



UNIVERSITY OF THE PHILIPPINES LOS BAÑOS

Master of Science in Wildlife Studies

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**IMPACTS OF LOWLAND RAINFOREST TRANSFORMATION TO
RUBBER AND OIL PALM ON MULTIPLE DIMENSIONS OF
CHIROPTERAN DIVERSITY**

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Date: JUNE 2017

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JUNE 2017

The thesis attached hereto, entitled "**IMPACTS OF LOWLAND RAINFOREST TRANSFORMATION TO RUBBER AND OIL PALM ON MULTIPLE DIMENSIONS OF CHIROP TERAN DIVERSITY**" prepared and submitted by **NEIL JUN SALA LOBITE** in partial fulfillment of the requirements for the degree of **MASTER OF SCIENCE (WILDLIFE STUDIES)** is hereby accepted.

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BIOGRAPHICAL SKETCH

I earned my Bachelors degree in Biology and graduated *Cum laude* at Caraga State University. Currently, I am pursuing my Masters degree in Wildlife Studies with Genetics as cognate at the University of the Philippines – Los Banos. My research interests include Community and Landscape Ecology, Evolutionary Genetics and Conservation Biology. I am particularly interested on the ecological mechanisms that structures bat community patterns along elevational and disturbance gradients. Currently, my research focused on the influence of land transformation (specifically to rubber and oil palm) to the community, trophic and genetic structure of Chiropteran fauna.

NEIL JUN S. LOBITE

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ABSTRACT

NEIL JUN SALA LOBITE. University of the Philippines Los Baños. June 2017.
Impacts of Lowland Rainforest Transformation to Rubber and Oil Palm on Multiple Dimensions of Chiropteran Diversity

Major Professor: **JUDELINE C. DIMALIBOT**

Drastic land-use transformations have occurred in the tropical forests of Southeast Asia, being logged and converted to rubber and oil palm plantations driven by strong global demand. While the overall impacts of these changes in land use on biodiversity are negative, relatively little research on this subject has been carried out particularly on its impact to the different dimensions of bat diversity. We assessed the impacts of lowland rainforest transformation to rubber and oil palm on the taxonomic, functional and phylogenetic diversity of bats in Sumatra, Indonesia and Palawan, Philippines, regions which are known as hotspots for biodiversity which has already undergone extensive land transformation. Bat surveys were carried out across different transformation systems with lowland rainforests as reference sites, jungle rubber and intensive rubber and oil palm plantations. Species diversity was highest in forest habitat and significantly decreased towards rubber and oil palm plantations. The bat community in oil palm plantation was compositionally distinct from those of Jungle rubber and forest with a shift of numerically dominant species (*Cynopterus brachyotis*), and the loss of numerous forest-roosting ensemble (Hipposiderids, Rhinolophids and Vespertilionid families). Jungle rubber had higher species richness than monoculture rubber and oil palm plantations supporting more forest specialist species comparable with that of forest.

Conversion to rubber and oil palm monoculture led to a marked reduction in functional diversity and a decline in phylogenetic diversity. Our study suggests that land transformation to rubber and oil palm plantation had negative impact on bat diversity. Further studies on bat taxonomic, functional and phylogenetic diversity incorporating additional biodiversity dimensions particularly genetic diversity, trophic structure and interaction networks are needed to better understand the impacts of land transformation to rubber and oil palm agriculture on Southeast Asian bat diversity.

CHAPTER I

INTRODUCTION

Background of the Study

Understanding how land use transformations affect biodiversity and what are the consequences on ecosystem functioning is one of the main challenges in ecology and conservation biology. Land transformation, mostly from land use change associated with agriculture becomes the key driver of the current trend in biodiversity loss (Sodhi *et al.*, 2004). Agricultural lands now cover a quarter of the Earth's land surface and are expected to increase to continue to feed the Earth's growing population (FAO, 2006). Such unprecedented demands necessitate land conversion particularly for agricultural expansion mostly in expense of the forests. Conversion, expansion and intensification of agriculture have been perceived as the greatest contributor of global forest loss and land cover change (Tilman *et al.*, 2001). Such transformation of land from forest to agricultural plantations particularly intensive monocultures could have an adverse impact on biodiversity and ecosystem functioning (Tscharntke *et al.*, 2005). This leads to changes in landscape composition and spatial configuration, thereby reducing habitat quality for many species (Fitzherbert *et al.*, 2008) and reduce landscape connectivity making populations vulnerable to local extinctions (Struebig *et al.*, 2011) and ultimately

results in nonreversible alteration in biodiversity and ecosystem functions (Barnes *et al.*, 2014).

Over the past decades, most of the land transformation is for rubber (*Hevea brasiliensis*) and oil palm (*Elaeis guineensis*) production driven by strong international demand. Rubber and oil palm are the most rapidly expanding plantation crop where production rate is continually increasing (FAO, 2015). Currently, there is a great concern regarding the detrimental effect of oil palm and rubber plantations on biodiversity in the tropical forests of South East Asia including Indonesia and the Philippines (Wilcove *et al.*, 2013). Indonesia has the fastest oil palm plantation growth rate in the world (FAO, 2015). Philippines has been cultivating and processing palm oil for the past three decades and the rising demand for crude palm oil has driven the growth of the local palm oil industry in the country (Villanueva, 2011). Same is true for rubber which covered an area equivalent to 71% of oil palm extent within Southeast Asia during 2012 (FAO, 2015).

The unprecedented and rapid expansion of intensive oil palm and rubber plantations in Indonesia (Tilman *et al.*, 2001) as well as the perceived and planned expansion in the Philippines (Villanueva 2011) has spurred considerable concern in the light of its adverse impact on the environment, biodiversity and local community. Coincidentally, these countries holds Southeast Asia's remaining primary forests (mainly Indonesia) which are considered one of the biodiversity hotspots supporting large numbers of endemic and highly threatened species (Mittermeier *et al.* 2005) making this an urgent issue of global conservation importance.

The impact of land transformation to biodiversity is complex (Gonzalez *et al.*, 2011). Transformation of habitat may not only change species richness, composition and diversity (Tscharntke *et al.*, 2005) but also the pattern of species interactions that link them in networks and the functions that the species performs (Morris, 2010) as well as the community's functional structure and diversity that defines a species ecological role in a community (Mouillot *et al.*, 2013). The effects of habitat conversion might even result in discontinuities in gene flow among potentially isolated populations which exacerbate rate of extinction (Struebig *et al.*, 2011).

In this perspective, multidimensional measures of diversity of communities (taxonomic, functional, phylogenetic and genetic diversity) is a cornerstone since it allows linking environment, community structure and ecosystem properties. Simultaneous consideration of multiple dimensions of biodiversity can provide evidence for the importance of particular ecological or evolutionary mechanisms in structuring communities (Meynard *et al.*, 2011) and will provide insights into the relative ecological impacts of land transformation to the faunistic community including bats which had suffered severe population declines driven by agricultural intensification and expansion (Kingston, 2013).

Bats are suitable indicators to assess the response to urbanization and land transformation (Park, 2014). Bats have a diverse array of dietary habits ranging from species that feed on insects and other arthropods to those that feed on fruit, nectar, and flowers and provide valuable ecosystem services (Kunz *et al.*, 2011). The tight link

between bat and plant communities through pollination and seed dispersion as well as the high level occupied by insectivorous bats in trophic chains make these mammals particularly responsive to habitat changes (Russo and Jones, 2015). There is a mounting evidence that intensification of agricultural practices can potentially affect bats through reductions in prey availability, loss of suitable roost sites and degradation of foraging areas (DEFRA, 2005) as well as changes in genetic structure and diversity (Struebig *et al.*, 2011). Furthermore, habitat modification through agriculture is one of the most important factors in increasing species' risk of extinction particularly to the loss of functional and genetic diversity (Struebig *et al.*, 2011).

While the overall impacts of land transformation and converting forest into oil palm plantation on biodiversity are negative (Fitzherbert *et al.*, 2008), relatively little research on this subject has been carried out particularly on its impact on bat fauna at multiple dimensions (Struebig *et al.*, 2011). The paucity of evidence for changes in taxonomic, functional and phylogenetic diversity in response to various land use transformation impedes effective conservation actions and formulation of management programs. In Indonesia which has been undergoing rapid and vast land use transformation particularly for oil palm plantation (Carlson *et al.*, 2012) and in the Philippines where rubber and oil palm industry is flourishing, no published studies to date have been conducted to explore the impact of land transformation to agricultural land use particularly to oil palm plantation on bat biodiversity at different dimensions.

This research ultimately aimed to assess and quantify the impact of tropical lowland rainforest transformation to rubber and oil palm plantations on taxonomic, functional and phylogenetic diversity having bats as indicator species. Through this research, I investigated the response and the influence of land use transformation system on multiple dimensions of bat diversity in Sumatra, Indonesia and in Palawan, Philippines by looking into the species richness, composition and abundance and assess the changes in the functional and phylogenetic structure of bat communities across land transformation systems. I hypothesized that if forest land transformation has a major impact on bat populations, then the species, functional and phylogenetic diversity of the focal bat species will be significantly lower in the transformed habitat (Jungle rubber, Rubber and Oil palm plantations) than in the forest habitat. The major findings of this research will provide understanding on the impact of land transformation from forest to rubber and oil palm plantations and will serve as a good basis for the formulation and implementation of policies, laws and ordinances to mitigate the adverse impacts of agriculture expansion and intensification particularly for monoculture crops such as rubber and oil palm on terrestrial biodiversity. Additionally, this will be of great help in formulating essential wildlife conservation measures in key agricultural areas in South East Asia where rubber and oil palm plantations are expanding.

Objectives of the Study

The study generally aimed to investigate, quantify and understand the impacts of tropical lowland rainforest transformation to rubber and oil palm plantations on the taxonomic, functional and phylogenetic dimension of bat diversity and to have a good basis for the formulation and implementation of policies, laws and ordinances to mitigate the adverse impacts of land transformation to agriculture particularly to rubber and oil palm on terrestrial biodiversity.

Specific Objectives are to:

1. Determine and compare the species richness, composition, evenness, relative abundance, diversity and dominance of bats between forest and different land use transformation systems (Jungle Rubber, Rubber and Oil Palm Plantation).
2. Assess and compare the functional diversity, functional divergence and functional dispersion of bat community between forest and different land use transformation systems.
3. Evaluate phylogenetic diversity and distinctness of bat community in forest and different land use transformation systems.

4. Determine the implications of the findings on bat conservation and land-use management in Sumatra, Indonesia and the Philippines.

CHAPTER II

REVIEW OF RELATED LITERATURE

Tropical Rainforest Transformation to Agriculture

Globally, one of the major pressures on biodiversity remains the transformations of natural habitats to agriculture, especially through forest clearance (Jenkins, 2003). It has been perceived that the rate of landscape change has accelerated during the past century. Perhaps the main reason for this is the increasing spatial scale of the human food chain. Land transformation driven by humans encompasses a wide variety of activities that substantially vary on intensity and many changes in land use are a consequence of the increase in human population and the resulting demand for more resources (Marzluff, 2008). Rising global demand for agricultural products such as palm oil remains the main factor driving up palm oil prices on the international commodity markets and this is encouraging further investment, stimulating trades in palm oil companies on the stock exchanges and accelerating land acquisition (Jenkins, 2003).

Drastic land-use transformations have occurred in the tropical forest landscapes of Southeast Asia in the past decades, leading to the disappearance of natural forests and the replacement of traditional land-use systems with monoculture plantations (Sandker *et al.*, 2007). While these rainforests are hotspots of biological diversity with a high rate of

endemism and hold important carbon stocks, they are also a major source of valuable timber, and are situated on lands that are very suitable for conversion to agricultural lands including oil palm and other large industrial plantations (Labrière *et al.*, 2015). The South East Asian region is subject to rapid rates of land-use conversion yet is characterized by high biodiversity and endemism and is of critical importance for global conservation efforts (Sodhi *et al.*, 2010).

Today's top form of agriculture is the establishment of oil palm plantations. Oil palm *Elaeis guineensis* is grown across more than 13.5 million hectares of tropical, high-rainfall, low-lying areas, a zone naturally occupied by moist tropical forests (Sandker *et al.*, 2007). Malaysia and Indonesia produce more than 80% of all palm oil (FAO, 2015) and together they also hold more than 80% of Southeast Asia's remaining primary forests (mainly in Indonesia), where many endemic species are threatened with extinction by some of the highest global rates of deforestation (Mittermeier *et al.*, 2005)

Oil palm plantations are estimated at 9.4 million ha in Indonesia, where the most vigorous expansion is underway. In 2008, Indonesia already has a reported 7.3 million hectares of land planted with oil palm. This represents a significant increase of 6 million hectares in 2006 (FAO, 2015). In addition a further 18 million hectares of land have been cleared for oil palm, but not subsequently planted. Regional development plans assign a further 20 million hectares of land for plantation expansion by 2020, primarily in Sumatra, Kalimantan (Indonesian Borneo), Sulawesi and West Papua (Carlson *et al.*, 2012).

Oil palm plantations in the Philippines occupy 46,608 ha during 2008, representing a 160% increase in plantation area in the span of just four years. This suggests that the Philippines may soon emerge as a key player in the palm oil industry of South East Asia. Although considered a fledgling industry in the Philippine agribusiness sector and while its size is certainly small compared to the millions of hectares of oil palm plantations in Malaysia and Indonesia, the Philippines has been cultivating and processing palm oil for the past three decades. In recent years, the rising demand for Crude Palm Oil and the high commercial value of the product has driven the growth of the local palm oil industry and the pressing demand from both the domestic and international markets is driving the industry to aggressively push for the expansion of oil palm plantations. Existing concentrations of oil palm plantations in the Philippines are found in various parts of Mindanao, the provinces of Bohol in the Visayas and Palawan in Luzon (Villanueva, 2011).

The establishment of oil palm cultivation in the Province of Palawan, considered the country's Last Ecological Frontier, began with the plans that took place only in 2003. The Provincial Government of Palawan was keen to open up certain areas in Palawan for oil palm cultivation with the belief that it would benefit the rural economy (Villanueva, 2011). According to a study conducted by the Philippine Coconut Authority (PCA) and the Palawan Palm Oil Industry Development Council (PPOIDC) for foreign investors, 37 out of the 454,405 hectares of agricultural area in Palawan, 208,997 hectares are appropriate for oil palm plantation. Current sources reveal that at first, the Provincial Government of Palawan identified some 80,000 ha for oil palm cultivation. However, out

of the 100,000 ha nationwide target for palm oil production in the country, Palawan was allocated 20,000 ha to be planted until 2011. Agusan Plantations Group, the Palawan Palm and Vegetable Oil Mills Inc. (PPVOMI) and the Agumil Philippines Inc. (AGPI) dominate the palm oil industry in Palawan and intend to cover 15,000 ha with oil palm plantations (Dalabajan 2010).

Impacts of Land Conversion to Oil Palm to Biodiversity

The conversion of natural forest to oil palm plantation is a major current threat to the conservation of biodiversity in South East Asia (Koh *et al.*, 2008). Optimal land to production ratio is achieved through oil palm monocultures over extensive areas of land, usually accompanied by the building of processing mills and roads for crop transport purposes (Fischer *et al.*, 2011). Forests in Southeast Asia are rapidly being logged and converted to oil palm. These changes in land-use are known to affect species diversity yet the ecological impact of oil palm depends crucially on the extent to which its expansion causes deforestation, and on the extent to which it is able to support biodiversity (Fitzherbert *et al.*, 2008).

The response of biodiversity to land-cover change depends upon the extent to which natural habitat features are replicated and upon variation in the sensitivities of species to change. Generalist species respond positively and may thrive in secondary habitats or managed plantations, while specialists decline and might become locally extinct (Yaap *et al.*, 2010). Oil palm plantations are structurally less complex than natural

forests, with a uniform tree age structure, lower canopy, sparse undergrowth, less stable microclimate and greater human disturbance and are cleared and replanted on a 25–30 year rotation (Tilman *et al.*, 2002), thus, environmental filtering of species with similar traits could lead to disproportionate reductions in trait diversity in degraded habitats and may support only selected species capable of tolerating such changes. Hence, the loss of virtually all forest vegetation during conversion to oil palm therefore lays the foundation for impacts on faunal groups (Yaap *et al.*, 2010).

Fitzherbert *et al.*, (2008) argued that the impacts of oil palm plantation agriculture on biodiversity have proven severe, leading to increased human–wildlife conflict, homogenization of structurally and species diverse ecosystems, and destruction of habitat for globally threatened species. Oil palm consistently held fewer than half as many vertebrate species as primary forests, whereas invertebrate taxa showed more variation (Koh and Wilcove, 2008). Most studies found large differences in faunal species composition between oil palm and forests (Fukuda *et al.*, 2005, Edwards *et al.*, 2013, Barnes *et al.*, 2014). The species lost were not a random subset of the original forest fauna, but tended to include species with the most specialised diets, those reliant on habitat features not found in plantations (such as large trees for cavity-dwelling species), those with the smallest range sizes and those of highest conservation concern. Plantation assemblages were typically dominated by a few abundant generalists, non-forest species (including alien invasives) and pests (Fitzherbert *et al.*, 2008).

Because oil palm and other tree crops are unsuitable habitats for most forest species, plantations - where they form part of the landscape matrix can act as a barrier to

animal movements (Turner *et al.*, 2008). This scenario was found in forest fragments isolated within oil palm plantations which only supported fewer than half as many ant species as nearby continuous forests, and a greater number of invasive species were found in the smallest fragments (Pfeiffer *et al.*, 2008). With respect to abundance, responses appear to vary depending on species and there is no clear overall effect in one direction. When the abundance results are considered in the light of the results on species richness and similarity, it appears that certain invertebrate species, e.g. generalist species, increase in abundance after forest conversion whereas others decline (Hassall *et al.*, 2006).

A recent study by Edwards *et al.*, 2013 calculated the functional diversity of birds across a gradient of disturbance from primary forest through intensively logged forest to oil palm plantations on previously forested land in Borneo, Southeast Asia. They found out that logged rainforest retained similar levels of functional diversity to unlogged rainforest but the conversion of logged forest to oil palm resulted in dramatic reductions in functional diversity. It was shown that few remaining species in oil palm filled a disproportionately wide range of functional roles but showed very little clustering in terms of functional traits, suggesting that any further extinctions from oil palm would reduce functional diversity even further.

Another research by Edwards *et al.*, 2014 showed that conversion of forest to oil palm greatly reduced taxonomic and functional diversity of dung beetles, with a marked decrease in the abundance of nocturnal foragers, a higher proportion of species with small body sizes and the complete loss of telecoprid species (dung-rollers), all indicating a decrease in the functional capacity of dung beetles within plantations. Their results

suggests that the transition from primary or logged forest to oil palm results in such environmental stresses, particularly due to microclimatic changes, that large subsets of forest species are driven to local extinction irrespective of their dietary breadth or specialization.

A study of Freudmann *et al.*, (2015) revealed the impacts of oil palm agriculture on phyllostomid bat assemblages by comparing phyllostomid bat assemblages in mature lowland forest interior, at forest margins and within oil palm plantations in southwestern Costa Rica. They found out that bat assemblages in oil palm plantations were clearly distinct from those at forest sites and exhibited lower species richness. The assemblage structure within oil palm plantations was characterized by increased relative abundance of common frugivorous Stenodermatinae and the loss of rare species, mainly disturbance-sensitive animalivorous Phyllostominae. They contend that oil palm agriculture may consequently reduce population connectivity and foster faunal impoverishment, which in turn can diminish crucial ecosystem services provided by bats.

Furthermore, a study on the effect of oil palm expansion on Neotropical avian phylogenetic diversity by Prescott *et al.*, (2016) showed that PD, a measure of phylogenetic richness, and MPD, a measure of the phylogenetic distance between individuals in a community in deep evolutionary time were significantly lower in oil palm than in forest suggesting its negative impact on biodiversity.

Impacts of Land Conversion to Rubber Plantations to Biodiversity

Worldwide demand and consumption of natural rubber (*Hevea brasiliensis*) has been increasing steadily for many decades. Although rubber is a native of the Amazon basin, 97 percent of the world's natural rubber supply today comes from Southeast Asia (Li and Fox 2012).

Natural forests have been recently converted to rubber plantations in mainland Southeast Asia and natural habitat conversion to rubber is set to continue (Li *et al.*, 2007). Regional scale simulation predicts the conversion of 4.25 million ha to rubber and other deciduous broadleaved plantations by 2050, mostly replacing evergreen broadleaf forest and forest-field mosaics (Fox *et al.*, 2012). Such areas support an assemblage of Critically Endangered and Endangered waterbirds, ungulates and primates which are likely to decline on clearance and fragmentation of currently contiguous forests (Tordoff *et al.*, 2005).

The distribution of rubber plantations across Southeast Asia coincides with four biodiversity hotspots in the region: Sundaland (Malay Peninsula, Borneo, Sumatra, Java, and Bali), Indo-Burma (Laos, Cambodia, Vietnam, most of Myanmar and Thailand, and parts of Southwest China, Wallacea (Indonesian islands east of Bali and Borneo but west of New Guinea, plus Timor Leste), and the Philippines (Myers *et al.* 2000), supporting large numbers of endemic and highly threatened species (Sodhi *et al.* 2004). Rubber cultivation occurs within multiple biogeographic realms and ecoregions, including subtropical montane rainforests and coniferous forests in Southwest China, moist and dry

evergreen and deciduous forests in Indo-Burma, and tropical and subtropical moist lowland forests in Sundaland, Wallacea and the Philippines (Olson *et al.* 2001).

Several researchers found that conversion of primary or secondary forest to rubber monoculture decreases the species richness of birds, bats and carabid beetles by 19–76% (Danielsen and Heegaard 1995; Aratrakorn *et al.*, 2006). Conversion also changes species composition, with forest specialists replaced by disturbance-tolerant, widespread species (Najera and Simonetti 2010). In lowland Thailand, 15 of 16 threatened bird species were restricted to forest, whereas species composition in rubber was similar to oil palm, representing a replacement of forest specialists (particularly frugivores and insectivores) with widespread generalists, usually of smaller body size (Aratrakorn *et al.* 2006). Moreover, bats in Indonesia (Danielsen and Heegaard 1995) recorded 13 species that were restricted to forest, and insectivorous bats showed 20-fold lower activity in rubber plantations attributed to lower insect biomass. Additionally, the study of Phommexay *et al.*, (2011) which compared the species diversity and activity of understorey insectivorous bats in forest and in nearby monoculture rubber plantations showed that species diversity and activity were much lower in rubber plantations than in forested areas and mean insect biomass was more than twice as high in the latter habitat than in the former.

While assessing impacts of primary forest conversion to rubber is relatively straightforward, more complex patterns of land-use change present a challenge in assessing biodiversity impacts. In mainland Southeast Asia, rubber agroforestry has been adopted and over half the current rubber plantation extent was established on mosaics of natural vegetation (grassland, shrubland and forest) and cropland, while in Indonesia

conversion of low-intensity rubber agroforest to monocultural plantations is an emerging trend representing leakage of biodiversity impacts beyond plantation boundaries (Li *et al.* 2013).

Agroforestry systems, through the maintenance and diversification of specific trees on farms, help maintain biodiversity in tropical landscapes. Agroforestry systems can have species richness equivalent to more than 60% of that of the natural forest (Bhagwat *et al.* 2008). Although there are negatives for species richness and composition of creating rubber agroforest on primary or secondary forest, rubber agroforest harbors greater biological value than monoculture rubber, supporting more forest specialist bird and plant species (Beukema *et al.* 2007), with increased bird diversity in plantations that have greater complexity in habitat structure (Aratrakorn *et al.* 2006). In some lowland areas of Indonesia, rubber agroforests are the only remaining forest-like habitats, supporting a subset of forest species not found in expanding monocultures (Ekadinata and Vincent, 2011).

Bat Diversity Response to Forest Disturbance and Land Transformation

By far the greatest proportion of the world's bat diversity resides in tropical ecosystems (Willig *et al.* 2003), but habitats in these ecosystems are some of the most imperiled in the world, subject to rapid degradation, extensive conversion to anthropogenic uses (Kingston, 2010). Southeast Asian bats play key ecosystem roles as

predators of insects, pollinators, and seed dispersers and are critical for forest regeneration (Hodgkison *et al.* 2003), the sustainability of commercial fruit crops (Bumrungsri *et al.* 2009), and control of insect crop pests (Leelapaibul *et al.* 2005).

Declines in local species richness and abundance and the concomitant changes in assemblage composition are likely to have profound effects on these services and compromise the integrity of both natural and production ecosystems. Studies that quantify the ecological and economic consequences of assemblage changes induced by anthropogenic activities are urgently needed (Kingston, 2010).

The forest-interior insectivorous ensemble, members of the Rhinolophidae, Hipposideridae, Kerivoulinae, and Murininae, is particularly vulnerable to forest loss and degradation, and this group can be further subdivided by their roosting ecology. By virtue of their greater vagility, cave-roosting forest interior species are somewhat more resilient to fragmentation and degradation than species that depend on forest structures for roosts (Kingston, 2010). It was first proposed by Kingston *et al.* 2003 that the ecomorphological adaptations that enable some insectivorous bats to forage in dense vegetation of the forest interior would preclude them from foraging successfully in more open habitats and, as a consequence, the forest-interior insectivore ensemble was predicted to be particularly vulnerable to human disturbance and degradation of forests that create monocrop plantations.

Intensification of agricultural practices can potentially impact upon bats through reductions in prey availability, reduced survival through loss of suitable roost sites, loss or degradation of foraging areas and exposure to toxic compounds used in agrochemicals

(DEFRA, 2005). Trapping studies in the tropics have shown reductions in abundance and species richness as previously forested land is converted to pasture and crop monocultures (Castro-Luna and Galindo-Gonzalez, 2012). Furthermore, there is evidence that bats benefit from lower intensity agricultural systems, specifically organic farming and shaded agroforestry: these systems tend to be associated with higher bat abundance, species richness and diversity, and are more heavily utilized by foraging bats (Heer *et al.*, 2015).

Study by Freudmann *et al.*, 2015 showed that species absent in oil palm plantations are usually those with specialized diets or roosting requirements and small home ranges, while assemblages in oil palm plantations are often dominated by a few abundant generalistic species and rather open-habitat tolerant. It was proposed that generally, those affected most by forest conversion are often rare and range-restricted species (Scales and Marsden, 2008).

Multiple Dimensions of Biodiversity

Understanding the processes shaping biological communities under multiple disturbances is a core challenge in ecology and conservation science. Biodiversity is a concept that embraces many aspects of biological variation, ranging from genetic and taxonomic differences to phenetic diversity among species (Jarzyna and Jetz, 2016). These different measures are thought to be related and, more importantly, to determine the resultant complexity of biological interactions which ultimately produce the patterns

of species coexistence, productivity, nutrient cycling, decomposition and energy flow in ecosystems (Cardinale 2014).

Most commonly, species richness (the number of species per unit area) has been used as a surrogate for the measurement of biodiversity. However, there is a growing consensus that species richness alone cannot appropriately describe the mechanisms involved in species coexistence and ecosystem processes and does not describe the differences in community structure well. Thus, using species richness as the sole measure of biodiversity may compromise our ability to understand the mechanistic basis linked to the spatial and temporal dynamics of biodiversity (Cardoso *et al.*, 2014).

Taxonomic diversity measures ignore the fact that communities comprise species with different phylogenetic positions and a range of ecological functions, and, thus, often miss information regarding ecosystem functioning and community evolutionary history (Safi *et al.*, 2011 , Cardoso *et al.*, 2014). The inadequacy of species richness in representing the differences in evolutionary history, how communities function, and how the network of interactions within communities are organized has led to the development of alternative measures, mainly phylogenetic diversity which reflects the assemblage evolutionary history and measured as the sum of the branch lengths of a phylogenetic tree connecting all species (Faith 1992) and functional diversity which reflects the diversity of ecological functions and often captured as the sum of branch lengths in a dendrogram representing differences among species in terms of forms or functions (Petchey and Gaston, 2006).

Phylogenetic and functional diversity can compensate for inadequate species diversity, and further describe the biodiversity of a community in evolutionary and functional terms, respectively. Phylogenetic diversity reflects the diversity of species in evolutionary terms by considering evolutionary and taxonomic hierarchies among species in a community (Mason *et al.*, 2005). Phylogenetic diversity is higher in communities with relatively distant phylogenetic relationships compared with those where phylogenetic relationships are close, given equal species richness. Phylogenetic diversity metric was initially proposed as a way of prioritizing species and areas for conservation. Because extinction risk is not phylogenetically random, there is, for instance a clumping of threat towards species which are slowly reproducing and with specialized habitats and high levels of endemism (Safi *et al.*, 2011). Consequently, the concern over the preservation of evolutionary history highlights the importance of determining whether priority sites for species conservation are also important in respect to evolutionary history (Faith 1992). Also, there has been a recent increasing effort to bring information about evolutionary relationships of species to elucidate questions of community assembly and diversity patterns (Devictor *et al.*, 2010).

Phylogenetic diversity measures the evolutionary differences among species based on times since divergence from a common ancestor (Faith 1992), and sometimes represents a comprehensive estimate of phylogenetically conserved ecological and phenotypic differences among species (Cavender-Bares *et al.* 2009). Thus, this dimension may represent the long-term evolutionary potential of a biota to respond or adapt to current and future environments. Depending on the nature of land use, human-modified

landscapes may become more homogeneous or more heterogeneous. With increasing landscape homogeneity, diversity of habitats or resources for particular taxa may decrease, ultimately increasing biotic homogenization (e.g. assemblages converge in species composition or in functional or phylogenetic attributes). Conversely, increased landscape heterogeneity may produce a greater diversity of habitats or resources for particular taxa, ultimately affecting the divergence in species composition along with attendant functional or phylogenetic attributes. The extent to which empirical values of FD or PD deviate from those expected due to empirical species richness or species diversity will facilitate assessment of whether landscape modification promotes or diminishes ecosystem functions and evolutionary potential along a landscape scale gradient in heterogeneity (Flynn *et al.* 2009).

As with phylogenetic diversity, functional diversity is also an important aspect of biodiversity (Petchey and Gaston, 2006), which reflects the diversity of functional traits of a group of species based on their morphological, physiological, reproductive, and phonological characteristics (Petchey *et al.*, 2004). The coexistence of species with various traits is beneficial in resource utilization, ecosystem stability, and restoration (Mason *et al.*, 2005). Hence, Trait-based and phylogenetic attributes of species are increasingly seen as vital components to better address the processes underlying spatial and temporal biodiversity dynamics and the potential consequences of biodiversity change.

Functional diversity measures variability in ecological attributes among species, and provides a mechanistic link to ecosystem resistance, resilience, and functioning

(Petchey and Gaston 2006). The loss of biodiversity due to anthropogenic activity can markedly modify the functional properties of ecosystems and the services they provide (Cardinale *et al.*, 2014). Biodiversity impacts ecosystem properties and processes because species (and individuals) differ in their productivity and contributions to ecosystem functions. These differences increase ecosystem functioning by increasing the odds of including more productive species when diversity increases (sampling effect), increasing the complementarity in how species use resources (resource partitioning), and/or in how they modify their surrounding environment in ways that impact other species (facilitation) (Petchey and Gaston 2006).

Acknowledging the trait-based and phylogenetic attributes of species, in both global and local context, is not only increasingly seen as vital for conservation prioritization but has also become a promising avenue to better address the processes responsible for spatial and temporal dynamics of species co-occurrence (Cardoso *et al.*, 2014). The rationale behind the use of these alternative diversity measures is to better identify the underlying processes determining species richness and ecosystem functioning (Jarzyna and Jetz, 2016).

Interest in, and opportunities to include functional and phylogenetic attributes of species in community ecology are rapidly growing and seen as vital for the assessment of status and trends in biodiversity. A recent study of Qin *et al.*, 2016 showed the application of species, phylogenetic and functional diversity for the evaluation of the effects of human activity and ecological restoration on biodiversity by investigating the species communities of a meadow pre- and post-restoration in the Lishan mountains, north China.

Their results showed that the relationships between species, phylogenetic and functional diversity changed due to human activity and community composition prerestoration and post-restoration suggesting that species, phylogenetic and functional diversity were all effective indices in evaluating on biodiversity from species abundance, phylogenetic relationship and functional traits.

Another study by Aguirre *et al.*, (2016) used different dimensions of biodiversity to assess spatial variation of bat assemblages of Bolivia and determined the changes in biodiversity as explained by the replacement of species or functional groups or by differences in richness (i.e., gain or loss of species or functional groups). Their research also evaluated the contribution of phylogenetic and taxonomic changes in the resulting patterns of functional diversity of bats. They found that bat assemblages differed from each other in all dimensions of biodiversity considered however, diversity patterns for each dimension were likely structured by different mechanisms. Their results suggest that whereas evolutionary processes create a template of diversity patterns across the country, ecological mechanisms modify these templates, decoupling the observed patterns of functional, taxonomic and phylogenetic diversity in Bolivian bats.

The study of Cisneros *et al.*, (2016) lead to the decomposition of biodiversity into different dimensions and functional components in order to facilitate the identification of the aspects of assemblages that are most affected by forest conversion and fragmentation. Their research identified the characteristics of a human-modified landscape that promote taxonomic (TD), functional (FD) and phylogenetic (PD) dimensions of bat biodiversity in Costa Rica. Additionally, Liu *et al.*, 2016 also applied taxonomic, functional, and

phylogenetic measures of diversity to study the reorganization of ant biodiversity after conversion to rubber plantation. They found a sharp decline of ant species richness in rubber plantations compared with nearby forest habitat, with low beta diversity indicating spatial homogeneity of communities in rubber plantations. In addition, patterns of both functional alpha and beta diversities suggested the emergence of a functionally distinct ant community in the agroecosystem compared to the forest habitats supporting the role of ecological filtering in structuring the taxonomic and functional composition of rubber and forest habitats. Their study highlights the need for a multidimensional approach to characterizing the loss of biodiversity in agroecosystems, as well as understanding the underlying mechanisms of community assembly driving biodiversity loss.

CHAPTER III

METHODOLOGY

Sampling Location and Design

This research was implemented in Jambi Province in Sumatra, Indonesia with the fastest and most complete transformation of tropical lowland rainforest and in Aborlan, Palawan Province, Philippines where oil palm plantation is currently expanding.

For sampling locations in Sumatra, Indonesia, two landscapes within Jambi Province were previously chosen for the Collaborative Research Center (CRC) research comprising large units of lowland rainforest: National Park Bukit Duabelas and Harapan Rainforest (Appendix 1). The transformation systems which were investigated include lowland rainforest as reference sites, jungle rubber (extensive rubber plantations), and intensive rubber and oil palm plantations. Lowland rainforest reference sites represent old-growth forest but have been subject to logging. Large sites of untouched natural rainforest are no longer existing in Jambi province, but the lowland rainforest reference sites selected represent large rainforest regions in a close to natural state. Jungle rubber represents an extensive management system which is established by planting rubber trees into rainforest. Its implementation dates back into the early 20th century but still covers large areas of Jambi. In each of the two landscapes (comprising blocks in a randomized

complete block design), four replicates of each of the four transformation systems (including the lowland rainforest as reference) were investigated. These 32 sites constituted the core sites.

The same sites were established in Aborlan, Palawan including lowland rainforest as reference sites, jungle rubber (extensive rubber plantations), and intensive rubber and oil palm plantations (Appendix 2 and 3). Four replicates were established in each of the transformation systems including the forest site.

Mist Netting

Mist netting and harp trapping methods were used to capture and record bats among the rainforest transformation systems. Bat sampling was done using mist nets (6m x 12m ; 6mm x 6mm mesh size) and harp traps for 2 nights in each of the selected sampling locations (Appendix 4). Nets were opened from 1800h until 0000h and were checked every 30 minutes. To maximize capture efficiency, nets were established across likely flight-paths in a variety of combinations such as “L” and “T” formations (Kunz *et al.*, 1996). Bat assemblages was surveyed from June, 2015 to August 2015 in Sumatra, Indonesia and from July 2016 to September 2016 in Palawan, Philippines.

The total sampling effort for mist netting was expressed as mist net hours (mn^h) where 1 mn^h equals to one – 12 by 6 m. mist net opened for one hour. Relative abundance of bats was calculated by dividing the number of bat individuals (n) with the total sampling effort (mn^h) and expressed as number of bats per mist net hour. For each

survey night, the location, weather conditions and time the nets were operational were noted. Geographic coordinates at each netting sites were recorded using a Global Positioning System (GPS).

A total of four (12 by 6 meters) mist nets were opened for 6 hours in each habitat in Sumatra, Indonesia. During the 64 nights of bat sampling, a total effort of 1,536 mist net hours (mnH) was obtained which was used to quantify relative abundance of bats per habitat and per every individual bat species. In Palawan, Philippines, a total of 8 (12 by 6 meters) mist nets were used and opened for 6 hours in each habitat. A total of 1,536 mist nets hours of sampling were rendered during the 32 nights of bat sampling in Palawan, Philippines.

Bat Identification

Captured bats were identified using the bat classification key of Philippine bats by Ingle and Heaney (1992) and the Field key to the Bats of Sumatra (Huang *et al.*, 2014). Bats were sexed by observation of genitalia and nipples, and were aged by assessment of the ossification of the joints of the digits of the wing (Ingle and Heaney, 1992). Female bats were classified as reproductive if they showed signs of pregnancy or lactation. Pregnancy was determined by palpation of the abdomen, whereas lactation was diagnosed by the presence of enlarged mammary glands, expression of milk, or hairless patches surrounding the mammary glands. Female bats that displayed no conspicuous signs of reproduction were classified as nonreproductive (Racey, 1988). To aid the bat

identification, standard morphometrics was measured including the total length, tail to vent length, hind foot length, external ear length, forearm length and body weight (Ingle and Heaney, 1992).

After identification, bats were marked with a water proof nail polish on its hindfoot nail using a coding system. It was released after morphometrics were taken or if the bat was weakened by the capture, it was nursed by feeding with sugar solution and allowed them to hang and rest.

Taxonomic Diversity (TD)

Species Richness and Diversity

Diversity indices for bats across land transformations was assessed using various parameters including Species richness, Species composition, Species evenness, Species relative abundance, Simpsons and Shannon's diversity index and Berger-Parker dominance and rarity index.

To facilitate comparisons, Shannon diversity index were transformed into its effective number of species or Hill's numbers based from the mathematical conversion proposed by Jost (2006). The equivalent number is the number of maximally dissimilar species with equal abundances that is required to produce the empirical value of a metric (Villeger *et al.* 2012). This transformation facilitates intuitive interpretation of differences

between assemblages or dimensions because indices are expressed in the same units (Jost 2006).

Species Accumulation and Abundance Curve

A rarefaction curve (species based and abundance based) was constructed to assess the completeness of bat assessment using the EstimateS software. Observed species richness (Sobs MaoTau) and the nonparametric species richness estimator Chao 2 (which accounts for non-registered species and differences in sampling effort) was used to examine species richness covered by samples. Additionally, a rank-abundance curves was constructed to explore the bat assemblage structure between forest habitat and land transformed habitat (Jungle rubber, rubber and oil palm plantations). Rank-abundance curves allow the comparison of number of species, relative abundances of species, number of rare species and equitability (Stoner, 2005). Rank abundance curves were compared with Kolmogorove Smirnov two-sample tests (Siegel, 1956). Species composition in each transformation system were compared with a nonmetric multidimensional scaling (NMDS) using Bray-Curtis similarity (McCune *et al.*, 2002).

Similarity of Bat Community Structure

To compare similarities of species composition among sites, the Bray - Curtis Index was used. This quantitative similarity index is based on the formula $BCd = 1 - (|xi$

$- |x_j| / (x_i + x_j)$), where x_i and x_j are the total number of individuals in sites a and b. The Bray–Curtis similarity is bounded between 0 and 1, where 1 means the two sites have the same composition (that is they share all the species), and 0 means the two sites do not share any species.

A cluster analysis of the Bray - Curtis values using group-average clustering was also performed to summarize relative similarity of bat community structure across habitat types.

Functional Diversity (FD)

Functional diversity quantifies the diversity of species traits in biological communities, and is widely regarded as a key to understanding ecosystem processes and environmental stress or disturbance (Mouillot *et al.*, 2013). A higher functional diversity signifies greater differences among species trait values, more distinct ecological functions, and thus potentially better functional stability to perturbations caused by human impacts or environment stresses (Flynn *et al.*, 2009).

Functional diversity was quantified at two levels : first by calculation of functional metrics considering only the functional group bearing of each identified species (frugivore, nectarivore, omnivore and insectivore) and second, by calculation of functional metrics using functional trait attributes including morphometric characters (forearm length, body length, body size, skull morphology, diet).

Functional Group Diversity

For the first case of functional diversity analysis in each of the land transformation systems, functional diversity was used as an inclusive term to describe aspects of the distribution of species among functional groups within communities. Other operational measures of aspects of functional diversity that was assessed includes the Richness of functional groups which represent the number of functional groups inhabiting a local community; the Diversity of functional groups which reflect the number of groups and equability of species richness among them and was estimated based on the Shannon index; the Evenness of functional groups which reflect the equability in the distribution of species among functional groups and was estimated using the Camargo evenness index; the Dominance of functional groups which describe the degree to which the number of species in the most species-rich functional group dominates the community in terms of species richness and was estimated by the Berger–Parker index.

Functional Trait Matrix

Chiropteran functional diversity was estimated using species abundances and two types of data: categorical (binary/discrete) and mensural (continuous) attributes using traits being functionally important to bats based on existing literature. For each data type, a suite of functional attributes were used to describe particular niche axes or the

functional components. Categorical components were associated with (1) diet (fruits, or plant, nectar or pollen, invertebrates); (2) habitat type (Forest, Agroforest, Rubber plantation, Oil palm plantation). Mensural components were associated with (1) body size (Mass, Forearm length, Head to Body length, Tibia Length), (2) masticatory mode/skull characteristics - Greatest length of skull (GTL), Condyllobasal length Mean value (CCL), Zygomatic breadth (ZB), Breadth of braincase mean value (BB), Palate width at canines (PC) and Mandibular length (MDL).

For each categorical attribute, a species was scored a “1” if it exhibited the characteristic or a “0” if it did not exhibit the characteristic. For each mensural attribute, an average value was obtained for each species based on measurements of multiple male and female adults. Information for all functional attributes were derived from the literature. Measurements of size attributes were augmented by field measurements from the study area.

Functional Diversity Metrics

To examine how the observed patterns of change following land transformation was affected by spatial scale, FD metrics were calculated separately for each habitat and then using summed data for each replicate (four per habitat/land transformation system). FD metrics was calculated using the FD package in R software. (R Development Core Team, 2016).

Having obtained trait data, formulae of Villéger *et al.*, 2008, Villéger *et al.*, 2010, Villéger *et al.*, 2011 were used to calculate four complementary measures of functional diversity: (1) functional richness (FRic), which quantifies the volume of functional space that a set of species occupies; (2) functional evenness (FEve), which describes how species' abundances are distributed throughout the occupied functional space; (3) functional divergence (FDiv), which summarizes the variation in species abundances with respect to the centre of functional space; (4) functional dissimilarity (FDis), which indicates the overlap of functional space between two or more communities; and (5) Rao's quadratic entropy (Q). In these methods, traits act as coordinates in functional space, thus identifying a species' functional niche (Villéger *et al.*, 2008).

Traits were given equal weighting and species were weighted by their relative abundance. Because the functional traits were a mixture of variable types, a distance matrix using the Gower distance measure were calculated before running a principal coordinates analysis (PCoA) to calculate a new trait matrix of transformed coordinates (Villéger *et al.*, 2008). Four PCoA axes were used to calculate the functional measures using a multidimensional convex hull to position species in functional trait space.

Functional diversity metrics were all calculated using the FD, geiger and picante package in R version 3.3.3 (R Core Team 2017).

Phylogenetic Diversity (PD)

Phylogenetic Tree

The phylogenetic dimension was evaluated based on branch lengths from a time-calibrated species-level phylogeny of bats (Agnarsson *et al.*, 2011). The time calibrated phylogenetic tree based on Cytochrome b was represented by 648 terminal bat taxa constructed through Bayesian analysis following a General Time Reversible with gamma distribution and variable sites (GTR – G + I) substitution model with separate model estimation for first, second, and third codon positions.

Five species (*Cynopterus minutus*, *Myotis sp*, *Hesperoptenus sp*, *Kerivoula pellusida*, *Kerivoula minuta*) from Sumatra, Indonesia and four species (*Rhinolophus arcuatus*, *Rhinolophus sp.*, *Murina sp*, *Glischropus tylopus*) from Palawan, Philippines were not present in the supertree and their positions were substituted by the most closely related congener in the tree. The effects of these substitutions on phylogenetic characteristics of strata likely are small because the lengths of terminal branches for congeners are often the same or very similar within the context of tree height (distance from root to tips) in the supertree. In general, analyses of phylogenetic biodiversity are robust with respect to variation in resolution of more recent phylogenetic relationships (Webb 2000); therefore, replacements of taxa missing from the tree with sister taxa will not greatly affect the results.

Phylogenetic Diversity Metrics

Tree-Based Measures of Phylogenetic Diversity and Distance-Based Measures of Phylogenetic Diversity were calculated to assess the phylogenetic diversity of bats in forest and land transformation systems.

Tree-based phylogenetic metrics calculated were (1) Faith's Index (PD) described as the sum of the branch lengths connecting all species in an assemblage; (2) Evolutionary Heritage (EH) that was designed to be different from Faith's Index by its inclusion of the root and provides more information regarding the long evolutionary history leading up to the species found in the community and (3) Weighted Faith Index (WPD) which include information regarding the relative abundance of individual species in the assemblages being analyzed.

Distance-based phylogenetic metric were Phylogenetic Species Variability (PSV) that quantifies how phylogenetic relatedness decreases the variance of this hypothetical unselected trait shared by all species in the community. To calculate PSV, only information about the phylogenetic relatedness of species in a community is needed, not information about any particular trait. Nonetheless, framing this measure in the context of a hypothetical neutral trait gives a metric that has not only an intuitive interpretation but also appealing statistical properties. The second metric quantifies Phylogenetic Species Richness (PSR) as the number of species in a community multiplied by the community's PSV. This metric is directly comparable to the traditional metric of species richness but includes phylogenetic relatedness. The third metric measures Phylogenetic Species

Evenness (PSE). It is the metric of PSV modified to incorporate relative species abundances. The maximum attainable value of PSE (i.e., 1) occurs only if species abundances are equal and species phylogeny is a star (i.e., a phylogeny that depicts a burst of radiation with each species evolving independently from a common starting point (Felsenstein 1985). Thus, PSE is a measure of both phylogenetic and species evenness.

Additionaly, MPD (mean pairwise distance) was calculated which is the average phylogenetic distance between individuals in a community. This is influenced by relationships in deep evolutionary time. Higher values suggest that species are distributed across a wide range of clades, and low values suggest phylogenetic clustering. Moreover, MNTD (mean nearest taxon distance) – the average distance between an individual and the most closely related (non-conspecific) individual was also calculated. High level of MNTD suggest that closely related individuals do not co-occur in the community, and low levels suggest that they do.

These tree-based and distance-based phylogenetic metrics were calculated using the picante package in R version 3.3.3 (R Core Team 2014).

Phylogenetic Assemblage Structure

Phylogenetic assemblage structure was investigated with the Net Relatedness Index (NRI) which is calculated as the inverse of the standardized effect size of the mean phylogenetic distance (MPD) between all taxon pairs in the assemblage phylogeny (Webb *et al.* 2002). To obtain NRI, the observed MPD value within each assemblage was

compared against the values from 999 sets of randomized assemblages created with the independent swap algorithm (Gotelli 2000), with all species present across habitat types as the source pool. This algorithm keeps the species numbers of the assemblages constant but randomizes the species occurrences across the assemblages, according to the occurrence frequencies of species in the original dataset. NRI was calculated as $NRI = -1 \times (\text{observed MPD} - \text{mean of MPD values from randomizations})/\text{standard deviation of MPD values from randomizations}$ (Webb *et al.* 2002). Therefore, NRI values > 0 indicate phylogenetic clustering, NRI value < 0 indicate phylogenetic evenness or over-dispersion, and NRI = 0 denotes random phylogenetic structure (Webb *et al.* 2002).

Phylogenetic Diversity Similarity among Communities

The phylogenetic similarity of the bat communities was assessed using PhyloSor UniFrac. UniFrac estimates the distance between communities as the fraction of the branch length of the phylogenetic tree that leads to descendants from either one environment or another, but not both. It seeks to quantify the unique fraction of the phylogeny contained in each of the two communities being compared. The PhyloSor and UniFrac indices can be both considered as ‘broad-sense’ measures of phylogenetic turnover (i.e. incorporating differences in evolutionary history between communities attributable to phylogenetic diversity gradients) (Leprieur *et al.*, 2012).

Both the PhyloSor and UniFrac indices range from 0 (the two communities are composed of similar species and hence share the same branches in the rooted phylogenetic tree) to 1 (the two communities are composed of distinct species that share no branch in the rooted phylogenetic tree). The two indices differ only because PhyloSor double weights the branch lengths shared by the two communities (i.e. the denominator of PhyloSor corresponds to the sum of phylogenetic diversity characterizing each community).

PhyloSor and Unifrac indices were calculated using the package GUniFrac and Picante in R version 3.3.3 (R Core Team 2014).

CHAPTER IV

RESULTS

Taxonomic Diversity

Species Richness and Composition

A total of 470 bat individuals representing 25 species, 13 genera and 6 families were recorded in Sumatra, Indonesia (Table 1). The most speciose family was Vespertilionidae with seven recorded species represented by *Hypsugo macrotis*, *Kerivoula hardwickii*, *K. minuta*, *K. pellusida*, *Tylonycteris robustula*, *Myotis* sp. and *Hesperoptenus* sp., followed by Pteropodidae with six species (*Balionycteris maculata*, *Cynopterus brachyotis*, *C. sphinx*, *C. minutus*, *Dyacopterus brooksi* and *Macroglossus sobrinus*) and Rhinolopidae with six species (*Rhinolophus affinis*, *R. sedulous*, *R. trifoliatus*, *R. acuminatus*, *R. luctus* and *R. lepidus*), Hipposideridae with four species (*Hipposideros bicolor*, *H. cervinus*, *H. diadema* and *H. orbiculus*) and Megadermatidae and Nycteridae with one species each are represented by *Megaderma spasma* and *Nycterus tragata* respectively.

The five most frequently captured species were *C. brachyotis*, *C. sphinx*, *B. maculata*, *R. trifoliatus* and *H. cervinus* representing 87.6% of total captures. *C.*

brachyotis alone accounted for 64.9% of total captures. The remaining 20 species had fewer than 10 captures each and accounted for 12.6% of captures with *C. minutus*, *R. affinis*, *R. acuminatus*, *R. lepidus*, *T. robustula*, *Myotis* sp. and *Hesperoptenus* sp. as singletons.

The taxonomic composition of the bat species assemblages varied among the four habitats, based on both total captures and captures in each habitat separately. In forest sites, Hipposiderids accounted for 47.8% of captures, Pteropodids for 22.1%, and Rhinolopids for 18.6%. In Jungle Rubber sites, Pteropodids represented 67.7% of captures, Rhinolopids 12.5%, and Hipposiderids 8.3%. In Rubber plantations, Pteropodids represented 95.9% of captures, Rhinolopids 3.1%, and Hipposiderids 1.03%. Oil palm plantations showed a more pronounced difference with Pteropodids accounting 97.5% of the captures in that habitat and the absence of Rhinolopids and Hipposiderids genera.

Species richness was highest in forest habitat (18 species), followed by Jungle Rubber (14 species), Rubber plantation (8 species) and Oil palm plantation (7 species) has the least number of recorded species. Species richness in Oil palm plantations is 61% lower than that of forest, 50% lower with that of Jungle rubber and 13% lower with that of rubber plantation. Four species were captured exclusively in forest sites (*H. orbicularis*, *R. affinis*, *R. acuminatus* and *T. robustula*), one species in Jungle rubber sites (*R. lepidus*), one species in Rubber plantations (*C. minutus*), and three species were captured only in the Oil palm plantations (*H. macrotis*, *Myotis* sp. and *Hesperoptenus* sp.).

Table 1. Summary of species and number of captured individuals per species across land transformation system in Jambi, Sumatra, Indonesia.

TAXONOMIC CLASSIFICATION		HABITAT			
Family	Species	Forest	Jungle Rubber	Oil Palm	Rubber
Pteropodidae	<i>Balionycteris maculata</i>	14	12	0	1
	<i>Cynopterus brachyotis</i>	3	12	208	82
	<i>Cynopterus sphinx</i>	0	8	21	5
	<i>Cynopterus minutus</i>	0	0	0	1
	<i>Dyacopterus brooksi</i>	2	0	0	1
	<i>Macroglossus sobrinus</i>	0	0	4	3
Hipposideridae	<i>Hipposideros bicolor</i>	6	2	0	0
	<i>Hipposideros cervinus</i>	30	1	0	1
	<i>Hipposideros diadema</i>	4	0	0	0
	<i>Hipposideros orbiculus</i>	1	1	0	0
Rhinolopidae	<i>Rhinolophus affinis</i>	1	0	0	0
	<i>Rhinolophus sedulus</i>	3	1	0	0
	<i>Rhinolophus trifoliatus</i>	10	4	0	0
	<i>Rhinolophus acuminatus</i>	1	0	0	0
	<i>Rhinolophus luctus</i>	1	0	0	3
	<i>Rhinolophus lepidus</i>	0	1	0	0
Vespertilionidae	<i>Hypsugo macrotis</i>	0	0	2	0
	<i>Kerivoula hardwickii</i>	1	1	0	0
	<i>Kerivoula minuta</i>	2	1	0	0
	<i>Kerivoula pellusida</i>	1	2	0	0
	<i>Myotis sp</i>	0	0	1	0
	<i>Tylonycteris robustula</i>	1	0	0	0
	<i>Hesperoptenus sp.</i>	0	0	1	0
Megadermatidae	<i>Megaderma spasma</i>	4	1	2	0
Nycteridae	<i>Nycteris tragata</i>	1	1	0	0
Total		86	48	239	97

In Palawan, Philippines, a total of 11 bat species were captured with a total abundance of 606 bat individuals under five Chiropteran families – Pteropodidae, Vespertilionidae, Hipposideridae, Rhinolopidae and Megadermatidae - representing 24% of the bat fauna known to occur in the Philippines (Heaney *et al.*, 1998) (Table 2). Four species belong to Family Pteropodidae including *C. brachyotis*, *M. minimus*, *Eonycteris spelaea* and *Rousettus amplexicaudatus*, three species belong to Family Rhinolopidae including *R. acuminatus*, *R. arcuatus* and *Rhinolophus sp.*, five species belong to family Vespertillionidae including *Glischropus tylopus*, *Murina cyclotis*, *Murina sp*, *Myotis macrotarsus* and *Pipistrellus javanicus* and a single species for family Hipposideridae and Megadermatidae represented by *H. diadema* and *M. spasma* respectively.

The same with Indonesia, *C. brachyotis* accounted for 60.3% of total captures mostly at Oil palm and rubber plantations. The five most frequently captured species in Palawan were *C. brachyotis*, *M. minimus*, *H. diadema*, *R. arcuatus* and *M. spasma* accounting 94.9% of the total captures. *H. diadema*, *R. arcuatus* and *M. spasma* had the highest number of captures in forest sites while *C. brachyotis* in oil palm plantations.

Bat species assemblages in Palawan varied among the four habitats. In forest sites, Pteropodids accounted for 39.64% of captures, Rhinolopids for 28.83%, Hipposiderids for 20.72% and Vespertilionids for 0.90% of captures. In Jungle Rubber sites, Pteropodids represented 91.04% of captures, Hipposiderids 3.73%, Vespertilionids 2.24% and Rhinolopids 0.75%. In Rubber plantations, Pteropodids accpunted for 95.86% of captures and Hipposiderids for 1.03%. In Oil Palm plantations, Pteropodids accounted for 98.96% of the captures while Hipposiderids and Rhinolopids accounted for 0.52%

Table 2. Summary of species and number of captured individuals per species across land transformation system in Aborlan, Palawan, Philippines.

TAXONOMIC CLASSIFICATION		HABITAT			
Family	Species	Forest	Jungle Rubber	Oil Palm	Rubber
Pteropodidae	<i>Cynopterus brachyotis</i>	29	77	173	123
	<i>Macroglossus minimus</i>	11	40	17	35
	<i>Eonycteris spelaea</i>	3	5	0	4
	<i>Rousettus amplexicaudatus</i>	1	0	0	0
Hipposideridae	<i>Hipposideros diadema</i>	23	5	1	3
Rhinolopidae	<i>Rhinolophus acuminatus</i>	11	0	0	0
	<i>Rhinolophus arcuatus</i>	20	1	0	0
	<i>Rhinolophus sp.</i>	1	0	0	0
Vespertilionidae	<i>Glischropus tylopus</i>	0	1	0	0
	<i>Murina cyclotis</i>	0	1	0	1
	<i>Murina sp</i>	0	1	0	0
	<i>Myotis macrotarsus</i>	1	0	0	0
	<i>Pipistrellus javanicus</i>	0	0	0	1
Megadermatidae	<i>Megaderma spasma</i>	11	3	1	2
Total		111	134	192	169

and 1.18% respectively. Such increase in frugivore percentage was due to an increase of abundance of a single species *C. brachyotis* rather than an increase in number of pteropodid species.

Having the same species richness pattern observed in Sumatra, Indonesia, species richness in Palawan was highest in forest habitat (10 species), followed by Jungle Rubber (9 species), Rubber plantation (7 species) and Oil palm plantation (4 species) having the least number of recorded bat species. Species richness in Oil palm plantation is 60% lower than that of forest, 56% lower with that of Jungle rubber and 43% lower with that of Rubber plantation.

A sample based rarefaction curve was constructed to see the completeness of sampling and facilitate meaningful comparison of species richness among the habitat types. In Sumatra, Indonesia, Forest and Jungle rubber habitat species rarefaction curves showed that species richness doesn't reached an asymptote and new species will likely be added to the list. In contrast, the land transformed habitat – Rubber and Oil Palm plantations showed an asymptotic trend (Figure 1a). The rarefied curve suggested that Forest had the most number species but Oil Palm plantation, in contrast, had the fewest species.

In Palawan, Philippines, sample based rarefaction curve showed the same trend with Forest and Jungle rubber habitat having the most number of species while Oil Palm Plantation having the least number of species recorded (Figure 1b). It is seen that new bats are likely to be captured in forest habitat. A similar situation occurred in Jungle Rubber habitat where the community seems to be underestimated. The rarefaction curves

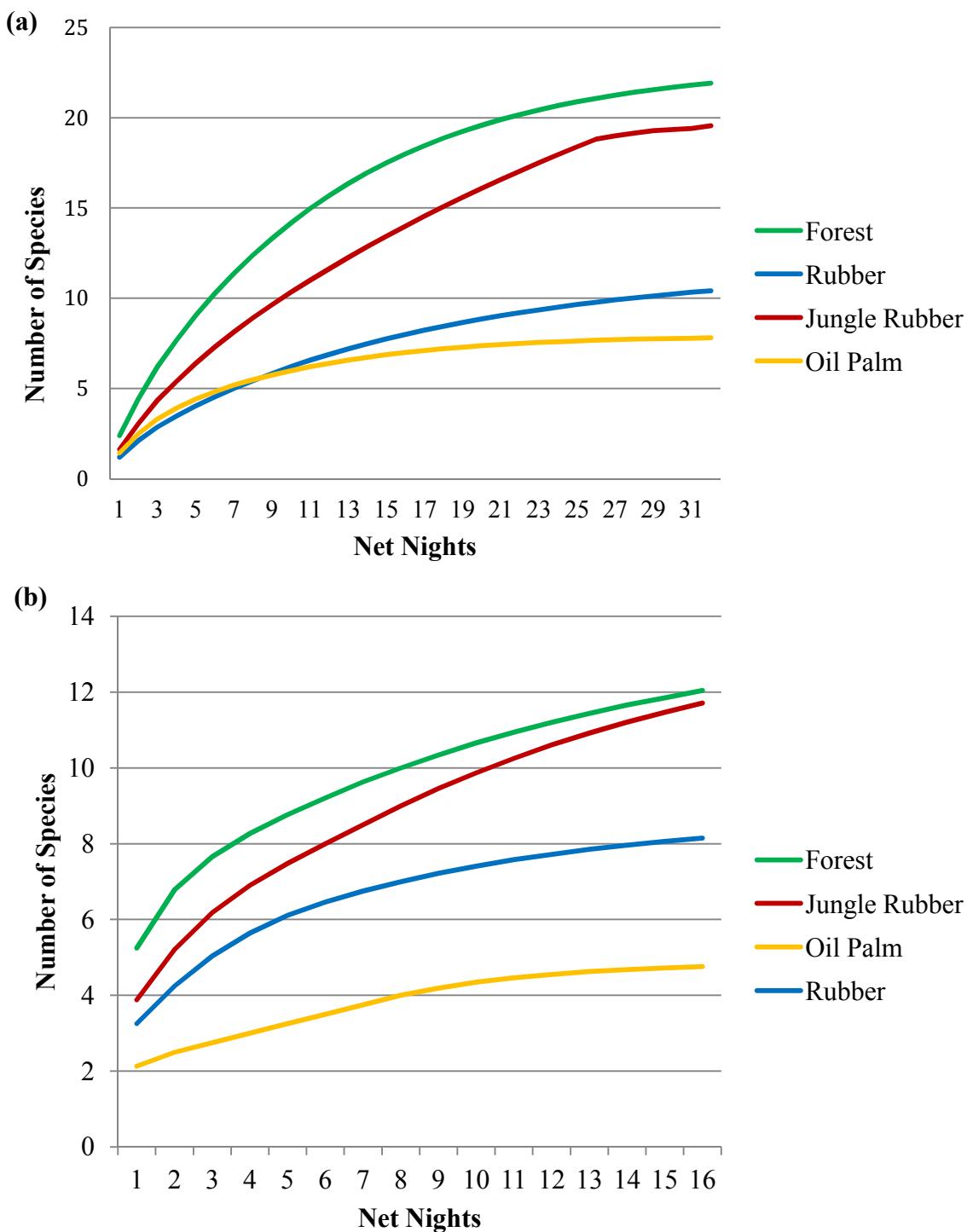


Figure 1. Sample based rarefaction curves showing the number of bat species expected from mist netting in (a) Sumatra, Indonesia and (b) Palawan, Philippines.

for the two land transformed habitat – Rubber and Oil palm plantations reached an asymptote indicating that no new bat species will likely be added on the list even at increased sampling effort on these sites.

The rarefaction curves for both Indonesia and Palawan across land transformed systems showed that the rate of species accumulation was comparable for both Forest and Jungle Rubber habitat. And the species accumulations for these two habitats were more than twice from that of Oil palm plantation.

Species Abundance, Rarity and Dominance

The rank-abundance curve of the bat community in Sumatra, Indonesia showed that the bat assemblages in transformed habitat – Rubber and Oil palm plantations were strongly dominated by a few species particularly generalist species – *C. brachyotis* and *C. sphinx* (Figure 2). The bat community in Forest and Jungle Rubber showed a small number of abundant species and a large proportion of rare species (*D. brooksi*, *H. orbiculus*, *R. affinis*, *R. sedulus*, *R. acuminatus*, *R. luctus*, *R. lepidus*, *K. hardwickii*, *K. minuta*, *K. pellusida*, *T. robustula* and *N. tragata*).

The following patterns could be observed in the rank-abundance plots across different habitats in Sumatra, Indonesia: (1) the bat species *C. brachyotis* was the most dominant in the transformed habitat - Oil palm and rubber plantations and showed a decreasing dominance in Forest and Jungle rubber habitat; (2) Rare species present in Forest habitat (*H. orbiculus*, *R. affinis*, *R. acuminatus* and *T. robustula*) tended to be

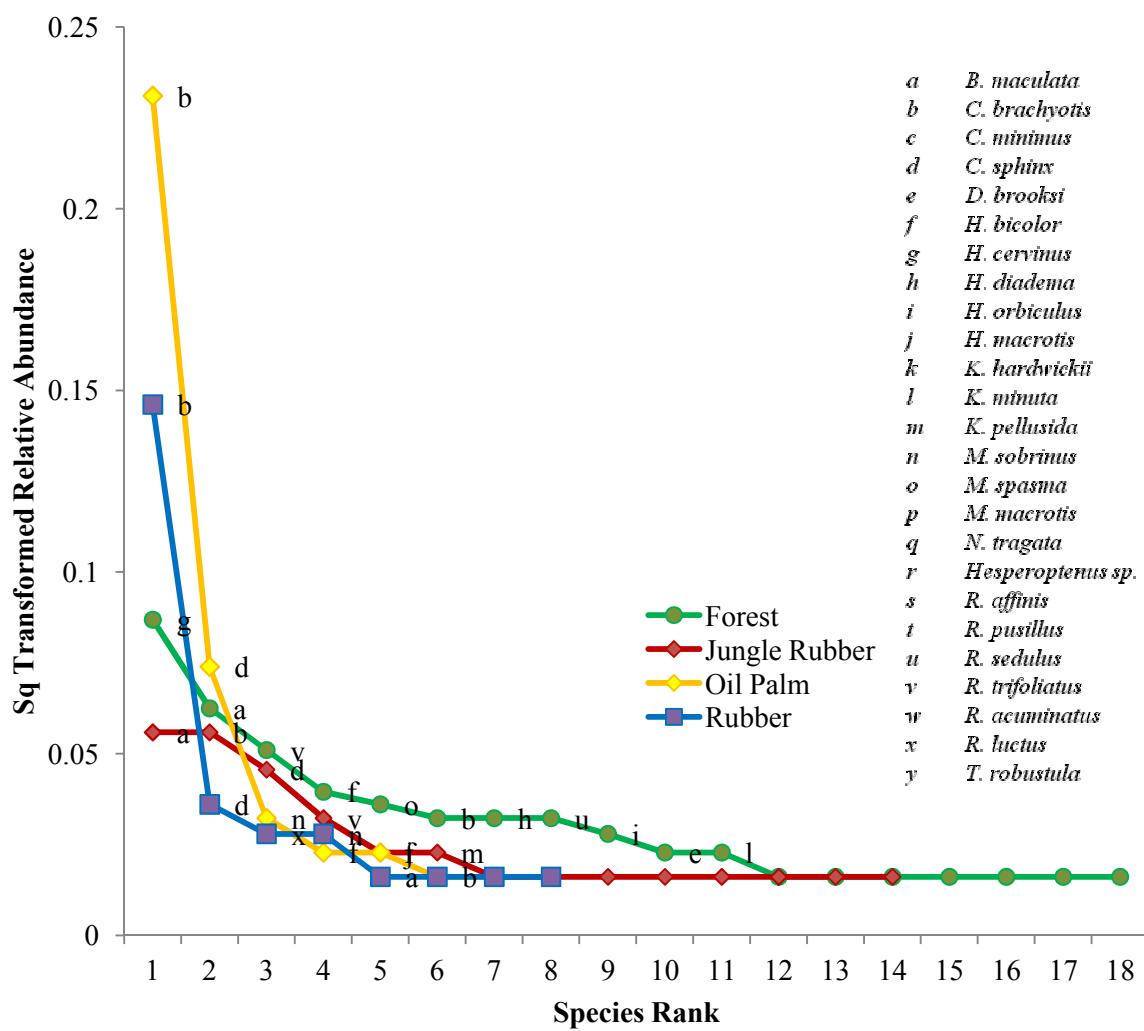


Figure 2. Rank-abundance curves for each habitat showing each bat species' position within the assemblage in Sumatra, Indonesia (species abundance are presented in the Appendix E)

absent in Rubber and Oil Palm habitat ; (3) Species that was the most dominant in forest (*H. cervinus*) was rare in Jungle Rubber and Rubber plantation habitat and tended to be absent in Oil palm plantations; and (4) some species in transformed habitat (Rubber and Oil Palm plantations) were not registered in Forest (*C. sphinx*, *M. sobrinus*, *H. macrotis*).

In Palawan, Philippines, the rank abundance curve showed the same trend in which few abundant species and a large proportion of rare species dominated the Forest habitat. Rubber and Oil palm plantation were dominated by disturbance tolerant species *C. brachyotis* and *M. minimus* (Figure 3). The following patterns could be observed in the rank-abundance plots across different habitats in Palawan, Philippines: (1) *C. brachyotis* had the highest capture rate in all habitat but gradually decreased in abundance from Oil palm, Rubber, Jungle Rubber and Forest having the least abundance of this species, (2) Some species with high dominance in the forest habitat were rare (*M. spasma*, *H. diadema*) and even absent (*R. arcuatus*) in transformed habitat - Rubber and Oil palm plantations (Figure 4), (3) A number of rare species (*E. spelaea*, *R. amplexicaudatus*, *R. acuminatus*, *Rhinolophus* sp., *G. tylopus* and *M. macrotarsus*) were present in Forest and Jungle Rubber but absent in Rubber and Oil palm plantations.

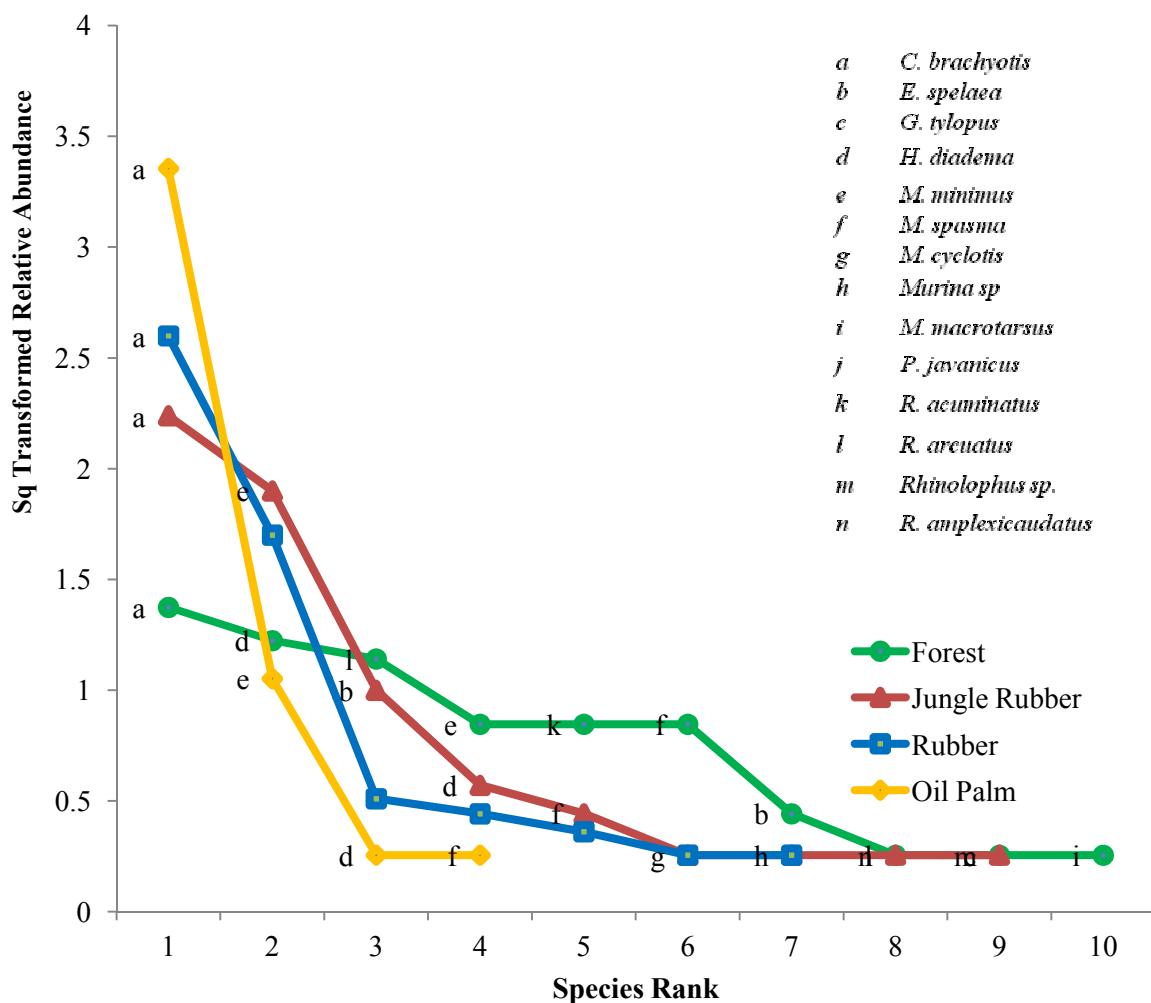


Figure 3. Rank-abundance curves for each habitat showing each bat species' position within the assemblage in Palawan, Philippines (species abundance are presented in the Appendix F)

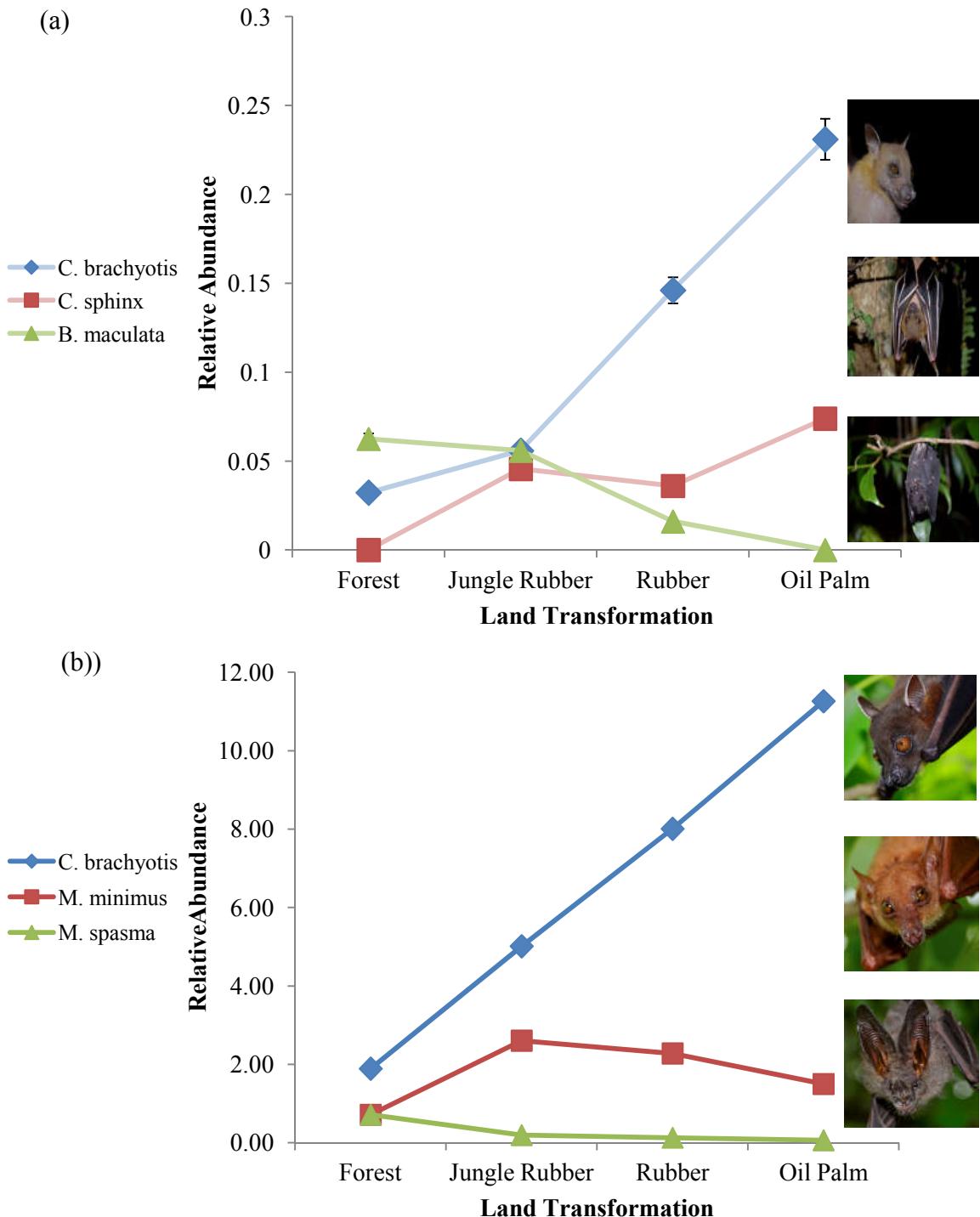


Figure 4. Abundance of the three most captured species across habitat in (a) Sumatra, Indonesia and (b) Palawan, Philippines

Species Diversity

Species diversity Analysis on the bat diversity in Sumatra, Indonesia based on several diversity metrics showed that bat diversity was highest in Forest (Shannon diversity = 2.21, Simpson diversity = 0.82, Simpson Inverse = 1.94, Fischer Alpha = 6.93) followed by Jungle Rubber (Shannon diversity = 2.11, Simpson diversity = 0.83, Simpson Inverse = 2.02, Fischer Alpha = 6.64), then Rubber plantation (Shannon diversity = 0.69, Simpson diversity = 0.28, Simpson Inverse = 0.81, Fischer Alpha = 2.07) and Oil palm plantation having the lowest diversity value (Shannon diversity = 0.53, Simpson diversity = 0.23, Simpson Inverse = 0.45, Fischer Alpha = 1.35) (Table 3). One sample t test showed that diversity value between Forest and Jungle rubber was similar ($P > 0.05$) while significant difference was observed between species diversity between forest and rubber plantation and between forest and Oil palm plantations ($P < 0.05$). Species evenness was comparable between Forest and Jungle rubber with an evenness value of 0.51 and 0.59 respectively showing that bat community was represented with even abundances of bat species. In contrast, evenness values for Rubber and Oil palm plantations were low with an evenness value of 0.25 and 0.24 respectively as this transformed habitat were dominated by few species with an extreme abundance value (i.e. *C. brachyotis*). Hence, the highest value for Dominance measure was observed in Rubber and Oil palm plantations ($D = 0.72$ and $D = 0.77$ respectively).

Table 3. Several species diversity metrics in each land transformation system in Sumatra, Indonesia and Palawan, Philippines.

ECOLOGICAL INDICES	INDONESIA				PALAWAN			
	F	JR	OPP	R	F	JR	OPP	R
Species Richness (SR)	18	14	7	8	10	9	4	7
Species Evenness (E)	0.51	0.59	0.24	0.25	0.67	0.35	0.36	0.33
Dominance (D)	0.18	0.17	0.77	0.72	0.17	0.42	0.82	0.57
Shannon Diversity (H')	2.21	2.11	0.53	0.70	1.89	1.16	0.36	0.83
Shannon Exponential (Effective Number of Species)	10	8	2	2	7	3	1	2
Simpson Diversity	0.82	0.83	0.23	0.28	0.83	0.58	0.18	0.43
Simpson Inverse	1.94	2.02	0.45	0.81	0.95	0.78	0.29	0.54
Fisher alpha	6.94	6.64	1.35	2.07	2.66	2.18	0.72	1.47
Chao-1	24.92	29.67	8	13.94	12.97	14.96	4.99	8.99
Chao-2	21.75	32.98	7.94	9.88	13.94	14.25	4.88	8.75

F= Forest, JR = Jungle Rubber, OPP = Oil palm plantation and R = Rubber plantation

To determine the true diversity of the bat community for all habitats, the effective number of species (ENS) or Hills number based on Shannon diversity index was computed. The Effective number of species magnified the differences in species richness between continuous forest and land transformed systems (Jungle Rubber, Rubber plantation and Oil palm plantations). Effective number of species declined across habitat with the pronounced decline at land transformed habitat – Rubber and Oil palm plantations (Figure 5). The reduction in species diversity from forest to Rubber plantations was on the order of 5 times. The same with Oil palm plantations which was 5 times less diverse with that of the forest.

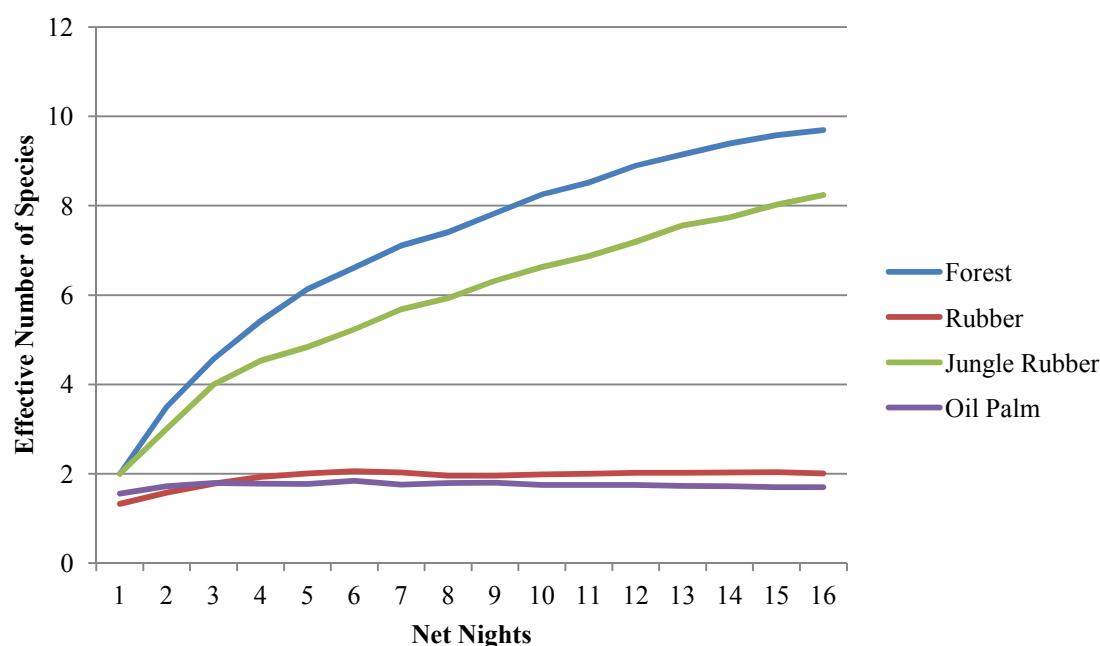


Figure 5. Species diversity curve based on the Effective Number of Species (Shannon exponential) in Sumatra, Indonesia.

In Palawan, Philippines, same species diversity trend was observed. Species diversity based on several diversity metrics was highest in Forest (Shannon diversity = 1.90, Simpson diversity = 0.83, Simpson Inverse = 0.95, Fischer Alpha = 2.66) followed by Jungle Rubber (Shannon diversity = 1.16, Simpson diversity = 0.58, Simpson Inverse = 0.78, Fischer Alpha = 2.18) and Rubber plantations (Shannon diversity = 0.83, Simpson diversity = 0.43, Simpson Inverse = 0.54, Fischer Alpha = 1.47) and Oil palm plantations having the lowest diversity value (Shannon diversity = 0.36, Simpson diversity = 0.18, Simpson Inverse = 0.29, Fischer Alpha = 0.72). Significant difference on species diversity was observed between Forest and Rubber plantations and between Forest and Oil palm plantations ($P < 0.05$).

Species evenness value was highest at Forest habitat ($E = 0.67$) exemplifying the even abundance distribution of each representative bat species recorded in forest habitat. Evenness value for Jungle Rubber, Rubber and Oil pal plantations were low ($E = 0.35$, 0.36, 0.33 respectively) which is indicative of the high abundance of few species. Dominance value was highest in Oil palm plantations ($D = 0.82$) followed by Rubber plantations ($D = 0.57$) and gradually decreased in Jungle rubber ($D = 0.42$) and Forest ($D = 0.17$).

Forest habitat had a true diversity of 7 effective species and Jungle rubber had a true diversity of 3 species while Rubber and Oil palm plantations had a true diversity of 2 and 1 effective species respectively (Figure 6). Species diversity in Rubber plantations was 3.5 times less diverse from that of the forest while an Oil palm plantation was 7 times less diverse.

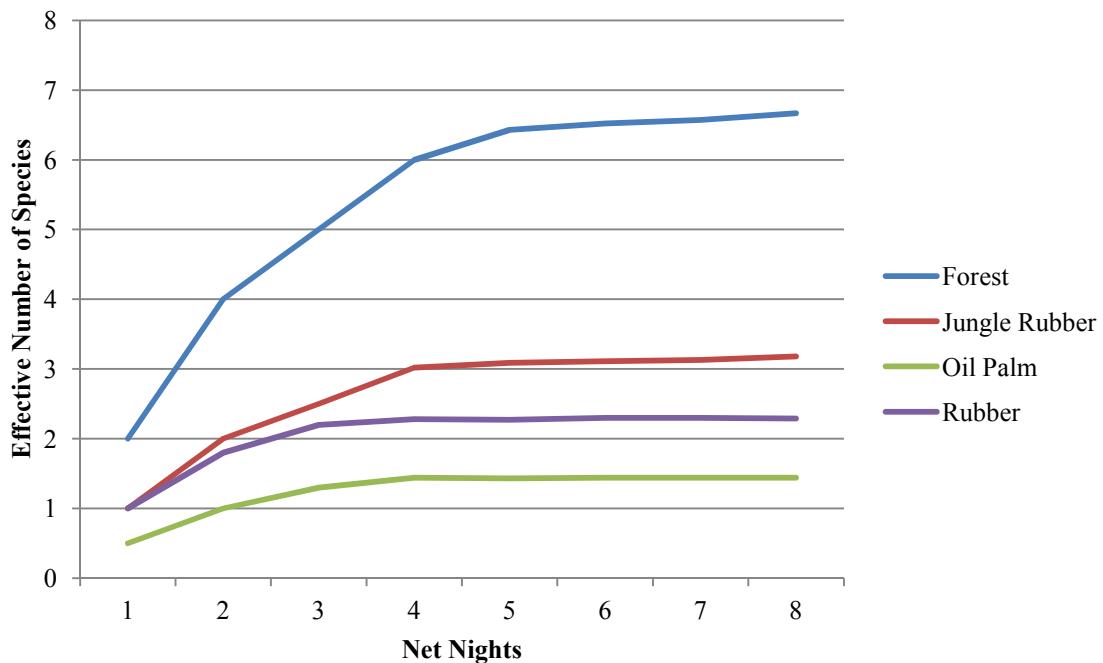


Figure 6. Species diversity curve based on the Effective Number of Species (Shannon exponential) in Palawan, Philippines.

Similarities of Bat Community Structure

Differences in community structure were linked with differences in species similarity among habitats. In Sumatra, Indonesia, community similarity was low between Forest and Oil palm plantation (0.031) and between Forest and Rubber plantation (0.077). Forest and Jungle rubber have a similarity value of 0.4 (Table 4).

Community structure of an Oil palm plantation had 53.6% degree of similarity with that of Rubber plantation, 14.6% with that of Jungle rubber and only 3% with that of Forest habitat. Rubber plantation had 26.2% similarity with Jungle rubber and only 7%

with Forest. The nonparametric Kruskal wallis test showed a significant difference on the community structure of chiropteran fauna between Oil palm plantation and forest ($P = 0.0086$) and between Rubber plantation and forest ($P = 0.0087$).

Table 4. Simmilarity of bat community between habitat types based on Bray-Curtis Index of Similarity in Sumatra, Indonesia.

COMMUNITY SIMILARITY	FOREST	JUNGLE RUBBER	OIL PALM	RUBBER
Indonesia				
Forest	1	0.43	0.031 *	0.077 +
Jungle Rubber		1	0.146	0.262
Oil Palm	* p = 0.0086		1	0.536
Rubber	+ p = 0.0087			1
Palawan				
Forest	1	0.425	0.277 *	0.343
Jungle Rubber		1	0.589	0.805
Oil Palm	* p = 0.0408		1	0.787
Rubber				1

For the community structure of bat fauna in Palawan, Philippines, same similarity pattern was observed in which community similarities in reference with forest habitat had gradually decreased across land transformed systems (Jungle rubber, Rubber plantation

and Oil palm plantation). Community structure of Palawan bat fauna in Oil palm plantation had 78.7% degree of similarity with that of Rubber plantation, 58.9% with that of Jungle rubber and only 27.7% with that of Forest habitat. Rubber plantation had 80.5% similarity with Jungle rubber, 78.7% with that of Oil palm and only 34.3% with Forest. Kruskal wallis test on the community structure of chiropteran fauna in Palawan showed a significant difference between Oil palm plantation and Forest habitat ($P = 0.0408$).

The relationship between survey sites was analysed using a Non-metric Multidimensional scaling (NMDS) ordination and showed a revealed distinct differences between an intact habitat (Forest and Jungle rubber) and land transformed to monoculture plantation habitat (Rubber and Oil palm plantations). Forest habitat clustered and showed an overlap with Jungle Rubber habitat while Rubber plantation clustered with Oil palm plantation indicating high similarity in assemblage structure (Figure 7).

In Palawan, Indonesia, three distinct clusters could be distinguished representing a gradient in species composition from Forest sites to transformed habitats – Rubber and Oil pal plantations. Forest and Jungle Rubber habitat clustered together while Rubber and Oil palm plantation had their own cluster.

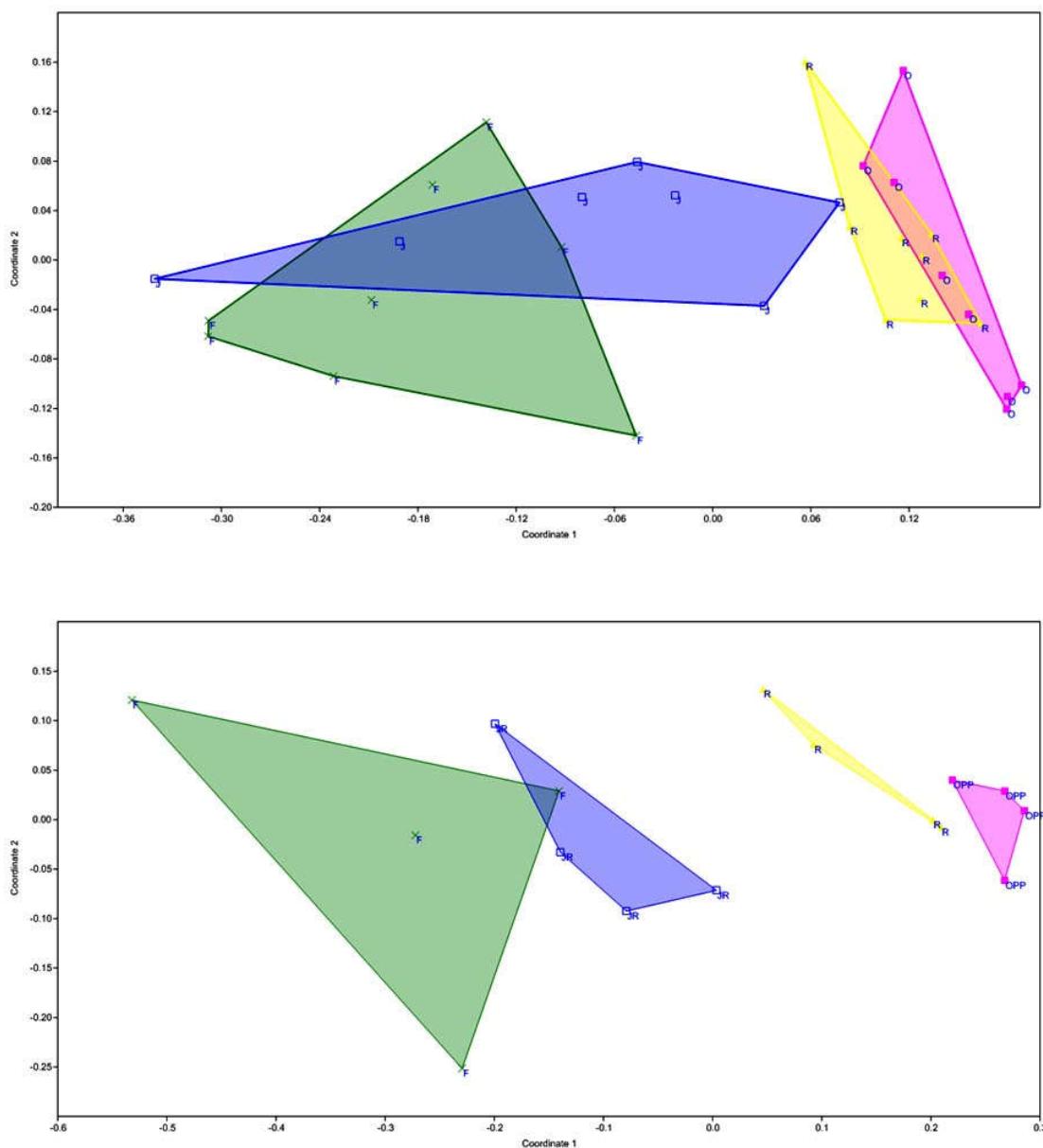


Figure 7. Species composition of bat assemblages in forest (green), at Jungle Rubber (blue), Rubber plantation (purple) and in Oil palm plantations (yellow) ordinated by non-metric multidimensional scaling (NMDS) based on BrayCurtis similarities in (a) Sumatra, Indonesia and (b) Palawan, Philippines.

Functional Diversity

Functional Guild Richness and Diversity

In Sumatra, Indonesia, classification of bats into foraging guilds showed that guild composition in forest habitat was comprised of 17% frugivore species and 83% insectivore species while in Jungle rubber, 21.4% were frugivores and 78.6% were insectivores. Rubber plantation showed an increased proportion of frugivorous species comprising 62.5% of captures while 12.5% were nectarivore and 25% insectivore. Oil palm plantation had a guild composition of 28.6% frugivore, 14.3% nectarivore and 57.1% insectivore. Fruit-eating bats (consuming fruits as primary items in their diets) were the most common in land transformed habitat (Rubber and Oil palm plantation) while insect-eating bats were the most common in Forest habitat and Jungle Rubber (Figure 8).

In Palawan, Philippines, insectivores comprised the most speciose guild throughout all habitat followed by frugivores and nectarivores. In the forest habitat, insectivores comprised 60% of captures while frugivores comprised 20% of the captures. In Jungle rubber, 67% were insectivores, 22% were nectarivore and 11% were frugivore. In Rubber plantations, 57% were insectivore, 29% were nectarivore and 14% were frugivore. Lastly, in oil palm plantations, 50% of the species were insectivores, 29% were nectarivore and 14% were frugivore.

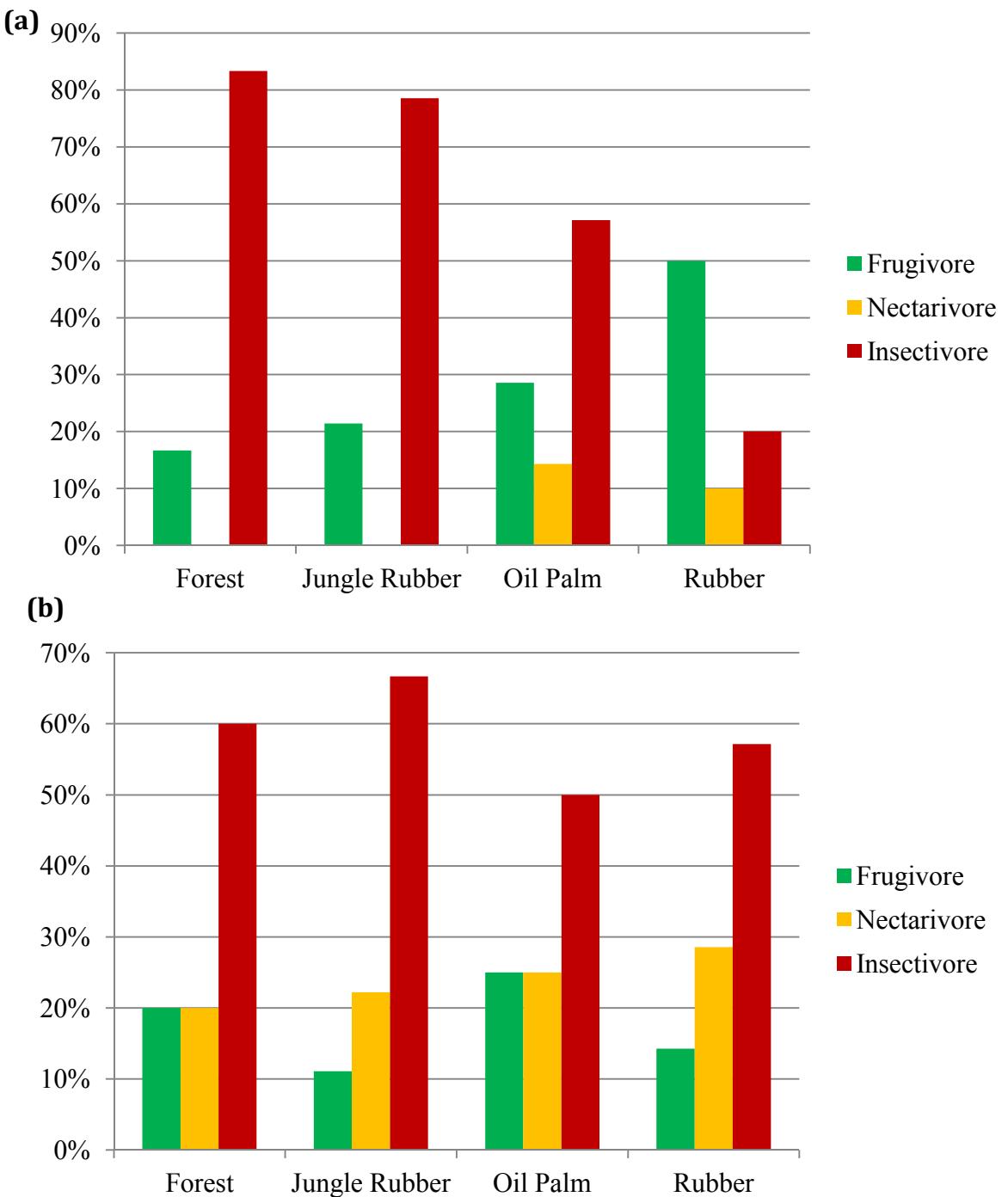


Figure 8. Functional guild composition in each habitat in (a) Sumatra., Indonesia and (b) Palawan, Philippines.

However in terms of number of bat captures per guild, frugivores accounted for the majority of the captures comprising 78.7% while insectivores was comprised only of 19.7% of the total captures. The differences were largely attributable to the pronounced increase in the capture rates of frugivorous and nectarivorous individuals as well as the decrease in capture rates of insectivorous species. Though insectivore guild was represented the most number of species, each insectivorous species were represented only by a few number of captured bat individuals as compared to frugivores which had high number of bat captures.

The functional guild diversity in Sumatra, Indonesia showed a higher diversity at Forest and Jungle rubber habitat and lower diversity for Rubber and Oil palm habitat (Table 5). For several diversity metrics, Jungle rubber had the highest functional group diversity (Shannon diversity = 0.64 , Simpson diversity = 0.44) followed by Forest (Shannon diversity = 0.53, Simpson diversity = 0.34). Rubber plantation had a Shannon diversity of 0.31 and Simpson diversity of 0.14 while Oil palm plantation had a Shannon diversity of 0.20 and Simpson diversity of 0.08. Functional group evenness were high at Forest and Jungle rubber with an evenness value of 0.85 and 0.95 respectively suggesting an even representation of number of species for each of the trophic guild. Species evenness for Rubber and Oil palm plantation were 0.45 and 0.41 respectively indicating a relatively unequal distribution of species representative for each trophic guild. Functional group dominance showed a high dominance value for the transformed habitat (Rubber plantation = 0.93 and Oil palm plantations = 0.96).

In Palawan, Philippines, functional guild diversity was highest in the Forest (Shannon diversity = 0.92, Simpson diversity = 0.55) with Jungle Rubber having a comparable level of diversity (Shannon diversity = 0.90, Simpson diversity = 0.55). Rubber plantation had a Shannon diversity of 0.70 and Simpson diversity of 0.42 while Oil palm plantation had the lowest diversity value (Shannon diversity = 0.36 , Simpson diversity = 0.18).

Table 5. Functional group diversity in each habitat in Sumatra, Indonesia and Palawan, Philippines.

FUNCTIONAL GROUP METRICS	INDONESIA				PALAWAN			
	F	JR	OPP	R	F	JR	OPP	R
Functional Group Diversity (Shannon, H')	0.53	0.64	0.20	0.31	0.92	0.90	0.36	0.70
Functional Group Diversity (Simpson)	0.34	0.44	0.08	0.14	0.55	0.55	0.18	0.42
Functional Group Evenness	0.85	0.95	0.41	0.45	0.84	0.82	0.48	0.67
Functional Group Dominance	0.66	0.56	0.92	0.86	0.45	0.45	0.82	0.59
Berger-Parker	0.78	0.67	0.96	0.93	0.60	0.58	0.90	0.73

F = Forest, JR = Jungle Rubber, OPP = Oil Palm and R = Rubber

The same trends were observed with the functional guild structure in Indonesia. The functional group evenness in Palawan, Philippines was high at both Forest and Jungle Rubber ($E = 0.84$ and $E = 82$ respectively) and lowest in Oil palm plantation ($E = 48$) while functional group dominance was highest in Oil palm plantation ($D = 0.90$) and moderate for both Forest and Jungle Rubber ($D = 60$ and $D = 58$ respectively).

Functional Diversity Measures

Functional diversity measures varied greatly among bat communities across habitat types in the Sumatra, Indonesia. Functional richness (Fric) was highest in Forest habitats (3.31) and lowest in Oil palm plantations (0.01). Functional evenness (Feve) were higher at both Forest and Jungle Rubber (0.71 and 0.74, respectively) and lower at Rubber and Oil palm plantations (0.32 and 0.37 respectively). Functional dispersion (Fdis) were higher at Forest and Jungle Rubber (3.26 and 3.70, respectively), lower in Rubber plantation (1.02) and lowest in Oil palm plantation (0.81). Same pattern was observed using RaoQ as measure functional diversity in which functional diversity was highest at both Forest and Jungle Rubber (12.19 and 14.41, respectively), lower in Rubber plantation (3.60) and lowest in Oil palm plantation (2.67).

Functional richness, divergence and evenness did not differ between Forest and Jungle Rubber ($P > 0.05$). Functional richness was significantly higher in forest than in Oil palm plantation ($P = 0.03$) (Figure 9). Functional evenness, dispersion and RaoQ were all much lower in oil palm than in forest habitat (Feve, $P < 0.004$; Fdis, $P = 0.004$;

RaoQ, $P < 0.003$) (Figure 10). Fdiv, however, was not significantly different in oil palm compared with other habitat ($P = 0.9$) (Figure 11).

Table 6. Functional diversity metrics of bat community across habitats in Sumatra, Indonesia and Palawan, Philippines

FUNCTIONAL DIVERSITY METRICS	INDONESIA				PALAWAN			
	F	JR	OPP	R	F	JR	OPP	R
Fric	3.31	0.66	0.01	1.64	0.04	0.03	0.00	0.02
Feve	0.71	0.74	0.37	0.32	0.51	0.57	0.19	0.48
Fdiv	0.75	0.89	0.99	0.40	0.72	0.92	0.81	0.71
Fdis	3.26	3.70	0.81	1.02	0.22	0.15	0.05	0.11
RaoQ	12.19	14.41	2.67	3.60	0.06	0.03	0.01	0.02

F = Forest, JR = Jungle Rubber, OPP = Oil Palm and R = Rubber

The different functional indices showed that functional diversity was comparatively higher in Forest habitat and Jungle Rubber. The five functional metrics showed the same change pattern in which functional diversity decreased significantly along land transformed habitat to monoculture plantations. The greater the disturbance intensity was, the less the functional diversity was.

In Palawan, Philippines, same trend was observed in which functional diversity measures of Forest (Fric = 0.04, Feve = 0.51, Fdis = 0.22, RaoQ = 0.06) and Jungle

Rubber ($\text{Fric} = 0.03$, $\text{Feve} = 0.57$, $\text{Fdis} = 0.15$, $\text{RaoQ} = 0.03$) were comparably higher than that of Rubber ($\text{Fric} = 0.02$, $\text{Feve} = 0.48$, $\text{Fdis} = 0.11$, $\text{RaoQ} = 0.02$) and Oil palm plantations ($\text{Fric} = 0.01$, $\text{Feve} = 0.51$, $\text{Fdis} = 0.05$, $\text{RaoQ} = 0.01$). Oil palm plantation had the lowest functional diversity.

Functional richness, divergence, dispersion and evenness did not differ between Forest, Jungle Rubber and Rubber ($P > 0.05$). Functional richness was significantly lower in Oil palm plantation than in forest ($P = 0.04$) (Figure 9). Additionally, functional evenness, dispersion and RaoQ were all much lower in Oil palm than in forest habitat (Feve , $P < 0.004$; Fdis , $P = 0.005$; RaoQ , $P < 0.003$) (Figures 10 and 11).

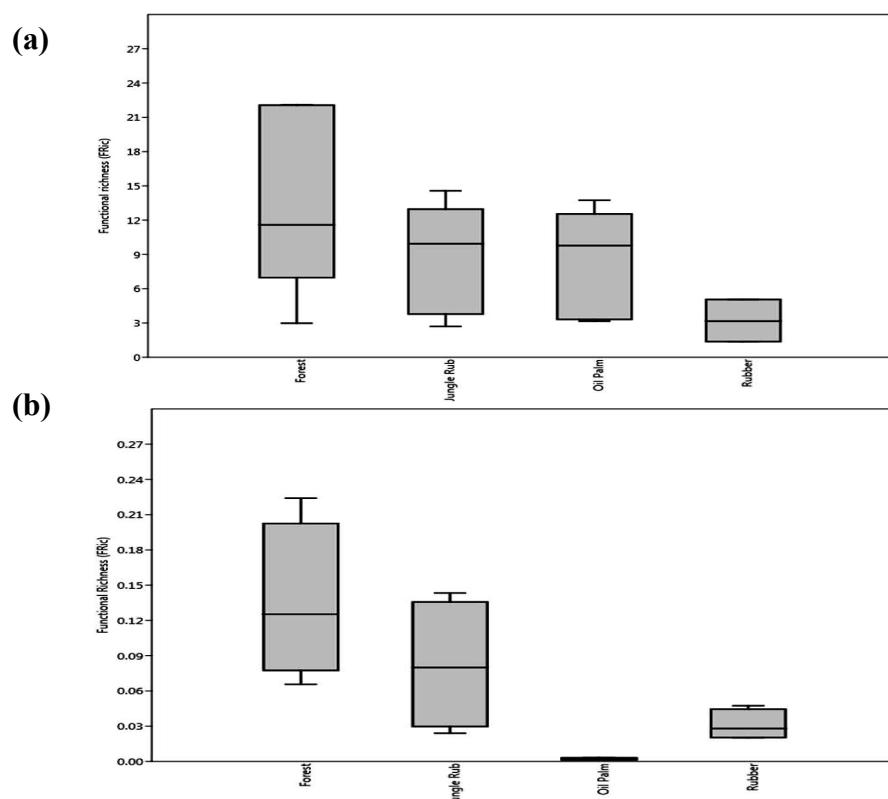


Figure 9. Functional Richness (FRic) (mean \pm SD) across habitat in (a) Sumatra, Indonesia and (b) Palawan, Philippines

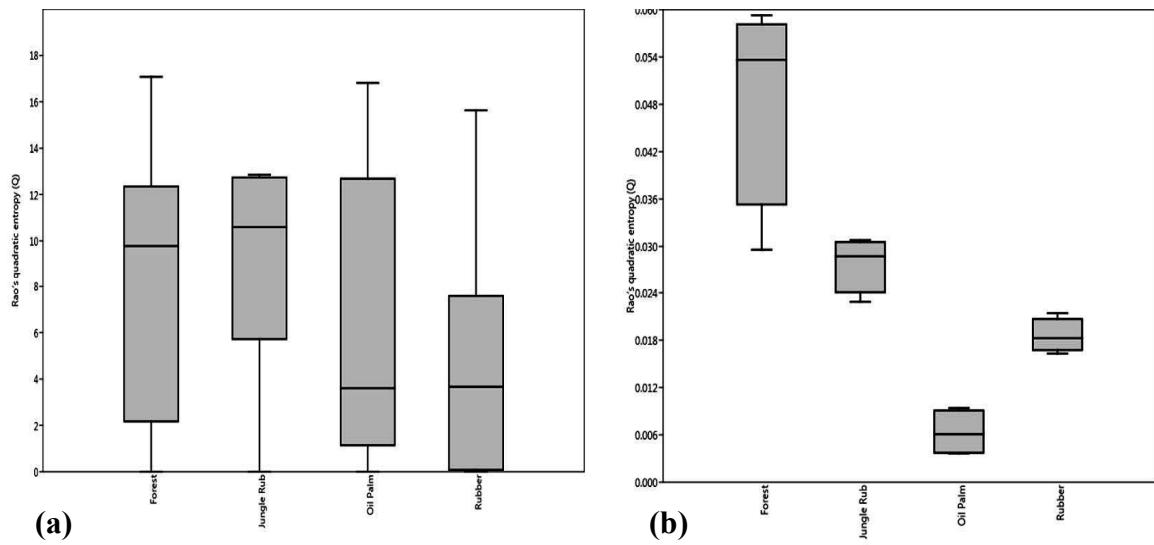


Figure10. Functional diversity based on Rao Quadratic Entropy (RaoQ) (mean \pm SD) across habitat in (a) Sumatra, Indonesia and (b) Palawan, Philippines

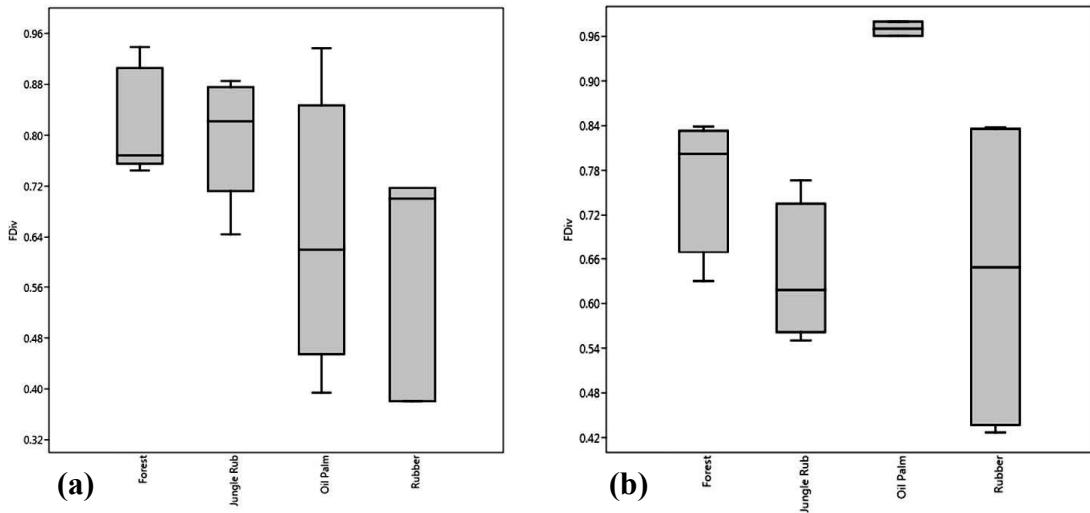


Figure 11. Functional divergence (FDiv) (mean \pm SD) across habitat in (a) Sumatra, Indonesia and (b) Palawan, Philippines

Phylogenetic Diversity

Tree-Based Measures of Phylogenetic Diversity

Faith Index (PD), Evolutionary Heritage and Weighted PD showed that Phylogenetic diversity of bat community in Sumatra, Indonesia was highest in Forest habitat (PD = 7.45, WPD = 8.14). Jungle Rubber showed a comparable phylogenetic diversity (PD = 5.90, WPD = 6.72). Rubber plantation had a lower phylogenetic diversity value (PD = 4.29, WPD = 5.89) while Oil palm plantations had the lowest phylogenetic diversity (PD = 3.78, WPD = 3.50). Despite the variety of lineages that were found in land transformed habitat to monocultures, average phylogenetic diversity was 42% lower in intensive Rubber plantation than in forest and 50% lower in Oil palm plantations than in forest habitat. Test for equal means showed that PD in Oil palm plantation is significantly lower from that of Forest ($P = 0.003$) (Figure 12). Same with Rubber plantation whose PD is significantly lower from that of forest habitat.

Forest and Jungle Rubber housed a higher value of evolutionary history (EH = 8.55 and EH = 7.0 respectively) while land transformed habitat – Rubber and Oil palm plantation had a lower evolutionary historical diversity (EH = 5.38 and EH = 4.88 respectively).

In Palawan, Philippines, phylogenetic diversity in the Forest habitat is slightly lower from that of Jungle Rubber (PD = 4.81, WPD = 4.02 and PD = 5.04, WPD = 4.96 respectively) though no significant difference on phylogenetic diversity was detected in

these two habitats ($P = 0.9$). Rubber plantation had a PD of 4.52 and WPD of 3.77 while Oil palm plantation had a PD of 2.49 and WPD of 1.72. PD in Oil palm plantation is significantly lower from that of Forest ($P = 0.004$) and Jungle Rubber ($P = 0.003$).

Level of historical diversity in an assemblage was comparable for Forest, Jungle Rubber and Rubber plantation with an Evolutionary Heritage value of 5.90, 6.14 and 5.62 respectively. Oil palm had the lowest EH with 3.59.

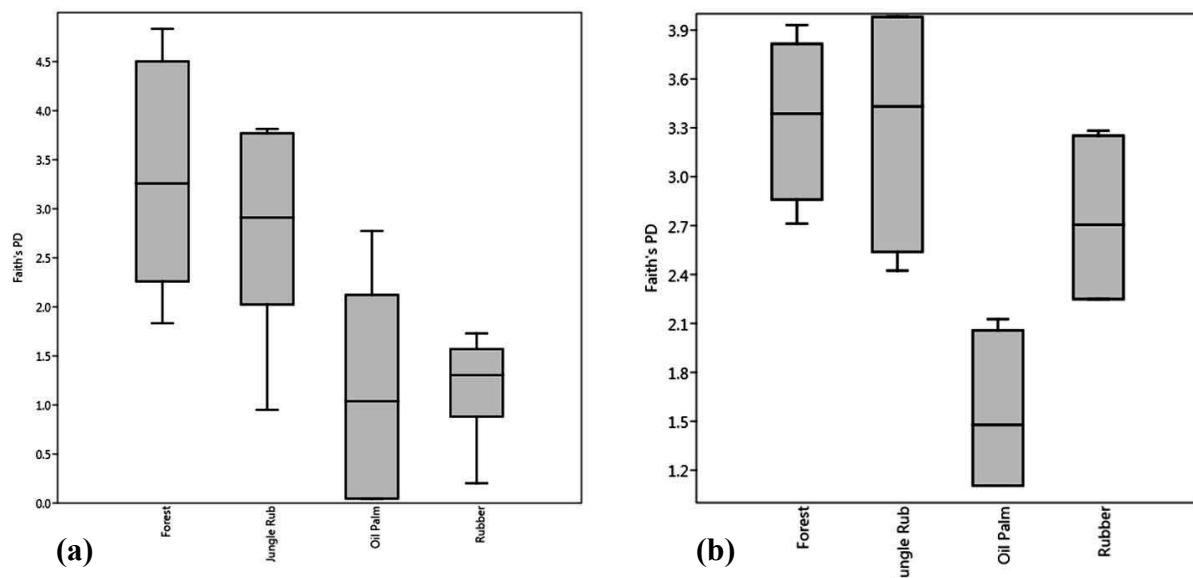


Figure 12. Faith's index of functional diversity (mean \pm SD) across habitat in (a) Sumatra, Indonesia and (b) Palawan, Philippines.

Distance-Based Measures of Phylogenetic Diversity

In Sumatra, Indonesia, distance based measures of phylogenetic diversity showed that Forest had the highest phylogenetic diversity while Oil palm plantation had the lowest phylogenetic diversity. Forest habitat had a Phylogenetic Species Richness (PSR), Phylogenetic Species Evenness (PSE) and Phylogenetic Species Variability (PSV) value of 14.28, 0.68 and 0.79 respectively. Jungle rubber had a comparable phylogenetic diversity value (PSR = 11.44, PSE = 0.66 and PSV = 0.82). Both Rubber and Oil Palm plantation had a lower phylogenetic diversity value – PSR = 5.91, PSE = 0.18 and PSV = 0.74 in Rubber and PSR = 5.87, PSE = 0.11 and PSV = 0.84 in Oil palm plantation.

MPD values across habitat ranged from 0.14 in Oil palm plantation, 0.24 in Rubber, 1.14 in Jungle Rubber and 1.23 in Forest with the highest phylogenetic diversity based on MPD. By comparing the values of MPD in a null model and calculating NRI which estimates the average phylogenetic relatedness between all possible pairs of taxa in an assemblage, NRI values on the bat assemblages in Forest habitat showed a negative value suggesting that bat assemblages in Forest are phylogenetically dispersed. NRI values in Jungle Rubber, Rubber and Oil palm plantations were positive suggesting that bat assemblages in these land transformed habitat were phylogenetically clustered.

In Palawan, Philippines, Phylogenetic Species Richness and Phylogenetic Species Evenness was highest in Forest habitat (PSR = 8.38, PSE = 0.78) followed by Jungle Rubber (PSR = 7.94, PSe = 0.51), then decreased in Rubber plantation (PSR = 6.34, PSE

= 0.37) and in Oil palm plantation (PSR = 3.64, PSE = 0.18). Phylogenetic Species variability (PSV) was comparable for all habitats.

MPD value was comparable between Forest and Jungle Rubber (MPD = 0.78 and 0.81 respectively) and between Rubber and Oil palm plantation (MPD = 0.99 and 0.90 respectively). Forest had a negative NRI value indicating that a vast majority of the chiropteran assemblages in forest habitats were phylogenetically dispersed. In contrast, NRI for Jungle rubber, Rubber plantation and Oil palm plantation were positive indicating a phylogenetic clustering of bat assemblage in these habitats.

Table 7. Phylogenetic diversity metrics of bat communities across habitat in Sumatra, Indonesia and Palawan, Philippines.

PHYLOGENETIC DIVERSITY METRICS	INDONESIA				PALAWAN			
	F	JR	OPP	R	F	JR	OPP	R
Faith Index (PD)	7.45	5.90	3.78	4.29	4.81	5.04	2.49	4.52
Evolutionary Heritage (EH)	8.55	7.00	4.88	5.38	5.90	6.14	3.59	5.62
Weighted PD	8.14	6.72	3.50	5.89	4.02	4.96	1.72	3.77
PSVs	0.79	0.82	0.84	0.74	0.84	0.88	0.91	0.91
PSEs	0.68	0.66	0.11	0.18	0.78	0.51	0.18	0.37
PSR	14.28	11.44	5.87	5.91	8.39	7.94	3.64	6.34
MPD	1.23	1.14	0.14	0.24	0.68	0.81	1.05	0.99
MNTD	0.51	0.43	0.70	0.67	1.01	0.70	0.20	0.50

F = Forest, JR = Jungle Rubber, OPP = Oil Palm and R = Rubber

Phylogenetic Similarities across Communities

Phylogenetic similarity of bat phylogenetic diversity in Sumatra, Indonesia based on Phylogenetic Sørensen (PhyloSor) similarity index showed that Forest and Jungle Rubber were 88.4% similar. Forest and Rubber plantation had a similarity of 0.657 while Jungle Rubber and Rubber plantation had a similarity of 0.646. Oil palm plantation had a low similarity with that of Jungle Rubber (0.492) and lowest similarity with that of Forest (0.465).

Consequently, the UniFrac dissimilarity index that quantify the unique fraction of the phylogeny contained in each of bat communities in Sumatra, Indonesia showed same trend where Jungle rubber had a lower dissimilarity value with that of forest (0.208). UniFrac values was highest between Forest and Rubber (0.674) and between Forest and Oil palm plantation (0.697) accentuating the degree of incongruence of bat phylogenetic structure between these habitats.

In Palawan, Philippines, Phylogenetic Sørensen (PhyloSor) similarity index showed the same phylogenetic similarity trend where land transformed habitat – Rubber and Oil palm plantation – shared the highest similarity. These transformed habitats had lower similarity in reference to forest habitat where Rubber and Forest phylogenetic diversity was 49% similar and Oil palm plantation and Forest was 46% similar.

Table 8. UniFrac index of dissimilarity of phylogenetic diversity in Sumatra, Indonesia and Palawan, Philippines

UNIFRAC	FOREST	JUNGLE RUBBER	OIL PALM	RUBBER
Indonesia				
Forest	0	0.208	0.697	0.510
Jungle Rubber	-	0	0.674	0.523
Oil Palm	-	-	0	0.653
Rubber	-	-	-	0
Palawan				
Forest	0	0.293	0.393	0.342
Jungle Rubber	-	0	0.416	0.239
Oil Palm	-	-	0	0.362
Rubber	-	-	-	0

Table 9. PhyloSor index of similarity of phylogenetic diversity in Sumatra, Indonesia and Palawan, Philippines

PHYLOSOR	FOREST	JUNGLE RUBBER	OIL PALM	RUBBER
Indonesia				
Forest	0	0.884	0.465	0.658
Jungle Rubber	-	0	0.492	0.646
Oil Palm	-	-	0	0.515
Rubber	-	-	-	0
Palawan				
Forest	0	0.829	0.756	0.794
Jungle Rubber	-	0	0.737	0.864
Oil Palm	-	-	0	0.779
Rubber	-	-	-	0

CHAPTER V

DISCUSSION

Impact of Land transformation on Taxonomic Diversity

The taxonomic diversity of bat communities in Sumatra, Indonesia and Palawan, Philippines did not differ greatly from other bat diversity studies in lowland forests in Southeast Asia (Heaney *et al.*, 2006, Fukuda *et al.*, 2009 and Shafie *et al.*, 2011) where forest harbored the highest bat diversity. Forest habitat in Sumatra and Palawan had the highest number of species recorded as compared to other habitat and some of these species were exclusively captured in forest habitat (Table 1 and 2).

The forest habitat provided roosting sites as well as high diversity of food items including fruiting trees and flowering plants and probably a myriad of insect species. Hence, forested areas tend to offer a greater diversity of food and roost sites for bats in Sumatra, Indonesia and Palawan, Philippines compared to agricultural systems and other habitat types. Similarly, Aguirre (2002); Heaney *et al.*, (2006) and Shafie *et al.*, (2011) found the highest species richness and diversity in the forested habitat. The greater incidence of bat species in the forest may be explained in terms of the heterogeneity of microhabitats that support species with varying ecological niches (Hodgkison *et al*, 2004b), the diversity of food resources(Hodgkison *et al.*, 2004a) and the availability of

roosting sites (Zubaid, 1993). Consequently, forests harbor bats that fly generally in gaps as well as those species that forage in highly cluttered space, whereas the more open and more homogenous understory in monoculture plantations such as rubber support mainly bats that fly customarily in gaps (Phommexay *et al.*, 2011).

Jungle Rubber had comparable species diversity with that of forest habitat for both bat communities in Sumatra, Indonesia and Palawan, Philippines. It has been reported that Jungle rubber systems in which rubber trees are grown in a secondary forest environment might maximize the occurrence of forest species in agricultural landscapes (Thiollay, 1995). Same is true with the bat fauna in Jungle rubber of Sumatra and Palawan where some forest species were shared by these two habitats and not on monoculture plantations.

Similarity analysis and NMDS for bat species composition in Sumatra and Palawan revealed that Jungle Rubber habitat clustered and showed an overlap with Forest habitat. It has been suggested that Jungle rubber is more beneficial to biodiversity with higher levels of species richness compared with monoculture plantations (Beukema *et al.*, 2007). The same result was shown in this study where Jungle Rubber habitat harbors a higher number of bat species and showed significant difference on varied metrics of species diversity (Tables 1, 2 and 3) from that of intensive Rubber plantation and Oil palm plantation.

This suggests that Jungle Rubber agroforest provides significant habitat and resources for the bat fauna in Sumatra and Palawan though less than those of the original forest. Hence, it has been considered that complex agroforests are the most forest-like of

all agroforestry systems and the ones that hold the highest potential for contributing to biodiversity conservation in tropical forest regions (Schroth *et al.*, 2004).

For intensive Rubber agricultural system, the data gathered indicate that rubber plantations have a negative impact on species diversity of bats in Sumatra, Indonesia and Palawan, Philippines. The number of bat species recorded in rubber plantations was significantly (about two to three times) lower than in forest. Based on Effective number of species or Hill's number which represents the true diversity of a community, the reduction in species diversity from forest to Rubber plantations was on the order of 5 times.

Results from other studies also suggested that forest conversion to rubber also causes serious losses on biodiversity. Studies of Aratrakorn *et al.* (2006) revealed most species of forest-dwelling birds including all but one of 16 IUCN Red-listed species, disappear, being replaced by widespread, smaller species. Additionally, bat species richness declines dramatically in rubber plantations where species diversity were found to be much lower in rubber plantations than in forested areas (Table 3). Danielsen and Heegaard (1995) had examined the response of bats to rubber plantations and showed that insectivorous bats are either extremely rare or absent in these monoculture plantations. Although bats are considered to be highly agile, which may mitigate the impact on them of these land use changes, not all species are as mobile as perceived (Struebig *et al.* 2008).

Oil palm plantations continue to expand rapidly in Southeast Asia and increasingly across the tropics (Fitzherbert *et al.* 2008). Conversion of forest to oil palm

creates a homogeneous canopy structure, open understory, and markedly altered microclimate (Luskin and Potts 2011), and drives a substantial reduction in species richness and significant shifts in species composition. Hence, it was suggested that oil palm plantations have a very limited biodiversity value and that the conversion of forest to oil palm results in major losses to conservation (Fitzherbert *et al.* 2008). Corroborating studies in South East Asian oil palm plantations (Danielsen and Heegaard 1995; Fukuda *et al.* 2009), species richness, composition and diversity of bat fauna was also lowest in Oil palm plantations in Sumatra, Indonesia and Palawan, Philippines.

Species composition in Oil palm plantation was clearly distinct from those at Forest and Jungle rubber sitesas shown by Bray-Curtis smimilarity and NMDS of bat community (Table 4, Figure 7). High sample coverage in Oil palm plantation and a leveled-off species accumulation curve indicate relatively complete sampling of the impoverished bat assemblages in this plantation. Increased relative abundances of certain Pteropodid species (i.e *C. brachyotis*) and declines of Rhinolopid, Hipposiderid and Vespertillionid species seem to shape the deviating assemblages in Oil palm plantation. These compositional shifts in the structure of bat assemblages are commonly observed in response to habitat disturbance (Fukuda *et al.*, 2009, Shafie *et al.*, 2011). The rank-abundance curve showed that the bat assemblages in the Oil palm plantation were strongly dominated by a few species (*C. brachyotis* and *C. sphinx* in Sumatra, Indonesia and *C. brachyotis* and *M. minimus* in Palawan, Philippines).

Based on the results, *C. brachyotis* accounted for almost half of the total captured individuals in Sumatra, Indonesia and Palawan, Philippines. Hence, *C. brachyotis* was

considered to inhabit a wide variety of habitats both forested and disturbed in both study locations. It was reported that *C. brachyotis* is typically found in agricultural areas and is most common on disturbed and residential areas (Heaney *et al.*, 1998). The high proportion of *C. brachyotis* in agricultural habitats were similar to the pattern observed by Heaney *et al.* (2006) in Camiguin Island, Philippines as well as for the other South East Asian countries such as in lowland dipterocarp forest of Borneo (Fukuda *et al.*, 2009) and on different habitat types in Malaysia (Shafie *et al.*, 2011) in which *C. brachyotis* accounted most of the total bat captures and constitutes a relatively large proportion in bat community. *C. brachyotis* is listed by Francis (2008) as a common species in disturbed areas. A study conducted in Camiguin Island, Mindanao, Philippines (Heaney *et al.* 2006), recorded *C. brachyotis* proportions up to almost 52% of the total catch of bats in the area. This species is highly adapted to their environments to take advantage of many available shelters such as caves, trees, rock shelters and occupies a variety of habitats including primary rainforest, disturbed forest, mangrove swamp, cultivated area, orchards, gardens and urban areas (Tan *et al.*, 1999).

Species absent in oil palm plantations were usually those with specialized diets or roosting requirements and small home ranges, while assemblages in Oil palm plantation were often dominated by a few abundant generalistic species (Fitzherbert *et al.* 2008). Similarly, species caught in high abundances in studied Oil palm plantations were mainly generalistic and rather open-habitat tolerant as dominated by *C. brachyotis*, *C. sphinx*. Generally, those affected most by forest conversion are often rare and range-restricted species (Scales and Marsden 2008).

Moreover, oil palm habitat showed a significant decrease on the abundance and number of *Rhinolophus* and *Hipposideros* species which were cluttered space forager. Previous intensive studies on insectivorous bat communities in Peninsular Malaysia and Borneo have indicated that most of the bats captured within the forest interior forage strictly or predominantly in the highly cluttered space of the forest understorey (Kingston *et al.* 2003; Struebig *et al.* 2006). These ‘narrow space’ bats are particularly susceptible to habitat destruction owing to their highly specialized wing morphology and echolocation call design, which may not allow them to forage effectively in the more open habitat found in plantations. This could lead accordingly to lower bat diversity in man-made environment (Kingston 2013).

Species adapted to highly cluttered environments and with small home ranges and comparably low mobility seemed to be the most threatened by habitat disturbance and fragmentation (Farneda *et al.* 2015) suggesting the significant decline of Rhinolopid and Hipposiderid species in Oil palm plantations in both Sumatra, Indonesia and Palawan, Philippines. The sparse understory of Oil palm plantations had no present woody plants in the study sites. The observed decrease in bat species richness towards lower structural habitat complexity illustrates negative impacts of habitat simplification and consequences such as reduced resource availability for many species foraging in the understory (Freudmann *et al.*, 2015).

In comparison with other studies on the impact of oil palm plantation of faunal diversity, Livingston *et al.* (2013) reported a decline in species richness, abundance, and similarity of bee communities in oil palm plantations with increasing distance from

forest. Similarly, oil palm plantations in Brazilian Amazonia were found to contain species-poor avian assemblages comparable to those of forest mainly consisting of generalistic species of low conservation concern and lacking range-restricted and forest associated species (Lees *et al.* 2015). Same pattern could be observed with the results of Danielsen and Heegaard (1995) reporting lower primate richness and abundance in plantations relative to primary forest, with macaques and gibbons absent, and a substantial reduction in the abundance of tree shrews and squirrels. Peh *et al.* (2006) also found that conversion of primary forests and logged forests to oil palm plantations decreases the species richness of forest birds by 77% and 73%, respectively, whereas the conversion of rubber plantations to oil palm plantations results in only a 14% decline in species richness of the remaining forest birds. Similar patterns hold for forest butterflies in Borneo where conversion of primary forests and logged forests to oil palm plantations decreases species richness of forest butterflies by 83% and 79%, respectively (Koh and Wilcove, 2008). Consequently, Oil palm plantation contribute to an impoverishment of the local fauna and may prevent the utilization of isolated forest remnants embedded in an agricultural matrix, conduced forest fragmentation and habitat degradation as well as deterioration of ecosystem services provided by bats (Koh and Wilcove, 2008).

Impact of Land Transformation on Functional Diversity

The functional guild diversity in Sumatra, Indonesia and Palawan, Philippines was highest in the Forest habitat and lowest in Rubber and Oil palm plantations. However, comparable level of functional guild diversity was observed between Forest and Rubber Jungle Rubber in both Sumatra, Indonesia and Palawan, Philippines. Fruit-eating bats (consuming fruits as primary items in their diets) were the most common in land transformed habitat (Rubber and Oil palm plantation) while insect-eating bats were the most common in Forest habitat and Jungle Rubber. It has been contended that the survival of functional groups in agricultural landscapes may depend upon the configuration of forested and non-forested patches. Metapopulation theory suggests that populations can be maintained in lower quality habitat patches by the influx of individuals from source populations, and this movement is facilitated by a high quality matrix (Vandermeer and Carvajal 2001). Biocontrol agents, pollinating bees, seed-dispersing frugivores and other functionally important species survive in many land-use systems within tropical mosaic landscapes only when these are connected to natural habitats (Schroth *et al.* 2004). In the case of Sumatra, Indonesia and Palawan, Philippines, the adoption of farmers towards rubber agroforestry and the proximity of this habitat to monoculture rubber and oil palm plantations in the area might be one of the contributing factors for the persistence of several functional groups in the completely transformed habitat such as monoculture rubber and oil palm plantations.

Of the 25 bat species present in Sumatra, Indonesia and 14 bat species in Palawan, Philippines, 5 species (*C. brachyotis*, *C. sphinx*, *C. minutus*, *B. maculata* and *D. brooksi*) and 2 species (*C. brachyotis* and *R. amplexicaudarus*) respectively were frugivores. Frugivores were highest in terms of the number of caught individuals though the guild insectivore was highest in terms of number of species. Frugivores play a major role in overall health of the forest (Kunz *et al.*, 2011) and so might be the case of the different habitat in Sumatra, Indonesia and Palawan, Philippines. Frugivores are one of the main spore and seed dispersers in tropical ecosystems, particularly in open areas and sites in the early stages of ecological succession (Garcia-Estrada *et al.*, 2011). They dominate most proportions of the bat community in a tropical ecosystem and constitute the most important trophic category in cloud forests (Soriano 2000). Frugivorous bats disperse the seeds of fruits they eat throughout the area mostly of the Ficus family and are important contributors of plant propagules in a tropical forest of which they disperse and pollinate trees in a forest environment (Muscarella and Fleming 2007). Pteropodids or fruit bats are known to pollinate flowers of about 168 plant species in 100 genera and 41 families and eat fruits from at least 139 genera in 58 families of plants (Fleming *et al.*, 2009). In the tropics, vertebrate frugivores have a much greater role in the dispersal of forest and successional woody plants than wind, and bats play the dominant role in dispersing early successional species (Kunz *et al.*, 2011). The relative high proportion of frugivorous bats in Sumatra, Indonesia and Palawan, Philippines is comparable with the results of Fukuda *et al.* (2009) in Borneo and Turner *et al.* (2006) in Negros Island, Philippines by which fruit bats contributes to the high abundance proportion of Chiropteran fauna in the area.

High abundance of frugivorous bats may be due to the availability and diversity of fruiting plants such as *Ficus sp*, *Muntingia sp.*, *Averrhoa sp.* and other fruiting trees that produced fruits and were available to fruit eating bats of throughout the year. Frugivorous bats in Palawan and Sumatra tend to inhabit various habitat types from forest habitat to human altered habitat such as rubber agroforest and monoculture rubber and oil palm plantations. It was reported that fruit bats (Pteropodidae) reached their greatest local densities in agricultural areas, and were least abundant in montane mossy forest (Heaney *et al* 1989). The fruit bats that are found to be common in agricultural areas are widespread in Southeast Asia and highly tolerant to human disturbance (Heaney *et al.*, 1998). Likewise, the nonendemic fruit bat *C. brachyotis* were abundant in agricultural habitat in Sumatra and Palawan.

Insectivorous bats was the guild with the most number of representative species with 19 species in Sumatra, Indonesia and 10 species in Palawan, Philippines. The presence of various insectivorous bats in Sumatra and Palawan provide a consequent ecological services in the area e.g. control both naturally occurring and anthropogenically-generated insect populations (such as agricultural pest species and insects that annoy or transmit specific pathogens to humans and other mammals) and contribute to the maintenance of ecosystem stability (Kunz *et al.*,2011).

Insectivorous bats had higher number of species than frugivores. However, each captured insectivorous bat species had the lower capture rate being represented mostly by one to ten individuals. Low abundance and capture rate of insectivorous bats in Sumatra and Palawan could be explained by the restriction of dietary requirements such as low

abundance of insects (Fukuda *et al.*, 2009) and probably the lack of suitable roost available for these bats in Sumatra and Palawan especially in monoculture plantations. This finding of insectivorous bat abundance was similar to the result of Shafie *et al* (2011) in which insectivorous bat species represented the lowest proportion of the bats captured from different habitat types. Furthermore, the result was also comparable to the fragmented tropical landscape in Mexico in which 85% of bats captured were frugivorous, compared to only 15% insectivorous bats (Galindo- González and Sosa 2003). Moreover, the ability of these insectivore bats of echolocation (Kingston *et al.*, 2003) allows them to detect the traps employed ahead making them difficult to capture in the field and could also be accounted for their low capture rates.

Nectarivorous bats had a greater value in terms of species abundance rather than species richness, this guild was only represented by a single species in Sumatra, Indonesia (*M. sobrinus*) and two species in Palawan, Philippines (*E. spelaea* and *M. minimus*).

The conversion of land from complex natural systems to simplified agricultural ecosystems is a major cause of the current unprecedented rates of global biodiversity loss (Matson *et al.* 1997). One biodiversity component that is greatly affected by this land conversion is functional diversity which seek to quantify the range of functional trait differences among species in a community (Petchey and Gaston, 2006) bridging the gap between species diversity and species composition, and giving insight into potential resilience and recovery of species in response to land-use change (Lynn *et al.*, 2009).

This study documented the decrease in the functional richness, functional evenness, functional dispersion of bat species along land transformation systems using functional traits. Bat functional diversity significantly decreased in Rubber and Oil palm plantations at Sumatra, Indonesia and Palawan, Philippines. The decrease in species, abundance and functional richness of bats with forest loss may have implications for the ecological processes they carry out such as seed dispersal, pollination and insect predation, among others (Kunz *et al.*, 2011). In contrary, bat community in Sumatra, Indonesia and Palawan, Philippines showed that forest habitat had the highest functional diversity and also harbored the highest number of representative bat species of different functional groups (Frugivore, Nectarivore and Insectivore). Moreover, functional diversity in Jungle Rubber is comparable with that of forest habitat. The apparent lack of substantial change in functional diversity or divergence in Jungle Rubber indicates that the bat community of Jungle Rubber maintained a similar diversity of resource-use traits as the community of Forest habitat. This study illustrates the potential of Jungle Rubber to retain a similar level of bat functional traits as in forest, and vastly more than Rubber and in oil palm plantations. It suggests therefore that ecosystem functioning is relatively stable in these Jungle Rubber habitat, adding weight to the argument that traditional agroforestry are of critical importance to the conservation of tropical biodiversity that underwent extreme pressure to agricultural expansion (Schroth *et al.*, 2004). However, degraded forests remain at serious risk of conversion to monoculture agriculture and are in urgent need of funding for protection.

The bat fauna in Rubber and Oil palm plantation had very low functional diversity (RaoQ) indicating that conversion of forest represents a dramatic loss of functional strategies (Azhar *et al.* 2013). The net loss of functional strategies could be a result in under-utilization of resources available within the oil palm (e.g. fruits or insects) or whether the resource base in oil palm contracted, such that those few resources available were being used just as effectively in oil palm as in forests. In Indonesia and Palawan, the shift in functional diversity was apparently driven partly by the reduction of number and abundance of representative species of particular functionally grouped species, especially insectivores in this homogenously transformed habitat.

Those functionally unique species that colonize the landscape after conversion to oil palm were typically generalists (i.e. *C. brachyotis*, *C. sphinx*, *M. minimus*, *M. sobrinus*) with very large geographical ranges and are of low conservation concern, whereas functionally unique species within forest were forest-interior specialists, often of global conservation concern (i.e. *Rhinolophus* species). The shifts in functional diversity across land transformation systems in Indonesia and Philippines mirror findings from the Neotropics, where a significant decrease in the species and functional richness of bat species along a gradient of habitat loss in Mexico using functional traits was reported (Devictor *et al.*, 2008)

The pattern of functional evenness also showed a decreasing trend from Forest habitat to Rubber and Oil palm plantation at both Sumatra, Indonesia and Palawan, Philippines. Considering that functional evenness takes abundance into account, the communities with a similar number of individuals (evenness) among functional groups

(i.e. groups of species that are similar in their functional traits), and regular distances between functional groups (similar lengths of the segments of the minimum spanning tree) have higher functional evenness values. That is, if a species disappears, but another that belongs to the same functional group is present, this second species can compensate for the species that is absent, and maintains functional evenness even though species richness is lower compared with that of other communities. The opposite occurs when a few species dominate the community and all belong to the same functional group, resulting in the overrepresentation of functional traits, or when some functional groups are underrepresented, functional evenness decreases. The functional evenness of the Rubber and Oil palm communities were lower than that of Jungle Rubber and Forest suggesting that the relative abundance of species with different functional traits is thus less even and the distances between these species is less regular within the functional space occupied by Rubber and Oil palm than Jungle rubber and forest communities.

The decrease in functional evenness within Rubber plantation and Oil palm plantation in Sumatra and Palawan reveals a shift in the relative abundance of species and thus trait combinations, and it could be assumed that this will influence functional processes by altering the strength of species interactions in tis community.

It may be regarded that those species that colonize or increase in abundance after land transformation provide a similar set of resource-use traits to those of the primary forest specialists that they replace and thus we might expect functional processes in Jungle Rubber forests to be similar to those in Forest. This contrasts with conversion of forest to monomulture plantation (Rubber and Oil palm), where changes in species

composition may be accompanied by concomitant changes in functional diversity (Lewis 2009).

Impact of Land Transformation on Phylogenetic Diversity

Phylogenetic diversity (PD, MPD, PSR and Evolutionary Heritage) were higher in forest than in Rubber and Oil palm plantations. Phylogenetic diversity also increased with extent of Jungle Rubber agrosystem showing the importance of Jungle Rubber for the maintenance of phylogenetic diversity in agricultural landscapes in Indonesia and Philippines. The results suggest that avoiding forest loss and conversion to monoculture plantations and preserving forest fragments within agricultural landscapes would minimize losses of chiropteran diversity in Sumatra, Indonesia and Palawan, Philippines including phylogenetic diversity.

Phylogenetic diversity is affected by both species richness and branch topology – adding species to a community increases the sum of branch lengths, and a community comprised of close relatives will have a lower branch length sum than one comprised of an equal number of distantly related species (Swenson 2014). After controlling for species richness (sesPD), PD did not differ across habitat types in Sumatra, Indonesia and Palawan, Philippines except for Oil palm plantation suggesting that on a per species basis, Jungle Rubber and Rubber plantations conserve comparable levels of evolutionary history to forest, but that different chiropteran clades are not more or less likely to survive in Oil palm plantations.

The higher MPD in forests suggests that the bat species recorded in forest sites are distributed across a wider range of clades than those recorded in Rubber and Oil palm plantation sites. Rubber and Oil palm plantation had low MPD at both Sumatra, Indonesia and Palawan., Philippines similar with the result of Frishkoff *et al.* (2014) where there is a significant reduction in bird MPD after conversion of forest to various types of agriculture.

Together with the finding that Rubber and Oil palm plantations have low MPD, this suggests that bat communities in Rubber plantation represent relatively few clades but contain many species within those clades, whereas bat communities in Oil palm plantation tend to have a broader representation of clades, but fewer occurrences of closely related species. Jungle Rubber and Forest comparably had higher MPD than oil palm and pasture which suggests that there is a broader representation of clades in forest points, but with many closely related species coexisting.

To determine the degree of phylogenetic relatedness among species between Forest and transformed habitat (Jungle Rubber, Rubber and Oil palm plantations), net relatedness index- NRI was computed. Forest habitat had negative values of NRI indicating that a vast majority of the chiropteran assemblages was phylogenetically dispersed. In contrast, Jungle Rubber, Rubber and Oil palm plantations had positive values of the NRI indicating that a vast majority of the chiropteran assemblages in these communities were phylogenetically clustered. A phylogenetic clustering pattern is commonly explained as a result of environmental filtering because ecological traits are generally phylogenetically conserved and thus more closely related species are expected

to be more ecologically similar (Webb *et al.* 2002). Conversely, a phylogenetic overdispersion pattern is commonly explained as a result of interspecific interactions because more closely related species are expected to have widely overlapping niches and thus to compete with one another strongly for similar resources, a process known as limiting similarity, which would lead to co-occurrence of distantly related species within a local assemblage. A lack of phylogenetic structure suggests that neutral processes structure local communities (Kembel and Hubbell 2006).

The fact that bat assemblage showed the tendency of increasing phylogenetic clustering across land transformed habitat (Jungle Rubber, rubber and Oil palm plantation) may suggest that the environmental filtering process has played a primary role in structuring species into communities for chiropteran fauna, although phylogenetic clustering may result from other processes (Cavender-Bares *et al.* 2009). Flynn *et al.* (2009) proposed that phylogenetic clustering may occur if functionally unique species are lost first in altered habitats. Distinct trait combinations and a turnover in species composition (Ndriantsoa *et al.*, 2017) indicate that although assemblages were equally clustered, they pass different environmental filters depending on resource availability in different habitats. Hence, bat species that thrives in Rubber and Oil palm plantation were mostly generalist species and of closer phylogenetic relationship. Rubber and oil palm habitat are highly homogenized and only a certain species of bats which are tolerant to disturbance could persist in this transformed habitat.

Implications for Conservation

One of the greatest challenges facing tropical biologists is how to conserve biodiversity within the agricultural landscapes that increasingly dominate the tropics and continue to encroach upon the remaining forests (Lewis 2009). Drastic land-use transformations have occurred in the tropical forest landscapes of Southeast Asia in the past decades, leading to the disappearance of natural forests and the replacement of traditional land-use systems with monoculture plantations (Fisher *et al.*, 2011).

Of the various land uses studied, agroforestry systems (those that intentionally combine trees within the cultivation of crops and/or animals) stand out as having a particularly high conservation potential, due to their structural complexity, high floristic diversity and close resemblance to forest ecosystems (e.g., Schroth *et al.* 2004). Results of this study adds to the growing consensus that agroforestry systems can contribute significantly to the conservation of biodiversity within fragmented landscapes by providing habitat for high number of species. Hence, Jungle Rubber showed a comparable level of taxonomic, functional and phylogenetic diversity with that of forest habitat in Sumatra, Indonesia and Palawan, Philippines. Results also highlight the fact that agroforestry systems have much greater conservation value than the monoculture crops that often replace them. However, the results also illustrate that the animal assemblages within agroforestry systems may be somewhat distinct from those in forest habitats and do not necessarily contain the same suite of species as the original forests. The protection of the remaining forest fragments will therefore be critical for the

conservation of intact animal assemblages in agricultural landscapes and should continue to form the backbone of conservation strategies.

In terms of conservation of bat diversity in reference to Rubber plantation, compared to other monoculture crops (e.g. oil palm, coffee, rice, cassava, and sugar cane), rubber plantations may be less detrimental to biodiversity as they retain a reasonably complex canopy and the period of rotation is long (more than 25 years) (Schroth *et al.* 2004). Rubber plantations in Sumatra, Indonesia and Palawan, Philippines support more species than Oil palm and showed a higher taxonomic, functional and phylogenetic diversity than Oil palm plantations. Although it is clear that rubber plantations cannot support the level of biodiversity found in forest, they can be effective as corridors between forest patches and as buffer zones around forested areas (Castro-Luna and Galindo-Gonzalez, 2012). Biodiversity may increase in rubber plantations if the ecological and economic management methods employed in other monoculture plantations are followed (Fisher *et al.* 2006).

The best alternative to monoculture rubber plantations is the adoption of Agroforest rubber plantations, which support not only rubber trees but also forest vegetation and edible and useful plants. They represent a compromise between economic and sustainable use of natural resources that lends itself more readily to biodiversity conservation (Beukema *et al.*, 2007). In order to balance the habitat requirements of indigenous fauna with the economic benefits of rubber production, it is suggested that strategies be implemented in plantations that enhance biodiversity conservation while preserving the economic value of the rubber crop.

For the conservation value of Oil palm plantations, converting forest to oil palm therefore leads to a significantly impoverished wildlife community (Fitzherbert *et al.*, 2008). Most forest species are lost and replaced by smaller numbers of largely non-forest species resulting in simpler, species-poor communities. The species that are lost tend to include taxa that rely on habitat features not found in plantations (e.g. large trees for cavity-dwelling species), those with the most specialized diets (e.g. frugivores), and those with the smallest range sizes and highest conservation concern (Peh *et al.*, 2006). While any conversion of natural forest is inevitably damaging to biodiversity, studies comparing several landcover types reveal that oil palm plantations support even fewer forest species than plantations of other tree commodity products such as Rubber, Cocoa and Acacia (Fitzherbert *et al.*, 2008). Same trend was observed in Sumatra, Indonesia and Palawan, Philippines where Oil palm plantation had the least value of taxonomic, functional and phylogenetic diversity and bat community in this habitat where primary composed and dominated by few generalist species.

It is unlikely that oil palm management practices could be improved enough to significantly increase the biodiversity value of plantations. This is because the main cause of massive biodiversity losses in oil palm areas is reduction of habitat complexity, and there are only limited opportunities to improve that while maintaining agricultural productivity (Koh and Wilcove, 2008). Hence, Yaap *et al.*, 2010 suggested that avoiding oil palm development on forested land in the first place is the best option for biodiversity conservation.

CHAPTER VI

SUMMARY AND CONCLUSION

The current study assessed the impact of tropical lowland rainforest transformation to rubber and oil palm plantations on taxonomic, functional and phylogenetic diversity having bats as indicator species and investigated the response and the influence of land use transformation system on multiple dimensions of bat diversity in Sumatra, Indonesia and in Philippines by looking into the species richness, composition and abundance and assess the changes in the functional and phylogenetic structure of bat community across land transformation systems. This study found a suite of changes across different dimensions of biodiversity resulting from the conversion of natural forest to rubber and oil palm plantations.

Taxonomic diversity of bats had decreased significantly from forest to Rubber and Oil palm plantations at both Sumatra, Indonesia and Palawan, Philippines. Species diversity was highest in Forest habitat while lowest in Oil palm plantation. Effective number of species which represents the true diversity of a community revealed a declined across habitat with the pronounced decline at land transformed habitat – Rubber and Oil palm plantations. The reduction in species diversity from forest to Rubber plantations was on the order of 3.5 to 5 times while Oil palm plantations was 5 to 7 times less diverse with that of the forest.

In terms of functional dimension of chiropteran biodiversity of Sumatra, Indonesia and Palawan, Philippines, the functional richness, dispersion and RaoQ were all much lower in oil palm than in forest habitat. The different functional indices showed that functional diversity was comparatively higher in Forest habitat and Jungle Rubber. Conversion to rubber and oil palm monoculture led to a marked reduction in functional diversity and a decline in functional evenness. The chiropteran fauna in oil palm had very low functional diversity indicating that conversion of forest represents a dramatic loss of functional strategies. The functional evenness of the oil palm community was also lower than that of Jungle Rubber and Forest communities. The relative abundance of species with different functional traits is thus less even and the distances between these species is less regular within the functional space occupied by oil palm than forest communities.

Phylogenetic dimension of chiropteran fauna in Indonesia and Philippines showed a decline in phylogenetic diversity (PD, MPD, PSR and Evolutionary Heritage) from forest to rubber and oil palm plantations. Similarity of bat phylogenetic diversity showed that Forest and Jungle Rubber were most similar (88.4%). Phylogenetic diversity also increased with extent of Jungle Rubber agrosystem showing the importance of Jungle Rubber for the maintenance of phylogenetic diversity in agricultural landscapes in Indonesia and Philippines.

In overall, the results indicated that conversion of forest to commercial plantations of oil palm or rubber resulted in a significant reduction of taxonomic, functional and phylogenetic diversiy of chiropteran fauna in Sumatra, Indonesia and Palawan, Philippines. This findings reinforce the growing consensus that conversion of either

primary forests or secondary forests to monoculture particularly oil palm plantations have detrimental impacts on Southeast Asia's biodiversity (Koh and Wilcove, 2008).

Further studies are needed to assess the impacts of land transformation to rubber and oil palm agriculture on Southeast Asian bat diversity. Aside from impact assessment at taxonomic, functional and phylogenetic level, incorporating additional biodiversity dimensions particularly genetic diversity, trophic structure and interaction networks will provide a mechanistic view of how land use transformation from forest to rubber and oil palm will translates into loss of bat species and changes in ecosystem functioning. Knowledge on species and genetic variation and insights on how land transformation to rubber and oil palm modifies species interactions will provide essential information in the formulation of appropriate management strategies directed towards the conservation of bat diversity in Sumatra, Indonesia and Palawan, Philippines as well for the preservation and management of their habitats.

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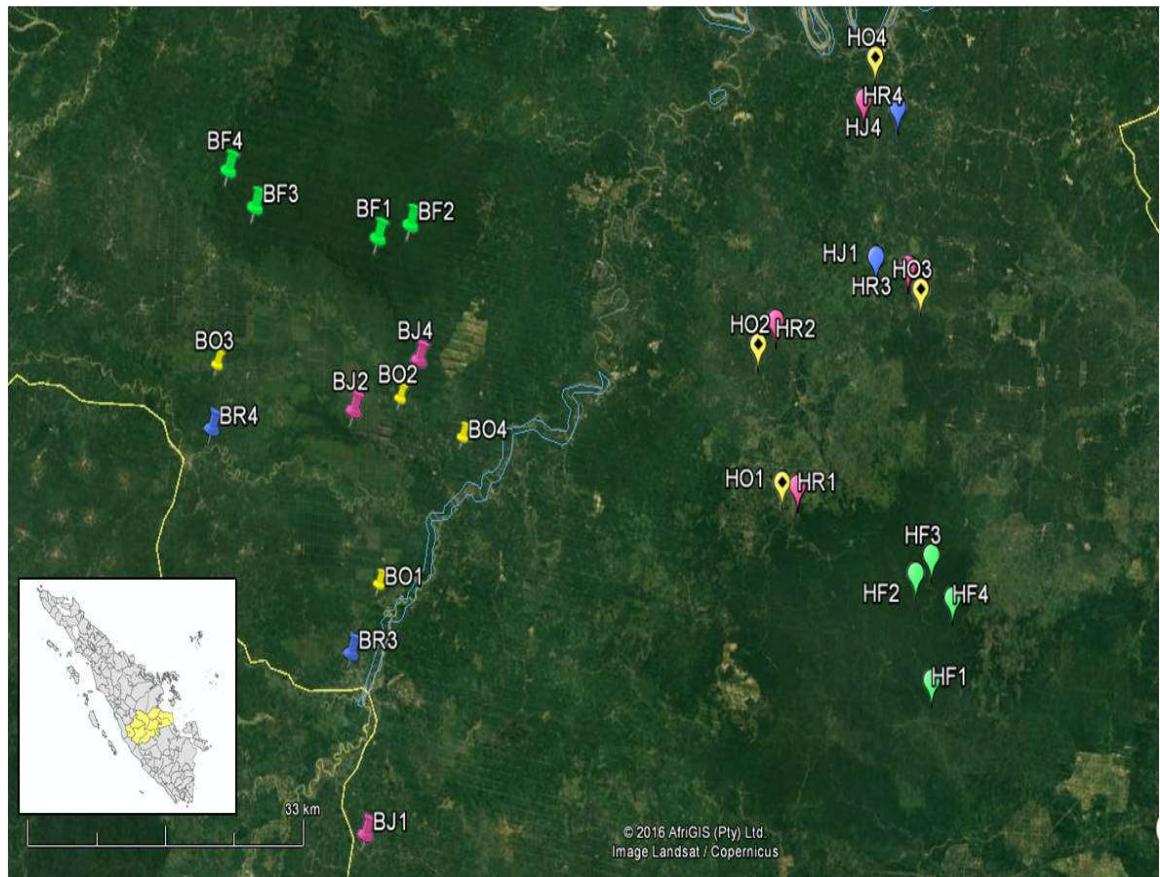
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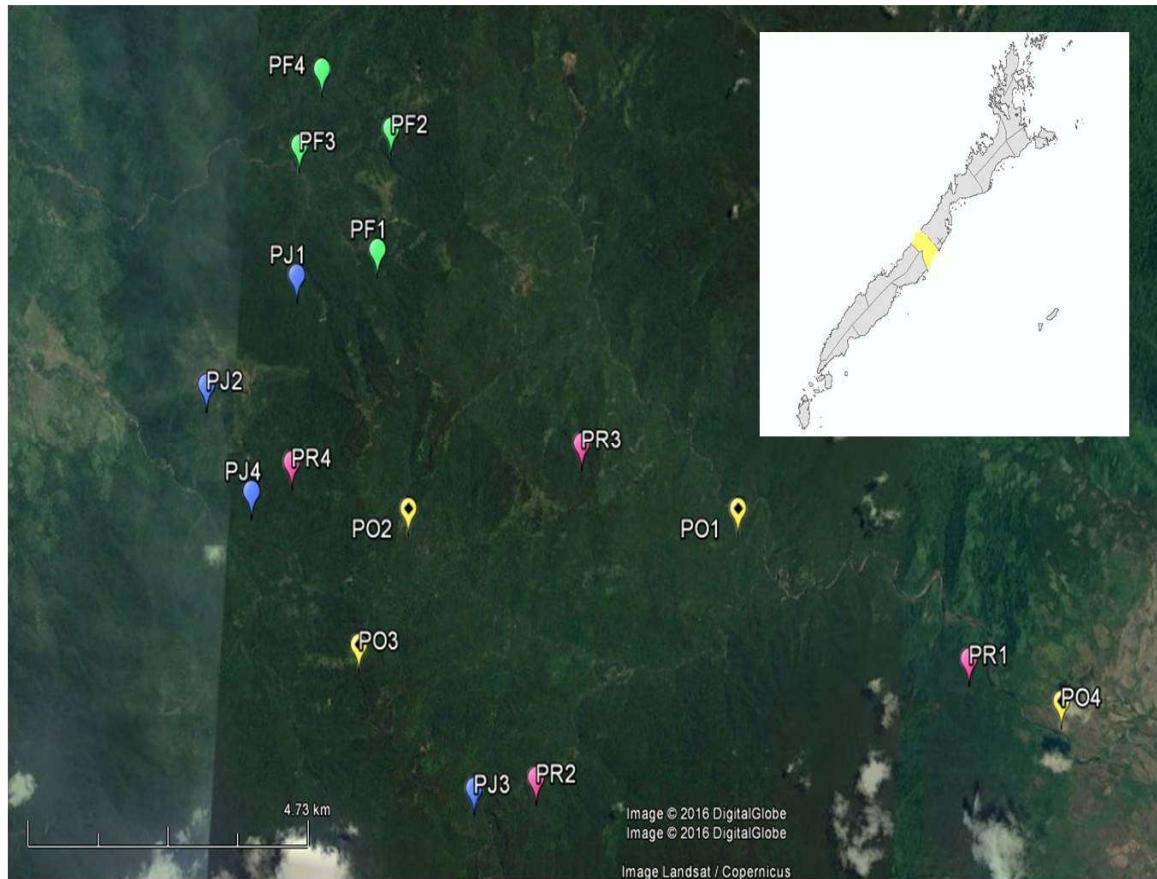
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APPENDICES

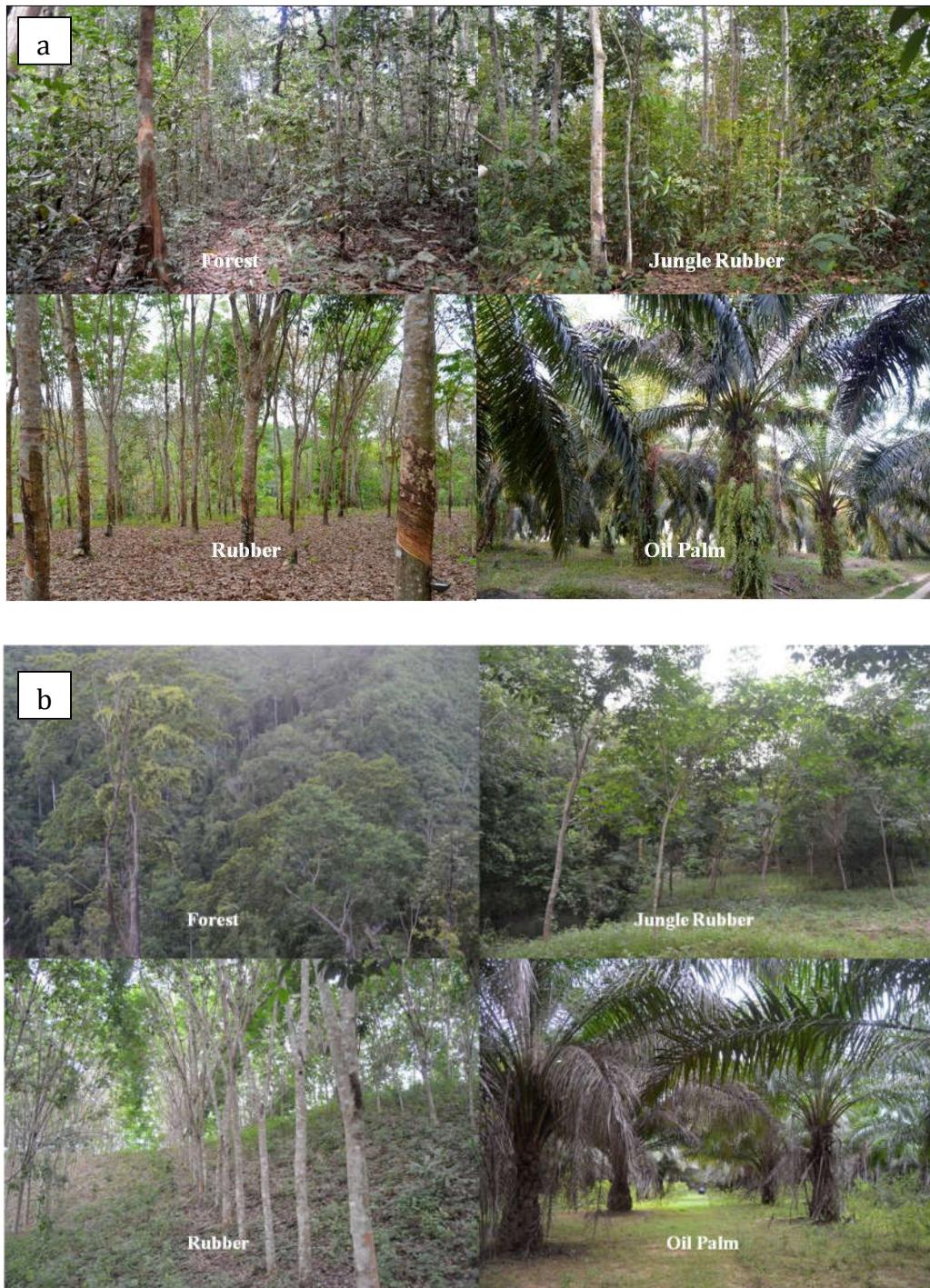
Appendix 1. Study area and location of 32 sampling sites in four habitat types in Jambi, Sumatra, Indonesia. Forest (green), Jungle Rubber (Purple), Rubber (blue) and Oil palm (yellow). Inset: Location of Jambi province in Sumatra, Indonesia.



Appendix 2. Study area and location of 16 sampling sites in four habitat types in Aborlan Palawan, Philippines. Forest (green), Jungle Rubber (Purple), Rubber (blue) and Oil palm (yellow). Inset: Location of Aborlan in Palawan, Philippines.



Appendix 3. Different habitats where bat sampling was conducted in (a) Sumatra, Indonesia and (b) Palawan, Philippines.



Appendix 4. Mist net (a) and Harp trap (b) Set up used for bat sampling.



Appendix 5. Relative abundance of bats captured in four habitat types in Sumatra, Indonesia.

Species	Forest	Jungle Rubber	Oil Palm	Rubber	Guild*	Species Codes
<i>Balionycteris maculata</i>	0.91	0.78	0	0.07	Fru	a
<i>Cynopterus brachyotis</i>	0.20	0.78	13.54	5.34	Fru	b
<i>Cynopterus minutus</i>	0	0.52	1.37	0.33	Fru	c
<i>Cynopterus sphinx</i>	0	0	0	0.07	Fru	d
<i>Dyacopterus brooksi</i>	0.13	0	0	0.07	Fru	e
<i>Macroglossus sobrinus</i>	0	0	0.26	0.20	Nec	n
<i>Hipposideros bicolor</i>	0.39	0.13	0	0	Ins	f
<i>Hipposideros cervinus</i>	1.95	0.07	0	0.07	Ins	g
<i>Hipposideros diadema</i>	0.26	0	0	0	Ins	h
<i>Hipposideros orbiculus</i>	0.07	0.07	0	0	Ins	i
<i>Rhinolophus affinis</i>	0.07	0	0	0	Ins	s
<i>Rhinolophus sedulus</i>	0.20	0.07	0	0	Ins	t
<i>Rhinolophus trifoliatus</i>	0.65	0.26	0	0	Ins	u
<i>Rhinolophus acuminatus</i>	0.07	0	0	0	Ins	v
<i>Rhinolophus luctus</i>	0.07	0	0	0.20	Ins	w
<i>Rhinolophus lepidus</i>	0	0.07	0	0	Ins	x
<i>Hypsugo macrotis</i>	0	0	0.13	0	Ins	j
<i>Kerivoula hardwickii</i>	0.07	0.07	0	0	Ins	k
<i>Kerivoula minuta</i>	0.13	0.07	0	0	Ins	l
<i>Kerivoula pellusida</i>	0.07	0.13	0	0	Ins	m
<i>Myotis sp</i>	0	0	0.07	0	Ins	p
<i>Tylonycteris robustula</i>	0.07	0	0	0	Ins	y
<i>Hesperoptenus sp.</i>	0	0	0.07	0	Ins	r
<i>Megaderma spasma</i>	0.26	0.07	0.13	0	Ins	o
<i>Nycteris tragata</i>	0.07	0.07	0	0	Ins	q

* Fru = frugivore, Nec = Nectarivore, Ins = Insectivore

Appendix 6. Relative abundance of bats captured in four habitat types in Palawan, Philippines.

Species	Forest	Jungle Rubber	Oil Palm	Rubber	Guild*	Species Codes
<i>Cynopterus brachyotis</i>	1.89	5.01	11.26	8.01	Fru	a
<i>Eonycteris spelaea</i>	0.20	0.33	0	0.26	Nec	b
<i>Glischropus tylopus</i>	0	0.07	0	0	Ins	c
<i>Hipposideros diadema</i>	1.50	0.33	0.07	0.20	Ins	d
<i>Macroglossus minimus</i>	0.72	2.60	1.11	2.28	Nec	e
<i>Megaderma spasma</i>	0.72	0.20	0.07	0.13	Ins	f
<i>Murina cyclotis</i>	0	0.07	0	0.07	Ins	g
<i>Murina sp</i>	0	0.07	0	0	Ins	h
<i>Myotis macrotarsus</i>	0.07	0	0	0	Ins	i
<i>Pipistrellus javanicus</i>	0	0	0	0.07	Ins	j
<i>Rhinolophus acuminatus</i>	0.72	0	0	0	Ins	k
<i>Rhinolophus arcuatus</i>	1.30	0.07	0	0	Ins	l
<i>Rhinolophus sp.</i>	0.07	0	0	0	Ins	m
<i>Rousettus amplexicaudatus</i>	0.07	0	0	0	Fru	n

* Fru = frugivore, Nec = Nectarivore, Ins = Insectivore

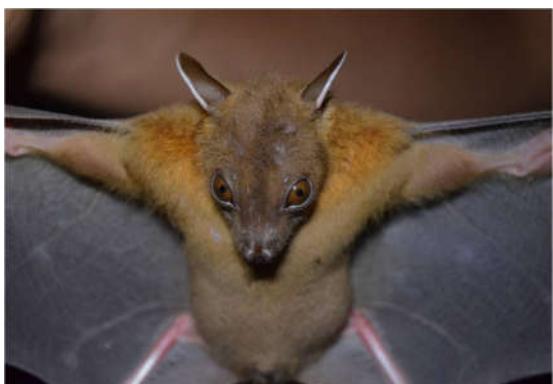
Appendix 7. Bat species recorded in Sumatra, Indonesia



Cynopterus brachyotis



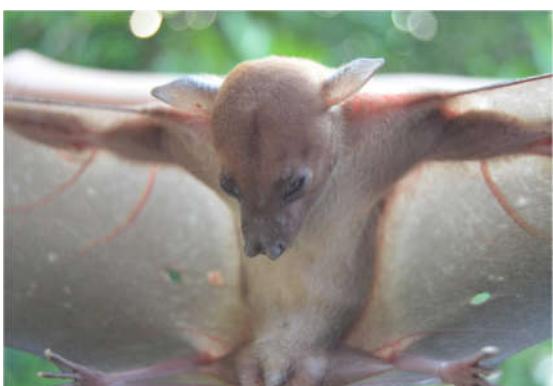
Cynopterus minutus



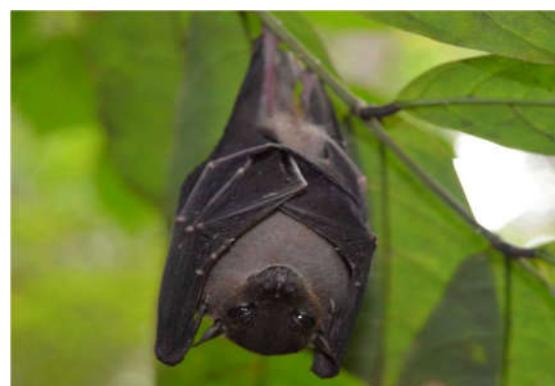
Cynopterus sphinx



Macroglossus sobrinus



Dyacopterus brooksi



Balionycteris maculata

Appendix 7 continued.



Rhinolophus trifoliatus



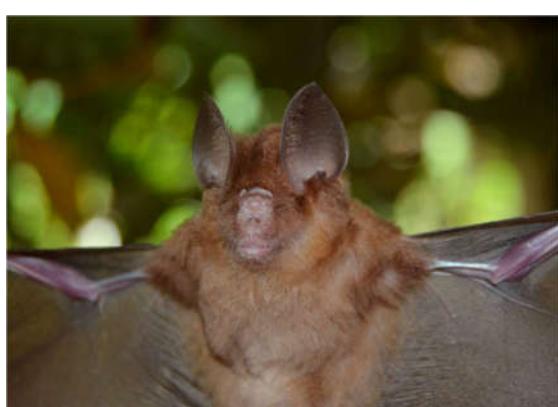
Rhinolophus luctus



Hipposideros orbiculus



Hipposideros bicolor



Hipposideros cervinus



Megaderma spasma

Appendix 7. Continued.



Kerivoula hardwickii



Myotis sp



Hypsugo macrotis



Hesperoptenus sp.



Kerivoula minuta



Nycteris tragata

Appendix 8. Bat species recorded in Palawan, Philippines



Cynopterus brachyotis



Eonycteris spelaea



Murina cyclotis



Murina sp.



Hipposideros diadema



Megaderma spasma

Appendix 8. Continued.



Rhinolophus arcuatus



Rhinolophus acuminatus



Glischropus tylopus



Myotis macrotarsus

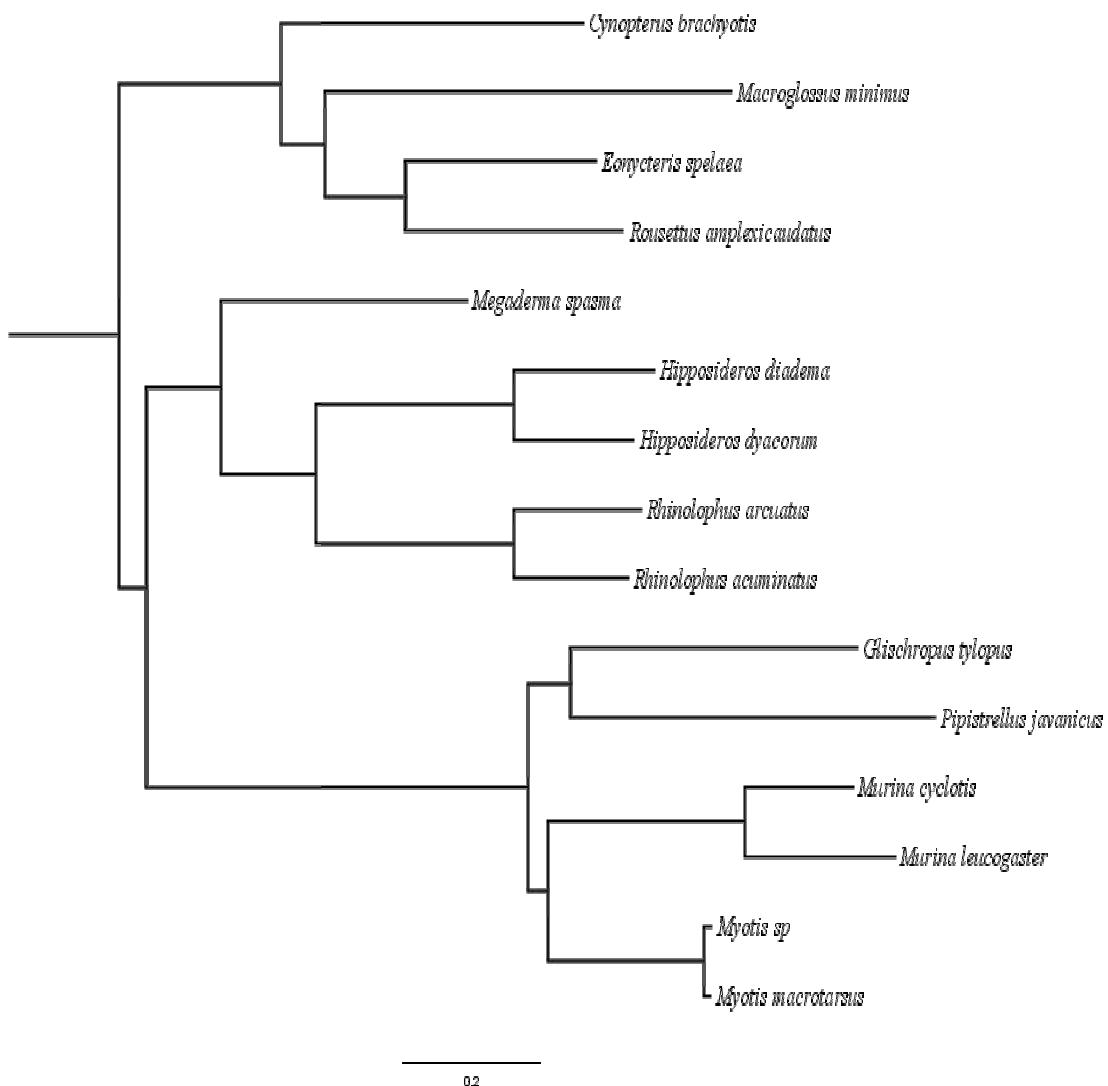
Appendix 9.

Phylogenetic tree of sampled bats in Sumatra, Indonesia pruned from the time calibrated bat phylogenetic supertree of Agnarsson *et al.*, 2011.



Appendix 10.

Phylogenetic tree of sampled bats in Palawan, Philippines pruned from the time calibrated bat phylogenetic supertree of Agnarsson *et al.*, 2011.



Appendix 11. Trait distance matrix of bat species in Sumatra, Indonesia used to calculate Functional diversity using a multidimensional convex hull.

	Cb	Cs	Db	Hs	Hb	Hc	Hd	Ho	Hm	Kh	Km	Kp	Ms	Msp	Mm	Nt	Rac	Raf	Rl	Rlu	Rs	Rt	Tb
Bm	0.27	0.39	0.39	0.54	0.37	0.30	0.50	0.32	0.56	0.35	0.41	0.36	0.40	0.38	0.54	0.31	0.37	0.38	0.43	0.47	0.34	0.33	0.44
Cb	-	0.14	0.30	0.57	0.36	0.43	0.41	0.44	0.61	0.51	0.57	0.50	0.35	0.28	0.59	0.38	0.50	0.49	0.57	0.36	0.48	0.40	0.61
Cs	-	-	0.28	0.58	0.45	0.57	0.48	0.58	0.63	0.65	0.71	0.63	0.36	0.41	0.60	0.50	0.64	0.63	0.59	0.46	0.61	0.53	0.74
Db	-	-	-	0.74	0.49	0.61	0.39	0.62	0.79	0.69	0.75	0.67	0.49	0.57	0.76	0.54	0.57	0.55	0.75	0.38	0.66	0.58	0.66
Hs	-	-	-	-	0.42	0.31	0.41	0.26	0.06	0.22	0.25	0.22	0.38	0.30	0.04	0.32	0.22	0.24	0.18	0.40	0.28	0.33	0.17
Hb	-	-	-	-	-	0.26	0.29	0.17	0.45	0.24	0.29	0.22	0.49	0.22	0.43	0.19	0.21	0.19	0.26	0.19	0.17	0.14	0.35
Hc	-	-	-	-	-	-	0.39	0.11	0.32	0.12	0.16	0.11	0.49	0.28	0.31	0.19	0.19	0.20	0.16	0.36	0.11	0.16	0.23
Hd	-	-	-	-	-	-	-	0.28	0.45	0.35	0.41	0.33	0.50	0.27	0.43	0.23	0.24	0.23	0.41	0.10	0.32	0.26	0.34
Ho	-	-	-	-	-	-	-	-	0.29	0.08	0.13	0.06	0.50	0.17	0.28	0.08	0.10	0.11	0.13	0.26	0.05	0.07	0.19
Hm	-	-	-	-	-	-	-	-	-	0.21	0.20	0.24	0.42	0.34	0.03	0.37	0.24	0.27	0.19	0.43	0.30	0.36	0.15
Kh	-	-	-	-	-	-	-	-	-	-	0.06	0.03	0.56	0.25	0.20	0.16	0.15	0.18	0.11	0.34	0.09	0.15	0.11
Km	-	-	-	-	-	-	-	-	-	-	-	0.08	0.62	0.30	0.22	0.21	0.19	0.23	0.14	0.39	0.13	0.20	0.10
Kp	-	-	-	-	-	-	-	-	-	-	-	-	0.56	0.23	0.22	0.14	0.14	0.15	0.11	0.31	0.07	0.12	0.14
Ms	-	-	-	-	-	-	-	-	-	-	-	-	-	0.39	0.40	0.46	0.44	0.44	0.50	0.43	0.53	0.49	0.53
Msp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.32	0.10	0.24	0.22	0.31	0.23	0.21	0.13	0.34
Mm	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.34	0.22	0.26	0.18	0.42	0.28	0.35	0.16
Nt	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.15	0.13	0.22	0.20	0.12	0.06	0.25
Rac	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04	0.19	0.20	0.11	0.12	0.14
Raf	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.20	0.19	0.11	0.09	0.17
Rl	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.39	0.11	0.18	0.21
Rlu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.29	0.21	0.33
Rs	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.08	0.20
Rt	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.26
Tb	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 11. Continued.

Legend: *Balionycteris maculata* (*Bm*), *Cynopterus brachyotis* (*Cb*), *Cynopterus sphinx* (*Cs*), *Cynopterus minutus* (*Cm*), *Dyacopterus brooksi* (*Db*), *Macroglossus sobrinus* (*Ms*), *Hipposideros bicolor* (*Hb*), *Hipposideros cervinus* (*Hc*), *Hipposideros diadema* (*Hd*), *Hipposideros orbiculus* (*Ho*), *Rhinolophus affinis* (*Ra*), *Rhinolophus sedulous* (*Rs*), *Rhinolophus trifoliatus* (*Rt*), *Rhinolophus acuminatus* (*Rac*), *Rhinolophus luctus* (*Rlu*), *Rhinolophus Lepidus* (*Rl*), *H. macrotis* (*Hm*), *Kerivoula hardwickii* (*Kh*), *Kerivoula minuta* (*Km*), *Kerivoula pellusida* (*Kp*), *Myotis sp* (*Mm*), *Tylonicteris robustula* (*Tr*) *Hesperoptenus sp.* (*Hs*), *Megaderma spasma* (*Msp*) and *Nycteris tragata* (*Nt*)

Appendix 12.

Trait distance matrix of bat species in Palawan, Philippines used to calculate Functional diversity using a multidimensional convex hull.

	Cb	Mm	Es	Ra	Mc	Ms	Rarc	Rac	Hd	Gt	Pj	Msp
Cb	-	0.28	0.31	0.36	0.51	0.60	0.49	0.51	0.26	0.62	0.62	0.21
Mm	-		0.28	0.58	0.38	0.48	0.39	0.43	0.37	0.51	0.50	0.22
Es	-	-	-	0.31	0.54	0.64	0.55	0.58	0.38	0.67	0.67	0.39
Ra	-	-	-	-	0.73	0.70	0.62	0.53	0.52	0.74	0.73	0.57
Mc	-	-	-	-	-	0.09	0.19	0.27	0.44	0.13	0.12	0.30
Ms	-	-	-	-	-	-	0.15	0.23	0.53	0.04	0.15	0.38
Rarc	-	-	-	-	-	-	-	0.11	0.41	0.17	0.29	0.28
Rac	-	-	-	-	-	-	-	-	0.45	0.25	0.25	0.31
Hd	-	-	-	-	-	-	-	-	-	0.55	0.55	0.17
Gt	-	-	-	-	-	-	-	-	-	-	0.16	0.41
Pj	-	-	-	-	-	-	-	-	-	-	-	0.41

Legend: *Cynopterus brachyotis* (Cb), *Macroglossus minimus* (Mm), *Eonycteris spelaea* (Es), *Rousettus amplexicaudatus* (Ra), *Hipposideros diadema* (Hd), *Rhinolophus acuminatus* (Rac), *Rhinolophus arcuatus* (Rarc), *Rhinolophus* sp. (Rs), *Glischropus tylopus* (Gt), *Murina cyclotis* (Mc), *Murina* sp (Msp), *Myotis macrotarsus* (Mmac), *Pipistrellus javanicus* (Pj) and *Megaderma spasma* (Msp)