflies discovered from this study was described in detail (Nada & Ballantyne, 2018). The chapter describes the taxonomic characters of the new species, *Pygoluciola dunguna* and details of its habitat and distribution based on collections made in the post-logging and the elevation studies. This species was one of the fireflies that did not occur above 900 m a.s.l and it was recorded to be between 90-630 m a.s.l. The collections made for this species were vast from this work, although prior to this study, the genus was considered to be rare due to the limited collections representing this genus (Ballantyne, 2008; Ballantyne & Lambkin, 2006).

We were also able to collect two pairs of mating *P. dunguna* therefore strong association of the females and the males was established, enabling reliable taxonomic description of the females. Such associations are seldom achieved for fireflies as most taxonomic description relied on male specimens.

6.7. Limitations of current study

Although considerable amounts of information on firefly species diversity and community structure in different forest types were gained from this study, several limitations are recognised. The low abundance and detectability of firefly species are probably the main reason limiting our ability to reveal associations that likely do exist. In contrast to many other studies of invertebrates across elevations (Bhardwaj et al., 2012; Carneiro et al., 2014b; Chamberlain et al., 2015), we were unable to detect strong statistical associations with habitat characteristics across elevational gradients that were hypothesized to be important to fireflies. However, substantial effect sizes of forest type and canopy closure suggest that these factors are important and that we likely lacked the power to detect significant relationships. For example, during the post-logging study, ten of the sixteen species collected consist of 1 or 2 individuals per compartment. Only five species had a collection of 3 or more individuals per compartment (mean: 5.6 individuals). Increasing sample sizes is, however, incredibly challenging given the landscape and the sparse distribution of the fireflies.

The firefly sampling method employed in this study captured a range of fireflies that are terrestrial, possible semi-aquatic and diurnal. Individuals occurring in three vertical stratifications of the tropical forest, i.e. ground layer, shrub and herb layer and lower canopy layer were collected via our method. It was not however sufficient to capture information of fireflies that were high flying more 5 m above ground or occurring in tree canopies. During the field sampling, fireflies were observed to be stationary on tree canopies while emitting their light flashes.

The firefly larvae collected in this study were not conclusively assigned to a species because taxonomic association of the adults and the larva of fireflies are limited.

A total of eight types of larvae were assigned to morphospecies. These details were not included in the analysis due to inconclusive association to species level. The reason for this is most firefly larvae do not have distinct morphological characteristics to enable them to be taxonomically identified to species unless after being reliably associated with a known male (Ballantyne & Lambkin, 2013; Ballantyne et al., 2015).

6.8. Prospects of future firefly diversity study in Malaysia

This is one of the first and most quantitative assessments of solitary fireflies conducted within the country. Previous research had focused on field sampling to increase discovery of species and expanding numbers in one's collection, termed "museum collecting" by Coddington et al. (1991) or specific to a species of interest for further in depth study, e.g. *Pteroptyx tener* in Malaysia (Case, 1980; Jusoh et al., 2013; Khoo et al., 2012) and aquatic fireflies in China (Fu, South et al., 2012; Fu, Wang et al., 2005; Ho et al., 2010). These approach would neglect a sampling design that could enable important information to conservation of biodiversity such as to estimate relative abundance or estimation of how many more to be discovered (Coddington et al., 1991; Longino & Colwell, 1997).

Methods of sampling in previous firefly biodiversity studies were not standardized across sites either in terms of duration, replication or area of coverage (Sartsanga et al., 2018; Viviani, 2001; Wattanachaiyingcharoen et al., 2016). This could hinder further exploration into understanding how a community changes across temporal and spatial scales (Coddington et al., 1991). Sampling in a standardised and systematic manner would assist in increasing the accuracy of estimating species of a community and minimise bias caused by different sampling intensity and approach (Longino & Colwell, 1997). Therefore it is timely to consider a standardised sampling protocol of fireflies especially in the tropical forests where much is still not understood although pressure of extinction and habitat loss are happening at an alarming rate. For other faunal groups i.e. birds, bats and dung beetles, their sampling protocol are applicable to various habitat types, e.g. point counts for birds, mist nets for bats and baited pitfall traps for dung beetles (Brosset et al., 1996; Hyvärinen et al., 2006; Larsen & Forsyth, 2005; Loos et al., 2014). The sampling protocol of fireflies detailed out in this study could have the potential of being extended to other habitats in future studies.

Most taxonomic identifications are based on adult males and conclusive association of larvae were only through *ex-situ* breeding or DNA confirmation (Ballantyne & Menayah, 2002; Fu, Ballantyne et al., 2012b). DNA barcoding has been shown to be effective tool to corroborate species identification of females and larvae of the mangrove fireflies (Jusoh et al., 2014) and future research could utilise this tool to link and confirm the species of the larvae and females collected from current study. At present, I am working in collaboration with a firefly researcher in National University of Singapore to explore the possibilities of associating the females and larvae of several firefly species collected including, the new species of firefly described from this study, the *Pygoluciola dunguna*.

6.9. Summary: New knowledge of solitary firefly diversity in Malaysia

1. Fireflies are understudied and more emphasize can be given to research and identify species diversity and environmental factors moderating their biodiversity.
2. The potential to discover more species of fireflies are high. The current study has substantially increased information on firefly species and the discovery of new species.

3. Independent of elevation or time since logging, canopy closure, leaf litter depth and presence of water bodies are effective habitat parameters to be measured in relation to firefly diversity. The availability of this abiotic parameters are important for the different firefly species, either terrestrial, semi-aquatic, or aquatic and help reveal patterns of community composition associated with habitats modified by logging or associated with elevation gradients.
4. Solitary Malaysian firefly community composition varies by elevation but does not vary by time since logging, per se. It is suggested that habitat characteristics, and not time since logging, drive firefly diversity in logged-over forests.
5. Proximity to primary forests could aid in firefly species recovery of habitats that have experienced disturbance.

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Appendices

Appendix Table 2.1: Information of mountains and forest types sampled

Mountain	Latitude, Longitude	Summit height (m a.s.l.)	Elevation range sampled (m a.s.l.)	Forest sampled with number of transects	Number of transects
Gunung Liang	3°48'7.38"N, 101°35'27.49"E	1933	250 - 1900	· Lowland dipterocarp -2	34
				· Hill dipterocarp -10	
				· Upper dipterocarp -8	
				· Oak laurel -6	
				· Montane ericaceous -8	
Bukit Kutu	3°32'31.65"N, 101°43'13.29"E	1051	200 - 1000	· Lowland dipterocarp -1	15
				· Hill dipterocarp -10	
				· Upper dipterocarp -4	
Gunung Nuang	3°15'59.94"N, 101°54'0.72"E	1459	200 - 1300	· Lowland dipterocarp -3	23
				· Hill dipterocarp -10	
				· Upper dipterocarp (8) -8	
				· Oak laurel (2) -2	
Gunung Besar Hantu	3°13'37.08"N, 102° 0'45.39"E	1409	250 - 1350	· Lowland dipterocarp -2	23
				· Hill dipterocarp -10	
				· Upper dipterocarp -8	
				· Oak laurel -3	
Gunung Berembun	2°48'10.55"N, 102° 3'21.74"E	1057	300 - 1000	· Lowland dipterocarp -1	15
				· Hill dipterocarp -10	
				· Upper dipterocarp -4	

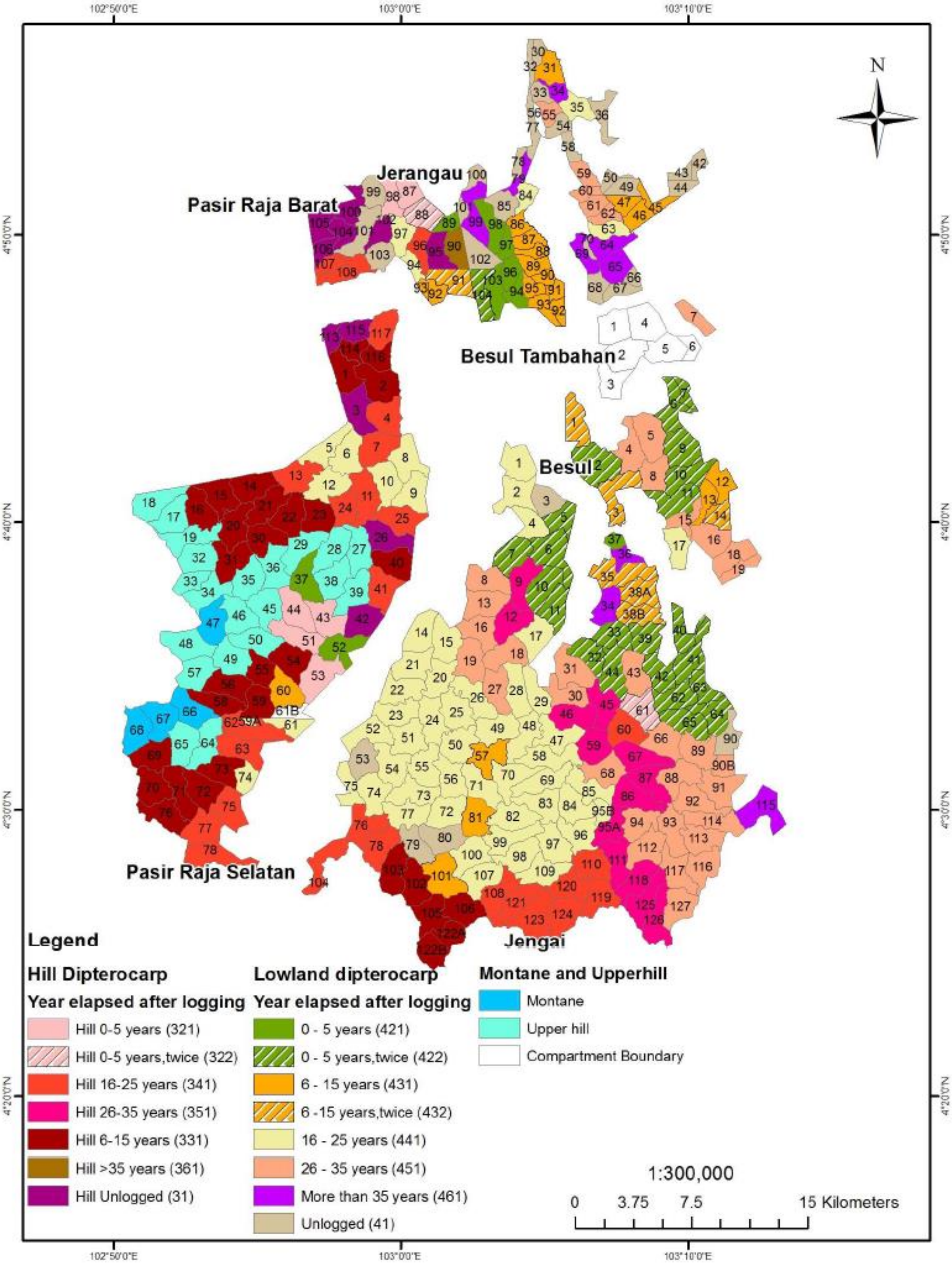
Appendix Table 2.2: Firefly species recorded in this study

No.	Subfamily	List of species	Collection made		New record		
			Elevational study	Post-logging study	For science	For Malaysia	For Peninsular Malaysia
1	Lampyrinae	*Diaphanes* sp. 1	●	●			●
2	Lampyrinae	*Diaphanes* sp. 2	●	●			●
3	Lampyrinae	*Pyrocoelia analis*		●			
4	Lampyrinae	*Pyrocoelia fumigata*	●	●			
5	Lampyrinae	*Pyrocoelia* sp. 1	●				
6	Lampyrinae	*Pyrocoelia* sp. 2	●	●			
7	Lampyrinae	*Pyrocoelia* sp. 3	●	●			
8	Luciolinae	*Abscondita berembun*	●		●	●	●
9	Luciolinae	*Abscondita jerangau*		●	●	●	●
10	Luciolinae	*Abscondita pallescens*	●	●		●	●
11	Luciolinae	*Colophotia brevis*	●	●		●	●
12	Luciolinae	*Curtos costipennis*	●	●		●	●
13	Luciolinae	*Curtos obscuricolor*	●	●		●	●
14	Luciolinae	*Curtos* sp. 1	●				●
15	Luciolinae	*Curtos* sp. 2		●			●
16	Luciolinae	*Curtos* sp. 3	●				●
17	Luciolinae	*Luciola liang*	●	●	●	●	●
18	Luciolinae	*Luciola pallidipes*	●			●	●
19	Luciolinae	*Luciola tiomana*		●	●	●	●
20	Luciolinae	*Pygoluciola dunguna*	●	●	●	●	●
21	Ototretinae	*Drilaster* sp.	●				
22	Ototretinae	*Stenocladius* sp. 1	●	●		●	●
23	Ototretinae	*Stenocladius* sp. 2	●			●	●
		Total species:	19	16	5	12	17

Appendix Table 3.1: Information of the forest compartments sampled in Dungun Timber Complex (DTC)

No.	Forest Block	Compartment ID.	Logging status	Area (ha)	Year of logging		Age after logging		Number of transect
					1st rotation	2nd rotation	1st rotation	2nd rotation	
1	Besul	12	Once	273.2	2006	None	10	None	6
2	Besul	17	Once	322.7	1992	None	24	None	17
3	Besul	18	Once	354.3	1984	None	32	None	6
4	Besul	19	Once	169.7	1986	None	30	None	6
5	Besul Tambahan	7	Once	228.1	1984	None	32	None	4
6	Hulu Terengganu Tambahan	35	Once	87.5	2014	None	2	None	6
7	Hulu Terengganu Tambahan	41	Once	233.3	2014	None	2	None	5
8	Jengai	4	Once	298.9	1993	None	23	None	11
9	Jengai	52	Once	394.3	1996	None	20	None	5
10	Jengai	64	Once	379.4	1985	None	31	None	6
11	Jerangau	93	Once	189.6	2010	None	6	None	16
12	Jerangau	31Y	Once	234.0	2005	None	11	None	11
13	Jerangau	31N	Once	61.0	1975	None	41	None	11
14	Pasir Raja Barat	87	Once	268.4	2011	None	5	None	12
15	Pasir Raja Selatan	52	Once	388.5	2011	None	5	None	9
16	Besul	3	Twice	445.3	1980	2006	36	10	6
17	Besul	10	Twice	392.1	1984	2014	32	2	11
18	Besul	14	Twice	229.8	1980	2006	36	10	6
19	Jengai	39	Twice	358.7	1985	2015	31	1	6
20	Jengai	40	Twice	305.1	1983	2013	33	3	10
21	Jengai	42	Twice	354.3	1983	2013	33	3	6
22	Jengai	38B	Twice	348.9	1980	2006	36	10	11
23	Jerangau	68	Twice	210.4	1970	2001	46	15	9
24	Hulu Terengganu Tambahan	27	Unlogged	327.7	None	None	None	None	11
25	Jerangau	100	Unlogged	141.6	None	None	None	None	11
26	Pasir Raja Selatan	26	Unlogged	418.9	None	None	None	None	11

Appendix Figure 3.1: Compartments in Dungun Timber Complex according to groups of ages after logged.



Appendix Table 3.2: Information on the compartments analysed in identifying possible influence of logging rotations on firefly species richnes

No.	Forest Block	Compartment ID.	Area (ha)	Logging status	Age after logging		Transect information		
					Previous	Latest	Total	Collection n = 0	Percentage transect n = 0
1	Hulu Terengganu Tambahan	35	87.5	Once	Unlogged	2	6	2	33.3
2	Hulu Terengganu Tambahan	41	233.3	Once	Unlogged	2	5	5	100.0
3	Pasir Raja Barat	87	268.4	Once	Unlogged	5	12	6	50.0
4	Pasir Raja Selatan	52	388.5	Once	Unlogged	5	9	6	66.7
5	Jerangau	93	189.6	Once	Unlogged	6	16	11	68.8
6	Besul	12	273.2	Once	Unlogged	10	6	5	83.3
7	Jerangau	31Y	234.0	Once	Unlogged	11	11	5	45.5
8	Jengai	52	394.3	Once	Unlogged	20	5	2	40.0
9	Jengai	39	358.7	Twice	31	1	6	3	50.0
10	Besul	10	392.1	Twice	32	2	11	5	45.5
11	Jengai	40	305.1	Twice	33	3	10	6	60.0
12	Jengai	42	354.3	Twice	33	3	6	5	83.3
13	Besul	3	445.3	Twice	36	10	6	1	16.7
14	Besul	14	229.8	Twice	36	10	6	5	83.3
15	Jengai	38B	348.9	Twice	36	10	11	10	90.9
16	Jerangau	68	210.4	Twice	46	15	9	7	77.8

Appendix Table 3.3: Post-logging study collections. Information on the number and percentage of collections; and information on the number and percentage of compartments for individual species.

No.	Subfamily	List of species	Unlogged compartments (n = 3)		Once logged compartments (n = 15)		Twice logged compartments (n = 8)		All compartments (n = 26)			
			Number of compartment	Number of collections	Number of compartments	Number of collections	Number of compartments	Number of collections	Number of compartments	Number of collections	Percentage of compartments	Percentage of collections
1	Lampyrinae	*Pyrocoelia* sp. 2	0	0	0	0	1	1	1	1	3.85	0.33
2	Lampyrinae	*Pyrocoelia* sp. 3	0	0	1	1	0	0	1	1	3.85	0.33
3	Luciolinae	*Curtos obscuricolor*	0	0	1	1	0	0	1	1	3.85	0.33
4	Luciolinae	*Luciola tiomana*	0	0	1	1	0	0	1	1	3.85	0.33
5	Lampyrinae	*Diaphanes* sp. 2	0	0	1	2	0	0	1	2	3.85	0.67
6	Lampyrinae	*Pyrocoelia analis*	0	0	2	2	0	0	2	2	7.69	0.67
7	Luciolinae	*Curtos* sp. 2	0	0	1	1	1	1	2	2	7.69	0.67
8	Luciolinae	*Luciola liang*	0	0	2	2	0	0	2	2	7.69	0.67
9	Luciolinae	*Abscondita jerangau*	1	2	1	1	0	0	2	3	7.69	1.00
10	Lampyrinae	*Pyrocoelia fumigata*	0	0	2	2	2	3	4	5	15.38	1.67
11	Ototretinae	*Stenocladius* sp. 1	1	2	3	4	2	3	6	9	23.08	3.00
12	Lampyrinae	*Diaphanes* sp. 1	2	4	4	10	2	2	8	16	30.77	5.33
13	Luciolinae	*Colophotia brevis*	0	0	3	5	2	21	5	26	19.23	8.67
14	Luciolinae	*Abscondita pallescens*	3	9	9	30	5	25	17	64	65.38	21.33
15	Luciolinae	*Curtos costipennis*	2	4	7	63	2	5	11	72	42.31	24.00
16	Luciolinae	*Pygoluciola dunguna*	3	14	3	62	4	17	10	93	38.46	31.00
			TOTAL:	**35**	**TOTAL:**	**187**	**TOTAL:**	**78**	**GRAND TOTAL:**	**300**		

Appendix Table 3.4: Species richness, Shannon diversity and Simpson diversity of fireflies according to forest compartments at 90 % sampling completeness and the asymptotic estima

No.	Forest block	ID no.	Logging cycle	Age after logging		Species richness		Shannon diversity		Simpson diversity	
				Previous	Latest	90% completeness	Asymptotic	90% completeness	Asymptotic	90% completeness	Asymptotic
1	Hulu Terengganu Tambahan	UTT35	Once	Unlogged	2	1.93	2.00	1.78	2.07	1.67	2.14
2	Hulu Terengganu Tambahan	UTT41	Once	Unlogged	2	0.00	0.00	0.00	0.00	0.00	0.00
3	Pasir Raja Barat	PB87	Once	Unlogged	5	1.73	6.91	1.31	1.67	1.18	1.21
4	Pasir Raja Selatan	PS52	Once	Unlogged	5	3.43	3.89	2.12	2.43	1.62	1.59
5	Jerangau	JU31N	Once	Unlogged	6	6.64	13.78	2.08	2.44	1.43	1.45
6	Besul	B12	Once	Unlogged	10	1.93	2.00	1.78	2.07	1.67	2.14
7	Jerangau	JU31Y	Once	Unlogged	11	3.13	5.93	1.69	1.97	1.35	1.38
8	Jengai	JI52	Once	Unlogged	20	8.52	10.57	3.48	3.95	1.96	2.02
9	Jengai	JI4	Once	Unlogged	23	4.72	5.00	4.04	4.99	3.51	4.69
10	Besul	B17	Once	Unlogged	24	3.50	3.86	2.46	2.87	1.89	1.82
11	Besul	B19	Once	Unlogged	30	1.67	3.48	1.36	1.65	1.23	1.29
12	Jengai	JI64	Once	Unlogged	31	1.90	2.00	1.77	2.19	1.67	2.50
13	Besul	B18	Once	Unlogged	32	0.00	0.00	0.00	0.00	0.00	0.00
14	Besul Tambahan	BT7	Once	Unlogged	32	0.00	0.00	0.00	0.00	0.00	0.00
15	Jerangau	JU93	Once	Unlogged	41	2.33	2.50	0.00	3.38	3.00	2.00
16	Jengai	JI38B	Twice	31	1	1.00	1.00	1.00	1.00	1.00	1.00
17	Besul	B14	Twice	32	2	1.00	1.00	1.00	1.00	1.00	1.00
18	Jengai	JI39	Twice	33	3	3.50	3.86	2.46	2.87	1.89	1.82
19	Jengai	JI40	Twice	33	3	4.69	5.82	3.06	3.64	2.29	2.50
20	Besul	B10	Twice	36	10	6.91	10.30	3.92	4.63	2.89	3.09
21	Besul	B3	Twice	36	10	3.20	4.48	2.05	2.40	1.63	1.71
22	Jengai	JI42	Twice	36	10	1.00	1.00	1.00	0.00	0.00	1.00
23	Jerangau	JU68	Twice	46	15	1.00	1.00	1.00	1.00	1.00	1.00
24	Hulu Terengganu Tambahan	UTT27	Unlogged	Unlogged	Unlogged	2.64	3.00	2.37	2.82	2.20	2.75
25	Jerangau	JU100	Unlogged	Unlogged	Unlogged	3.83	4.00	3.33	4.04	2.95	3.90
26	Pasir Raja Selatan	PS26	Unlogged	Unlogged	Unlogged	4.78	5.23	4.43	5.84	4.16	6.88

Appendix Table 3.5: Effect size analysis based on Partial η2 values and the Type II sum of squares analysis to estimate the significance of each habitat variables on the firefly species richness and diversity. Significant level at $p < 0.05$. (a) Unlogged compartments assigned as 200 years old, (b) Unlogged compartments assingned as 100 years old.

(a) Oldest Age = 200 years old

Habitat characteristic	Species Richness					Shannon Diversity					Simpson Diversity				
	Partial η2	Sum Sq	Df	F value	Pr(>F)	Partial η2	Sum Sq	Df	F value	Pr(>F)	Partial η2	Sum Sq	Df	F value	Pr(>F)
Forest age	*0.1403*	5.1122	1	1.7952	0.20731	0.04133	0.4888	1	0.4311	0.5263	*0.10629*	1.3774	1	1.3082	0.277
Canopy closure	**0.3518**	16.9993	1	5.9694	**0.03263**	*0.131726*	1.7203	1	1.5171	0.2462	0.015902	0.1872	1	0.1778	0.6814
Leaf litter depth	**0.2444**	10.1313	1	3.5577	0.08593	0.065734	0.7978	1	0.7036	0.4212	0.000001	0	1	0	0.9977
Understory height	0.0865	2.9672	1	1.042	0.32929	0.005102	0.0581	1	0.0513	0.8254	0.000372	0.0043	1	0.0041	0.9501
Number of water	0.0894	3.0758	1	1.0801	0.32098	0.045399	0.5393	1	0.4756	0.5061	0.002627	0.0305	1	0.029	0.8679
Distance to primary forest	**0.4532**	25.9648	1	9.1178	**0.01166**	**0.270399**	4.2024	1	3.7061	0.0831	*0.151921*	2.0747	1	1.9705	0.188

(b) Oldest Age =100 years old (No Change in Results)

Habitat characteristic	Species Richness					Shannon Diversity					Simpson Diversity				
	Partial η2	Sum Sq	Df	F value	Pr(>F)	Partial η2	Sum Sq	Df	F value	Pr(>F)	Partial η2	Sum Sq	Df	F value	Pr(>F)
Forest age	0.10247	3.734	1	1.2558	0.28632	0.029727	0.3516	1	0.3064	0.59207	*0.075888*	0.9835	1	0.9033	0.3623
Canopy closure	**0.32533**	15.77	1	5.3042	**0.0418**	*0.126968*	1.669	1	1.4543	0.25559	0.016194	0.1971	1	0.1811	0.6787
Leaf litter depth	**0.23392**	9.986	1	3.3588	0.09403	0.066015	0.8112	1	0.7068	0.42015	0.000016	0.0002	1	0.0002	0.9897
Understory height	0.07062	2.485	1	0.8359	0.38018	0.007531	0.0871	1	0.0759	0.78856	0.000036	0.0004	1	0.0004	0.9845
Number of water	0.09518	3.44	1	1.1571	0.30509	0.040902	0.4894	1	0.4265	0.52846	0.004503	0.0542	1	0.0498	0.8276
Distance to primary forest	**0.42947**	24.618	1	8.2804	**0.01504**	**0.289502**	4.6762	1	4.0746	0.07115	*0.175092*	2.542	1	2.3348	0.1547

Appendix Table 3.6: Summary table of ANOVA .

Habitat characteristics	Species Richness					Shannon Diversity				Simpson Diversity			
	Estimate	Std. Error	t value	Pr(>|t|)		Estimate	Std. Error	t value	Pr(>|t|)	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-1.6177198	3.779179	-0.428	0.6769		4.79E-01	2.30E+00	0.208	0.839	-3.56E-01	2.40E+00	-0.148	0.8849
Forest age	-0.0097219	0.007256	-1.34	0.2073		5.05E-03	4.41E-03	1.144	0.277	3.02E-03	4.59E-03	0.657	0.5263
Canopy closure	0.1590294	0.0650894	**2.443**	**0.0326**	*	1.67E-02	3.96E-02	0.422	0.681	5.12E-02	4.16E-02	1.232	0.2462
Leaf litter depth	-1.6396641	0.8692996	-1.886	0.0859		-1.58E-03	5.29E-01	-0.003	0.998	-4.79E-01	5.70E-01	-0.839	0.4212
Understory height	-0.0357073	0.034981	-1.021	0.3293		1.36E-03	2.13E-02	0.064	0.95	-5.01E-03	2.21E-02	-0.226	0.8254
Number of water	3.6743341	3.5354671	1.039	0.321		-3.66E-01	2.15E+00	-0.17	0.868	1.67E+00	2.42E+00	0.69	0.5061
Distance to primary forest	-0.0003602	0.0001193	**-3.02**	**0.0117**	*	-1.02E-04	7.25E-05	-1.404	0.188	-1.46E-04	7.56E-05	-1.925	0.0831

Appendix Table 3.7: Estimation of species richness using iNEXT for (a) Once logged forest group and (b) Twice logged forest group. Values underline showed the estimated species richness at 93% coverage in both groups.

(a) Once logged group

	m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
1	1	interpolated	0	1.000	1.000	1.000	0.277	0.224	0.329
2	6	interpolated	0	3.279	2.939	3.619	0.770	0.698	0.842
3	11	interpolated	0	4.200	3.538	4.862	0.859	0.794	0.923
4	16	interpolated	0	4.850	3.894	5.805	0.882	0.824	0.941
5	22	interpolated	0	5.528	4.243	6.812	0.892	0.838	0.947
6	27	interpolated	0	6.057	4.513	7.601	0.897	0.844	0.949
7	32	interpolated	0	6.566	4.770	8.362	0.900	0.849	0.952
8	37	interpolated	0	7.058	5.017	9.099	0.904	0.853	0.954
9	43	interpolated	0	7.628	5.297	9.958	0.907	0.857	0.957
10	48	interpolated	0	8.086	5.518	10.655	0.910	0.860	0.960
11	53	interpolated	0	8.532	5.728	11.336	0.912	0.863	0.962
12	59	interpolated	0	9.050	5.965	12.134	0.915	0.865	0.965
13	64	interpolated	0	9.468	6.150	12.786	0.918	0.868	0.968
14	69	interpolated	0	9.876	6.325	13.427	0.920	0.870	0.970
15	74	interpolated	0	10.274	6.490	14.058	0.922	0.871	0.972
16	80	interpolated	0	10.739	6.675	14.804	0.924	0.873	0.974
17	85	interpolated	0	11.118	6.820	15.417	0.925	0.874	0.976
18	90	interpolated	0	11.490	6.956	16.024	0.926	0.875	0.978
19	96	interpolated	0	11.928	7.110	16.746	0.928	0.876	0.980
20	97	observed	0	12.000	7.134	16.866	0.928	0.876	0.980
21	98	extrapolated	0	12.072	7.158	16.985	0.928	0.876	0.980
22	103	extrapolated	0	12.429	7.276	17.581	0.929	0.877	0.982
23	108	extrapolated	0	12.780	7.386	18.173	0.930	0.878	0.983
24	113	extrapolated	0	13.126	7.490	18.762	0.931	0.879	0.984
25	118	extrapolated	0	13.467	7.588	19.346	0.932	0.879	0.985
26	123	extrapolated	0	13.803	7.680	19.926	0.933	0.880	0.986
27	128	extrapolated	0	14.134	7.767	20.501	0.934	0.881	0.987
28	133	extrapolated	0	14.460	7.849	21.072	0.935	0.882	0.988
29	138	extrapolated	0	14.781	7.925	21.638	0.936	0.883	0.989
30	143	extrapolated	0	15.098	7.997	22.199	0.937	0.884	0.990
31	148	extrapolated	0	15.410	8.064	22.756	0.938	0.885	0.991
32	153	extrapolated	0	15.717	8.127	23.308	0.939	0.886	0.992
33	158	extrapolated	0	16.020	8.186	23.855	0.940	0.887	0.993
34	163	extrapolated	0	16.318	8.240	24.397	0.941	0.888	0.993
35	168	extrapolated	0	16.612	8.291	24.934	0.942	0.889	0.994
36	173	extrapolated	0	16.902	8.339	25.465	0.943	0.891	0.995
37	178	extrapolated	0	17.187	8.382	25.992	0.943	0.892	0.995
38	183	extrapolated	0	17.468	8.423	26.514	0.944	0.893	0.996
39	188	extrapolated	0	17.745	8.460	27.031	0.945	0.894	0.996
40	194	extrapolated	0	18.072	8.501	27.644	0.946	0.895	0.997

(b) Twice logged group

	m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCI
1	1	interpolated	0	1.000	1.000	1.000	0.221	0.176	0.266
2	5	interpolated	0	3.290	3.021	3.560	0.665	0.586	0.744
3	9	interpolated	0	4.371	3.814	4.928	0.806	0.742	0.870
4	13	interpolated	0	5.056	4.280	5.833	0.857	0.807	0.907
5	17	interpolated	0	5.587	4.645	6.529	0.881	0.840	0.923
6	22	interpolated	0	6.140	5.038	7.242	0.900	0.865	0.936
7	26	interpolated	0	6.521	5.315	7.726	0.912	0.879	0.945
8	30	interpolated	0	6.858	5.561	8.154	0.922	0.890	0.953
9	34	interpolated	0	7.157	5.779	8.535	0.930	0.900	0.961
10	39	interpolated	0	7.486	6.012	8.959	0.940	0.910	0.970
11	43	interpolated	0	7.717	6.171	9.263	0.946	0.917	0.976
12	47	interpolated	0	7.924	6.306	9.542	0.952	0.922	0.981
13	51	interpolated	0	8.110	6.421	9.799	0.956	0.927	0.986
14	55	interpolated	0	8.278	6.517	10.039	0.961	0.931	0.991
15	60	interpolated	0	8.466	6.612	10.319	0.965	0.934	0.996
16	64	interpolated	0	8.601	6.671	10.531	0.968	0.937	0.999
17	68	interpolated	0	8.725	6.717	10.734	0.970	0.938	1.002
18	72	interpolated	0	8.841	6.750	10.931	0.972	0.939	1.005
19	77	interpolated	0	8.974	6.776	11.172	0.974	0.940	1.009
20	78	observed	0	9.000	6.780	11.220	0.975	0.939	1.011
21	79	extrapolated	0	9.025	6.781	11.270	0.975	0.939	1.011
22	83	extrapolated	0	9.123	6.779	11.467	0.976	0.941	1.012
23	87	extrapolated	0	9.216	6.772	11.661	0.977	0.943	1.012
24	91	extrapolated	0	9.305	6.760	11.850	0.979	0.944	1.013
25	95	extrapolated	0	9.389	6.742	12.036	0.980	0.946	1.013
26	99	extrapolated	0	9.469	6.720	12.217	0.981	0.948	1.014
27	103	extrapolated	0	9.544	6.695	12.394	0.982	0.949	1.014
28	107	extrapolated	0	9.616	6.666	12.567	0.983	0.951	1.014
29	111	extrapolated	0	9.685	6.634	12.736	0.983	0.952	1.015
30	115	extrapolated	0	9.750	6.599	12.900	0.984	0.954	1.015
31	119	extrapolated	0	9.811	6.562	13.060	0.985	0.955	1.015
32	123	extrapolated	0	9.870	6.523	13.216	0.986	0.957	1.015
33	127	extrapolated	0	9.925	6.483	13.367	0.987	0.958	1.015
34	131	extrapolated	0	9.978	6.441	13.515	0.987	0.959	1.015
35	135	extrapolated	0	10.028	6.398	13.658	0.988	0.961	1.015
36	139	extrapolated	0	10.076	6.354	13.797	0.988	0.962	1.015
37	143	extrapolated	0	10.121	6.310	13.932	0.989	0.963	1.015
38	147	extrapolated	0	10.164	6.265	14.063	0.990	0.964	1.015
39	151	extrapolated	0	10.205	6.219	14.190	0.990	0.965	1.015
40	156	extrapolated	0	10.253	6.161	14.344	0.991	0.967	1.015

Appendix Table 4.1: Collections made during the elevation study. Number of collections according to species for each mountain and its specific forest types.

Mountain/ Forest type	Number of transect	*Luciola pallidipes*	*Abscondita berembun*	*Abscondita pallescens*	*Curtos obscuricolor*	*Curtos costipennis*	*Curtos* sp.1	*Curtos* sp. 3	*Pygoluciola dunguna*	*Pyrocoelia fumigata*	*Pyrocoelia* sp. 1	*Pyrocoelia* sp.2	*Pyrocoelia* sp.3	*Diaphanes* sp.1	*Diaphanes* sp.2	*Colophotia brevis*	*Stenocladius* sp.1	*Stenocladius* sp.2	*Drilaster* sp.
Bukit Kutu	**15**						**1**		**2**								**1**		
• Lowland dipterocarp	1																		
• Hill dipterocarp	10						1		2										
• Upperhill dipterocarp	4																1		
Gunung Besar Hantu	**23**			**2**												**3**	**2**	**1**	
• Lowland dipterocarp	2															3			
• Hill dipterocarp	10			1														1	
• Upperhill dipterocarp	8			1													2		
• Oak-laurel	3																		
Gunung Berembun	**15**		**6**	**2**					**2**					**3**	**2**				
• Lowland dipterocarp	1													1	2				
• Hill dipterocarp	10			1					2					1					
• Upperhill dipterocarp	4		6	1										1					
Gunung Liang	**34**		**1**	**4**	**1**	**1**			**10**	**3**	**4**		**4**						**2**
• Lowland dipterocarp	2			1					4										
• Hill dipterocarp	10			3					6										
• Upperhill dipterocarp	8																		
• Oak-laurel	6		1																
• Motane ericaceous	8				1	1				3	4		4						2
Gunung Nuang	**23**	**4**		**4**	**1**	**4**		**1**	**1**			**3**			**1**	**5**	**9**	**5**	
• Lowland dipterocarp	3	4										1				1	6	1	
• Hill dipterocarp	10			3					1			2			1	4	2	4	
• Upperhill dipterocarp	8			1		3		1									1		
• Oak-laurel	2				1	1													
Grand Total	**110**	**4**	**7**	**12**	**2**	**5**	**1**	**1**	**15**	**3**	**4**	**3**	**4**	**3**	**3**	**8**	**12**	**6**	**2**

Appendix Table 5.1(a): Abreviations for taxonomic characters

Abbreviations	Description
ASD	distance between antennal sockets
ASW	antennal socket greatest diameter
B	pronotal dimension measured from above; width across middle
C	pronotal dimension measured from above; width across posterior third
FS	antennal flagellar segments
GHW	greatest head width (across eyes, measured parallel to ASD)
L	length
Legs 1, 2 etc	Legs and parts of legs are referred to by their segment number e.g. legs 1 are prothoracic legs; tarsi 2 =mesothoracic tarsi; femora 3 = metathoracic femora.
LL	lateral lobes, aedeagus
LO	light organ
ML	median lobe of the aedeagus
MN	mesonotal plates
MPP	median posterior projection ventrite 7 male only
MS	mesoscutellum
SIW	smallest interocular width (measured horizontally, may be on the same level as ASD, ASW, above it if the eyes are closer there)
T7, 8 etc	abdominal tergites
V6, 7 etc	abdominal ventrites, referred to by actual, not visible number

Appendix Table 5.1(a): Depositories of specimens

Acronym	Depositories
ANIC	Australian National Insect Collection Canberra
BEIJING	Natural History Museum, Beijing
BPBM	Bernice Bishop Museum, Honolulu, Hawaii
CMG	Museo Civico di Storia Naturale, Genoa
FRIM	Insect Reference Collection, Forest Research Institute Malaysia
LEIDEN	National Museum of Natural History, Naturalis, Leiden
MZUM	Zoology Museum University of Malaya
NHML	Natural History Museum, London
ZRC	Raffles Museum, Singapore