Phylogeography and Demography of Common Plant Species from the Philippine Islands

by

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I dedicate this dissertation to my family, Simplicio, Virgilia, Valerie, Sarah, Vivien, Vanessa, John Simon, and Vincent Rupert Yap

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Table of Contents

Chapter

List of Figures

Figure

List of Tables

Table

ABSTRACT

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Effects of historical and current environmental conditions on plant populations from the Philippine Archipelago are investigated. The complex geologic history of the Philippines creating a diverse and highly endemic flora is reviewed. Apart from tectonic activity, the islands were subjected to changes in topography, temperature, and precipitation from Pleistocene glacial and interglacial periods (Heaney, 1991). Comparative phylogeography is used to determine the effects of Pleistocene events on the population genetic structure of two endemic species, *Daemonorops mollis* (Arecaceae) and *Macaranga bicolor* (Euphorbiaceae). Limited variation and the distribution of unique haplotypes in both species suggest that during periods of lowered sea levels, rainforest habitats were maintained as refugia throughout the archipelago. A land barrier between eastern and western Luzon and water surrounding each island restricted dispersal among populations. A potential route of island colonization in the south- and west- ward direction from northeast Luzon was recovered in *M. bicolor*. An eastern Luzon population was studied to document spatial distributions and species-habitat associations, and determine possible mechanisms facilitating coexistence in species-rich communities. Torus translation tests showed contrasting patterns of stream- and elevation- microhabitat associations between three palm tree species and *D. mollis*, a liana, suggesting a potential for niche differentiation between growth forms. In 30 dominant tree species, each was associated with at least elevation, slope, or stream at one or more life stages (saplings, juveniles, or adults), but associations varied across life stages in most species. Species sharing a microhabitat are shown to partition the niche, in time if not in space. Distributions at different life stages were also analyzed to infer what processes resulted in the observed spatial patterns. Aggregation was exhibited in all species at multiple scales, and decreased with species abundance and long-distance dispersal. Correlation analyses measured the relationship between clusters of saplings, or juveniles, with clusters of adults or distance to the nearest conspecific adult. Results show greater clustering of saplings around adults in three species, attributed to negative density dependent effects on juveniles. In ten species, juveniles clustered more around adults indicating negative density dependence before the sapling stage, while recruitment into the juvenile stage was successful for saplings located in suitable habitats near adults. Seed dispersal, negative density dependence, and niche differentiation, are therefore important in maintaining the diverse tree community in Palanan, Philippines.

Introduction

Phytogeography of the Philippine Islands

Islands fascinate scientists. They inspired Alfred Russell Wallace to develop the field of biogeography from his knowledge of the fauna of the Malay Archipelago (Wallace, 1869). Wallace discovered a distinct zoological break, famously called Wallace's Line, which distinguishes the origin of the fauna of the islands west of the line as predominantly Asian and the fauna of islands east of the line as Australian (Wallace, 1860). The placement of the Philippine Archipelago to the west of Wallace's Line however, was contested and the line redrawn such that the Philippine Islands excluding the Palawan group lies to the east of Wallace's Line, now called Huxley's Line (Dickerson *et al.,* 1928). Many other lines have been drawn through the Philippines and the eastern Indonesian islands, an area Simpson (1977) acknowledges as having a complex mix of Asian, Australian, and endemic species. In fact, Simpson (1977) proposed not assigning this area to either Asian or Australian regions, or even defining it as a transitional or intermediate zone, believing this would encourage research into the biota of these islands.

At present, Philippine phytogeography is still poorly understood. The majority of biogeographic research on Philippine species is on terrestrial mammals, birds, or marine animals (Jones & Kennedy, 2008). For example, a search on the Web of Science using the keywords "biogeography + Philippines" resulted in 134 articles, only seven of which were on plants. Of these seven articles, five were restricted to either a single site (Linis, 2009; Tan, 1996) or included a single Philippine species (Keppel *et al.*, 2008; Ladiges *et al.*, 2003; Vanwelzen *et al.*, 1992). Only two papers analyzed the phylogenetic relationships of multiple Philippine species, the first studying the genus *Cyrtandra* (Gesneriaceae) that documented some support for Huxley's Line (Atkins *et al.*, 2001). The second paper included eight species of *Rhododendron* (Ericaceae), which presented a set of species-area relationships that neither conformed to Huxley's nor Wallace's Line (Brown *et al.*, 2006). A collection of similar studies is needed to conclusively determine whether the flora of the Philippine Islands belong to the Asian or Australian phytogeographic region.

Several factors must have contributed to the assembly of the Philippine flora, including the complex geological history of the 7,107 islands that comprise the archipelago (Hall, 2002), species diversification, stasis, and endemism within islands, and the effects of climate change throughout the Cenozoic (Morley, 2000). Clearly, colonization of the oceanic islands by plants occurred via dispersal from nearby Asian and Australian sources, but the timing of dispersal events and the routes taken by propagules remain uncertain (Jones & Kennedy, 2008). Tectonic activity gradually formed the islands that comprise the Philippine Archipelago and plate movements shifted island positions (Hall, 2002). Therefore, dispersal events occurred at different times and between different islands beginning 50 million years ago with the formation of Luzon Island. The extraordinarily high endemicity in plants, estimated between 45 to 76.5 percent (Heaney & Mittermeier, 1997; Myers *et al.*, 2000), suggests localized diversification occurred after colonization early in the Philippines' history. However, distributions of some taxa limited to Borneo and Palawan (e.g., two recently diverged *Cyrtandra* species) also indicate dispersal during recent times, possibly during periods of low sea level during the Pleistocene (Atkins *et al.,* 2001). For two endemic species, *Daemonorops mollis* (Arecaceae) and *Macaranga bicolor* (Euphorbiaceae), I examined the effects of land connections between islands that formed aggregate island complexes during the Pleistocene and the drier climate during this same period, on the genetic composition of island populations.

Historical conditions allowed for the dispersal and establishment of insular populations of the current diverse Philippine flora. Sadly, forests that were logged from the mid-1500s (Bankoff, 2007) until today have very little remaining area intact (Myers *et al.*, 2000). The Philippines is one of the 25 megadiversity countries (Caldecott *et al.,* 1994) but is also one of the 25 hotspots identified for conservation based on the high number of endemic species and extent of habitat loss in the country (Myers *et al.,* 2000). The previous statement and other data collected by the scientific community have been used to increase awareness within public and government agencies, as well as non-government organizations of biodiversity and conservation. The hope is to provide an impetus for the development of conservation programs. A review of current conservation projects reports some success with increasing populations of endemic animals like the *Cacatua haematuropygia* (Philippine cockatoo), *Aceros waldeni* (Visayan wrinkled hornbill), *Crocodylus mindorensis* (Philippine crocodile)*,* and *Pithecophaga jefferyi* (Philippine eagle) (Posa *et al.,* 2008). In an effort to preserve these animals, each respective agency managing these projects lobbied for protection of natural habitats for each species (Posa *et al.,* 2008). In addition, Republic Act. No. 7586 was enacted in

1991, establishing protected areas under the National Integrated Protected Areas Systems (NIPAS). As of 2007, approximately 3,330,810 hectares have been proclaimed as protected areas and this number is still increasing (PAWB, 2007).

My dissertation also included evaluation of present-day environmental conditions that may dictate the observed distribution and abundance of species. I collected and analyzed data from a 16-hectare plot in Palanan, Isabela, which is part of the largest protected area under NIPAS, the Northern Sierra Madre Natural Park (PAWB, 2007). Implementation of forest protection however, is very poor, so illegal logging of timber species such as *Pterocarpus indicus* (Fabaceae) and *Shorea guiso* (Dipterocarpaceae) still occurs within the park (Van der Ploeg *et al.,* 2008). Fortunately, the Palanan plot is guarded so tree populations are maintained. Still, I am concerned that human disturbance in nearby areas of the forest have reduced animal visitation to the plot, and therefore potentially pollination and seed dispersal processes that visitation facilitates. Research must be conducted to find evidence to confirm or refute this. Below, I will describe how results from studying the demography of 30 dominant tree species can be applied in the rehabilitation of disturbed habitats.

Overview of the Dissertation and Application in Conservation

This dissertation examines the effects of Pleistocene geographic change, Pleistocene climatic change, and current environmental conditions on plant populations in the Philippine Islands. Extant plant populations are highly threatened particularly by deforestation. Understanding the effects on island plant populations of a reduced population size within isolated rainforest refugia during the Pleistocene, provides insight into the potential response of plant populations to today’s fragmented forests.

Furthermore, research into the ecology of common, native tree species at local scales identifies specific environmental factors associated with species distributions that might be mimicked in reforestation to ensure a successful recovery of deforested areas.

Chapter One of this dissertation provides a review of the geologic and climatic history of the Philippine Islands from the initial island formation 50 million years ago up to the present. Geologic reconstruction of the Southeast Asian region indicates that intense tectonic activity resulted in the formation of the oceanic islands that ultimately moved to their current positions (Hall, 2002). The historical assembly of the modern Philippine flora occurred through the climatic fluctuations of the Cenozoic, culminating in the increase of global temperatures to present levels after the Last Glacial Maximum (Morley, 2000). Colonization from both Asian and Australian floras combined with isolation in islands resulted in a highly diverse and endemic flora (Morley 2000). Despite threats to the Philippine flora from habitat loss (Fernando *et al.*, 2008), new species are still discovered in remnant primary and even in secondary forests (Barcelona *et al.*, 2009), emphasizing the need for conservation of forest habitats.

Chapter Two documents the effects of changes in climate and geography during the Pleistocene on two widespread endemic Philippine plants, *Daemonorops mollis* (Arecaceae) and *Macaranga bicolor* (Euphorbiaceae). Both species occur in sympatry, bird-dispersed, and dioecious yet represent two separate evolutionary lineages. Lowered sea levels during the Last Glacial Maximum of the Pleistocene created land connections between present-day islands where savanna vegetation is hypothesized to have replaced rainforest habitats due to a cooler and drier climate (Heaney, 1991). Phylogeographic structure is recovered only in *M. bicolor* and in neither species does present-day nor

Pleistocene island boundaries reflect the distribution of genetic variation. Haplotypes with restricted distributions demonstrate the unique contributions of most of the sampled populations to the total genetic pool in *M. bicolor*, making prioritizing sites for conservation difficult. More information from comparative phylogeographic analyses of additional species is needed to further distinguish distinct genetic characteristics among sites. My initial recommendations would be to begin conservation initiatives with the Palanan and Bislig sites, not only based on the genetic features of the populations but also because of the better quality of forest relative to other sites. Better forest quality would increase the chances of a successful conservation effort.

The preservation of natural habitats and biodiversity in the Philippines spans a century with some success as reviewed in Chokkalingam *et al.* (2006). Forest rehabilitation efforts purportedly increased forest cover in 28 of 46 sites studied, however, in most sites trees were planted in open grasslands as part of short-term projects (< 25 years) with limited funding (Chokkalingam *et al.,* 2006). The likelihood of planted seedlings reaching maturity and establishing closed canopy forest cover in this time is suspect. In addition, despite the objectives of these programs to increase forest cover, conserve biodiversity, decrease soil erosion, and improve watershed management, non-native tree species, such as the neotropical tree *Swietenia macrophylla* (Meliaceae), were extensively planted, and no baseline soil and water measurements were taken (Chokkalingam *et al.,* 2006). Published silvicultural methods guided the planting and subsequent care of planted trees, typically limited to a few timber species and the ubiquitous *S. macrophylla* (Dayan *et al.*, 1995; Chokkalingam *et al.,* 2006). To properly re-establish native forests, the ideal plan would mimic natural communities and gather data on soil, light, and nutrient conditions. This type of plan would avoid creating monoculture timber plantations or forests with little total biodiversity. A detailed demographic study of the distributions of common native species should be completed deriving data from the environmental attributes of the species' habitat that could be used to model reforestation initiatives.

Chapters Three to Five analyze 35 species in association with environmental features that influence species distributions within the 16-hectare plot in Palanan. Chapter Three focuses on palms, which are dominant components of tropical forests (Henderson *et al.*, 1995). In the Palanan plot, palms are speciose, abundant, and include a large proportion of the basal area. From among the 14 palm species present on the plot, four palm trees and one climbing palm were included in the demographic study here. Morisita's Index, a statistical measure of dispersion, shows all five species have clumped distributions influenced by the patchiness of suitable microhabitats. *Caryota cumingii, Orania decipiens,* and *Pinanga maculata* are positively associated with low elevations, whereas the fourth tree species, *P. insignis* is not associated with any elevation, and the lianous *Daemonorops mollis* is preferentially found at high elevations. In addition, *P. maculata* is positively associated with stream habitats while *D. mollis* is positively associated with non-stream habitats, suggesting a potential niche distinction of the two growth forms. Non-timber forest products include canes for furniture from climbing palms and some palm trees provide food for humans and other animal species. Further development of this potential in a sustainable manner would suggest that knowledge of the habitats best suited to each palm species is important for community-based reforestation programs that provide economic incentives for shareholders.

Chapter Four analyzes the association of 30 dominant tree species with topographic features such as elevation, slope, and stream location. All species associated with at least one topographic feature, which typically changed with age. Only four species were consistently associated with the same elevation microhabitat from saplings, to juveniles, and finally as adults. In contrast, seven species associated with one stream microhabitat across all the three life stages. This result indicates that the habitat best suited to a species may change as they age, suggesting careful monitoring of planted seedlings is necessary to ensure successful establishment of trees into maturity. Site selection for planting, is therefore key to plant survival. It is also clear that soil nutrients, soil moisture, and light availability are some of the environmental factors that must be measured so that these can be adjusted accordingly for each species during their development, because adjustment of the location of planted seedlings is not possible.

Chapter Five explores the spatial patterns in distributions of 30 dominant tree species and the potential roles of dispersal and density dependence on recruitment. Aggregation is observed in all species at multiple spatial scales in the three life stages: saplings, juveniles, and adults. The 15 most abundant species showed a peak of clustering at the scale of $45m^2$ while clustering at a smaller scale ($25m^2$) was exhibited by less abundant species. Negative density dependent effects are observed at the sapling stage in three species and at the juvenile stage in ten species. These results provide guidelines for the proper placement of the appropriate number of seedlings to enhance recruitment into maturity of each species.

Results from my research provide several important guidelines in designing forest conservation programs. Limited genetic variability and restricted distribution of haplotypes in the sampled populations shows that conservation should be intensified and include as many populations in as many islands as possible. In addition, collecting seedlings from many populations to rehabilitate a forest would ensure that the genetic diversity of a species is preserved if not all populations can be protected.

The ideal site to apply the findings from my research for rehabilitatation of disturbed forests and reforest cleared areas is the area surrounding the plot in Palanan. As previously stated, I recommend conservation efforts that begin with the forests in Palanan and Bislig. Fortunately, the lowland dipterocarp forests of Palanan are already protected by law, if not in practice. Surrounding the 16-ha plot are logged forests and less than 1500 meters from the plot are open clearings from abandoned agricultural fields. It is expected that the 30 dominant trees should also be dominant in the disturbed forest adjacent to the plot. An area with heterogeneous topography should be selected to facilitate coexistence of a diverse set of species. A census of the trees in the disturbed forest would identify which species are missing or in lower abundance than anticipated, based on plot data. Individuals of these species can then be supplemented by planting of trees in appropriate topographic or soil habitats. For example, selective logging would have removed dipterocarp species in the disturbed forest and therefore require additional individuals. Seedlings of *Shorea guiso* and six other dipterocarp species should thus be planted in the highest elevations within the disturbed forest while *S. philippinensis* may be planted at any elevation. Seedlings planted may be collected from the Palanan plot in sites where an over abundant population subject to negative density dependent effects exists. *Shorea guiso* juveniles are found farther from adults than saplings, indicating some negative density dependence effects, but the difference is not statistically significant. However, mortality of individuals transitioning from juveniles to adults is high with juveniles showing only 32% survivorship. At the minimum, the same number of adults in the plot (assuming a 16-ha disturbed forest), comprising 12% of the total *S. guiso* population, may be collected as seedlings, saplings, or juveniles to be planted in the disturbed forest. Constant monitoring is required to assess the status of planted trees. At the same time, measurements of soil nutrients, soil moisture, and light availability can be conducted for the 30 most abundant species within the plot and the recorded conditions for the same species duplicated to the extent possible in the regenerating forest. Moreover, demographic analyses must also be completed for the other 293 tree species found in the plot to incorporate as many species as possible in this biodiversity conservation program. A similar methodology using the same data may be adapted to other sites like Bislig if the species composition is similar between sites. In other habitat types, such as limestone, mangrove, or ultramafic forests, baseline data must be gathered first before implementing the same methodology.

The species included in this dissertation were observed under natural conditions and not in disturbed habitats, therefore the response of the 30 species to the drastically different environmental conditions found in completely cleared forests is uncertain and requires further study. Nevertheless, I would recommend prioritizing cleared areas near a water source to avoid deficiency in soil moisture from extreme exposure to the sun. In addition these preliminary reforestation efforts are more likely to succeed if water for seedlings is easily available to workers implementing the plantings. Among the 30 species, five are abundant close to a stream. These are the candidate species to be planted with the addition of the palm tree, *Pinanga maculata*, also found in stream habitats. Gaps in the plot should also be studied to identify species that are key in the natural regeneration process, so that these may be included in reforestation of open habitats. Keeping in mind that the area was farmed and abandoned, the soils must be nutrient poor. If necessary, these soils must be replenished to ensure growth of planted trees. Upon establishment of some forest cover, other species may be added following the same guidelines as in the rehabilitation of the disturbed forest.

The proposed biodiversity conservation program requires a long-term investment in time, effort, and money. Successful programs also require cooperation from other scientists, the government, and the local community. Educating the public on the importance of biodiversity conservation must be a priority as well as economic incentives to encourage the local community to develop and maintain the program. For example, rattans, particularly *D. mollis*, which is abundant in the plot, should be incorporated into the planting design with the intention of sustaining a population that can be selectively harvested. Intensive research on topics such as pollination and dispersal are also needed to enhance the development and sustainability of the forest.

Plant conservation programs from tree plantations to reforestation require prior knowledge of plant ecology, but equally require support from interested parties in the government and society. Perhaps difficult to attain, this is nevertheless the main agenda in order to successfully preserve the rich biodiversity in the Philippines.

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Chapter 1
Origin, Evolution, and Future of the Philippine flora

The origin and evolution of the Philippine flora was influenced by the complex geological and climatological history of the archipelago throughout the Cenozoic Era (65-0 million years ago). Although very little is known about the evolutionary history of Philippine plants, some information has been published on the Philippine fauna, so inferences can be made from these data as well as the more extensive Southeast Asian floristic history. Here, I provide a review of the geological history of Southeast Asia, and the Philippines in particular, to illustrate the origins of the existing landmasses in the Indo-Malayan region. I present documented biogeographic histories of some of the region's flora and fauna that give insight into the assembly of the modern Philippine biota. Finally, the future prospects of tropical forest taxa in the Philippine Islands will be addressed.

Palaeogeography of the Philippines

The palaeogeography of Southeast Asia, including the Philippines, during the Cenozoic was very complex, due to tectonic activity. Through the interaction of the Australian, Caroline, Eurasian, Indian, Pacific, and Philippine Sea Plates, plate collisions were common and widespread occurring between island arcs, island arcs and continents, and between continents (Hall, 2002). Two collision events played major roles in the geological development of Southeast Asia, and subsequently influenced the evolutionary history of plants and animals in the region. The first major Cenozoic event occurred 50 million years ago (Ma) involving the rafting of the Indian subcontinent toward the Asian mainland, colliding with the Eurasian Plate (Figures 1.1 & 1.2; Hall, 2002; Lomolino *et al.*, 2006). The second event occurred in the late Oligocene (25 Ma) with the collision of Australia and the eastern Philippines-Halmahera-New Guinea arc system resulting in major changes in plate boundaries, rotation of the Philippine Sea Plate, and closing of the passageway between the Indian and Pacific Oceans (Hall, 1996, 1998, 2002; Lomolino *et al.*, 2006).

The geologic history of the islands that comprise the Philippine Archipelago parallels the complex history of Southeast Asia. The amalgam that is now called the Philippine Islands is the result of several areas with separate origins and underwent distinct historical developments different histories. Fragments of continental crust from the southern margin of China make up the islands of Palawan and Mindoro (Figure 1.1; Hall, 2002). A small portion of Mindanao Island, the northwestern tip called Zamboanga, is also of continental origin, but from the Sunda Shelf (Hall, 1996). The rest of the Philippine Archipelago is volcanic in origin (Hall, 2002). Subduction zones surrounding the Philippine Sea Plate were responsible for the formation of the oceanic islands of the Philippines, Moluccas, and northern New Guinea beginning 50 Ma in the Eocene (Figures 1.1 & 1.2; Hall, 2002) and are still active today (Yumul *et al.*, 2008). The Philippine Archipelago is now situated on the eastern margin of the Eurasian Plate, separated from the western border of the Philippine Sea Plate by the Philippine Trench (Queano *et al.*, 2007).

The current arrangement of islands in the Philippines resulted from the convergence of northern and southern groups of islands primarily caused by the subduction and rotation movements of the Philippine Sea Plate (Figures 1.1-1.5, see also Hall's animated plate tectonic reconstruction at www.searg.rhul.ac.uk). The oldest volcanic island, Luzon, appeared 50 Ma followed by the eastern Philippine islands 45 Ma (Hall, 2002). Luzon, initially located near Borneo, then moved in a northeast direction and rotated counter-clockwise before colliding with the Palawan-Mindoro block of continental crust. That crust separated from the Asian mainland in the mid-Oligocene as the seafloor spread, creating the South China Sea (Hall, 2002; Queano *et al.*, 2007). Close to the end of the Miocene (10 Ma), the Palawan-Mindoro Block reached the Sunda Shelf and was lifted above sea level (Hall, 1998). Islands in the eastern Philippine arc, at the same latitude as present-day Sulawesi, began moving north 25 Ma and then northwest 5 Ma until reaching their current position and completing the existing arrangement of Philippine islands (Hall, 2002). Geological features responsible for the continuing tectonic activity in the Philippines are reviewed in Yumul *et al.* (2008).

Palaeoenvironment of the Philippines: Insight from the broader Southeast Asian region

Tropical rainforest habitats have occupied the Southeast Asian region at least since the beginning of the Cenozoic Era. In fact, global climate was warmer and more humid than today which supported tropical rainforests as far north as Japan, 35° north of the equator (Woodruff, 2003). Paleoclimate data for the Philippines is lacking, so records from surrounding areas are evaluated to provide insight into the climatic conditions across the Archipelago during the Cenozoic. Special attention is placed on the Pleistocene and Holocene epochs when conditions are better understood.

Periodic contraction of tropical rainforests with replacement by more open savanna-like vegetation, accompanied by increasing or decreasing land area resulting from changes in sea levels characterize the changing Southeast Asian environments throughout the Cenozoic, particularly during the Pleistocene. Palynological studies reviewed by Morley (2000) have pointed to a low diversity moist, warm climate in Myanmar, Sarawak, and Eastern Java in the Paleocene (60 Ma). At this time and through the early Eocene, when the first islands of the Philippines were being formed from volcanic activity on the ocean floor, sea levels were higher than today, often as much as 75m higher, and at one point more than 120m, above current sea level (Miller *et al.*, 2005). Fewer and smaller fluctuations occurred in the middle and late Eocene, a period during which Morley (2000) contends that the Philippine island arc system situated between Sundaland and the western Melanesian arc developed a local flora from colonizing species and autochthonous speciation, possibly serving as a dispersal pathway for Laurasian and Gondwanan taxa. The Philippines may even have been a minor floristic source for the Malesian and South Pacific region. No fossil evidence substantiates this (Morley, 2000). Furthermore, some geological reconstructions of the Philippines hypothesize that prior to the late Miocene, the majority of the land area of the Philippine islands was beneath shallow waters (Hall, 1998).

In the Oligocene, after the collision of India with Asia, an everwet period was followed by a drier seasonal climate, with low sea levels (minus 50-65 m from present levels) associated with ice formation in Antarctica (Wade & Palike, 2004). Subsequent ice growth (Miller *et al.*, 1986; Woodruff, 2003) corresponded with periods of sea level lowering of 50 to 120 m below current levels in the late Miocene and the Pleistocene, respectively (Voris, 2000; Miller *et al.*, 2005). During periods of lowered sea levels, much of the Sunda Shelf was exposed, creating landbridges across many islands in the region. In the Philippine Archipelago during the Pleistocene, this created a grouping of six Pleistocene Aggregate Island Complexes (PAIC) at the maximum decrease of 120 m (Heaney, 1986; Brown & Diesmos, 2002). However, Voris (2000) estimates that only 15,000 of the last 250,000 years were sea levels 120m below present levels. Furthermore, at the Last Glacial Maximum (LGM, 17000 ya) sea levels were below 120m only 6% of the time (~1,000 years) and decreased by only 20 meters.for 9,200 years (54%).

Pleistocene glacial and interglacial periods subjected the Southeast Asian islands to changes in topography, temperature, and precipitation. As a result, the islands underwent a turnover in vegetation types. Heaney (1991) proposed that during the glacial period, cooler and drier conditions from decreased evaporation and moisture content of monsoonal winds reduced the extent of tropical rainforest and opened a savanna corridor from Thailand to Peninsular Malaysia. The savanna corridor included the newly exposed interior Sunda Shelf, extending to Java and the southern Lesser Sunda Islands, which today have seasonal climates with low rainfall. The same savanna corridor was interpreted based on the primate fauna (Brandon-Jones, 1998) and termite communities (Gathorne-Hardy *et al.*, 2002) in Sundaland. It is hypothesized that rainforest habitats were maintained as fragmented refugia in northeast Indochina, north Borneo, north Sumatra, west Java, and in parts of Peninsular Malaysia (Heaney, 1991; Brandon-Jones, 1998; Gorog *et al.*, 2004). The savanna corridor hypothesis is supported by evidence from geomorphology, biogeography, palynology, and vegetation modeling of the LGM, but the width of the corridor is still contentious (Flenley, 1998; Bird *et al.*, 2005).

Palynology records across Southeast Asia and the West Pacific demonstrate the appearance of savanna vegetation during the LGM where previously only lowland rainforest taxa were present (Flenley, 1998). Additional pollen records of the LGM from a part of the raised Sunda Shelf north of Borneo show an assemblage of lowland rainforest and lower montane rainforest taxa, suggesting that despite the cooler climate, humidity was sufficient to maintain rainforest habitats at low elevations (Wang *et al.*, 2009). Thus, rainforest habitats could have occupied large areas including the exposed Sunda Shelf or contracted to small refugia in Sumatra and Borneo. However, it is clear from pollen records that open vegetation separated rainforest habitats during Pleistocene glaciations, creating a dispersal barrier for closed canopy dependent species between Borneo and Sumatra. It is also possible that the same conditions were present during periods of lowered sea levels before the Pleistocene.

Modern molecular techniques have been used to analyze the evolutionary histories of rainforest taxa in the Malesian region, providing a potential representation of the region's paleoenvironment. The phylogeographic pattern in the rainforest tree genus *Lithocarpus* indicates persistence in Southeast Asia since the late Eocene, with fragmentation of Asian mainland and Bornean populations, and development of unique evolutionary lineages in several isolated populations most likely predating the Quaternary (Cannon & Manos, 2000). Although the timing of events is not clear, the research of Cannon & Manos (2000) does not contradict the idea that open vegetation habitats (non rain forest) appeared during dry intervals in the Miocene and Pliocene. This would have fragmented forest populations, reducing dispersal across rainforest refugia, and resulting in locally endemic evolutionary lineages.

The palaeoenvironment of the Philippine Archipelago, if representative of the Southeast Asian region's environmental history, was therefore most likely wet and moist in the early Cenozoic. Tropical rainforest species would have dispersed to newly exposed islands later developing into the widespread tropical rainforest habitats found across the archipelago. Periodic changes in the vegetation must have subsequently occurred in response to climatic fluctuations. Only the recent Pleistocene palaeoenvironmental history has been analyzed in the Philippines, but it is possible that the Philippine islands underwent events analogous to those that occurred in Sundaland. The western half of the Philippines has been reconstructed with a drier climate during the LGM (Heaney, 1991). The western islands are presently categorized as having Type I (pronounced dry season November-April) and Type III (relatively dry season November- April) climate (PAGASA, 2009). Bird *et al.* (2007), using a novel method of gathering palaeoenvironmental information based on carbon isotope data from guano deposits in the island of Palawan, postulate that the areas surrounding the collection sites were grasslands suited to the drier climate during the LGM. By the mid-Holocene, tropical forest, much like the modern forest in the area today developed and replaced the savanna-like vegetation. In contrast to the grasslands in the west, a reconstruction by Heaney (1991) shows the eastern half of the Philippines with an everwet climate coinciding with areas of Type II (aseasonal, with pronounced rainfall November-April) and Type IV (evenly distributed rainfall) climate (PAGASA, 2009). The proposed vegetation distribution during the Pleistocene implies that the range of tropical rainforest flora and fauna was increasingly restricted in the western islands, whereas tropical rainforest habitats in the eastern islands were only slightly contracted at the glacial maximum.

Inferring from Heaney's savanna hypothesis (1991), tropical forest taxa in the Philippines today exist primarily due to the persistent rainforest habitats in the eastern islands, and probable introductions from Borneo or other nearby landmasses. In order to account for the extremely rich and endemic modern flora of the Philippines (76.5% endemicity, Myers *et al.*, 2000), significant pockets of rainforest habitat must have existed during the LGM even within the savanna corridor, as it seems highly unlikely that the eastern islands hosted all the extant endemic species. Therefore, it is more probable that during glacial periods, rainforest species persisted in fragments of forest habitat throughout the Philippines, but mainly in the eastern islands, coupled with some disjunct rainforest refugia within the widespread savanna vegetation in the western islands.

Origin of the modern Philippine flora

Species-rich tropical rainforests are the dominant habitats throughout the Philippine archipelago, extending from 5° to 21° N latitude (Heaney & Regalado, 1998; Co *et al.*, 2006). Several areas with highly diverse floras exist along the boundaries of the Philippines. These areas may have contributed to the current diverse Philippine flora. The Asiatic flora of Taiwan and mainland China form the northern border, Borneo is immediately to the southwest, and Sulawesi and New Guinea are in the southeast. It is unfortunate that there is no fossil record of the vegetation that appeared following the emergence of the current Philippine islands in the Eocene (Ashton, 1993; Morley, 2000) to signal which phytogeographic region contributed the majority of colonizing species to the Philippines. The fossil record could contribute to a clearer picture of the floristic history of islands during the Cenozoic and clarify how the flora underwent change due to plate tectonics. Nevertheless, modern floristic similarity analyses and phylogenetic studies give insight into events that have led to the development of the present flora.

Floristic distributions suggest that the Philippine flora is largely Sundaic in origin (Peninsular Malaysia+Borneo+Sumatra), with some temperate Asian and tropical Australasian elements (Merrill, 1926, 1943). Wallace's Line (Figure 6) was drawn in recognition of the zoological boundary between the Asian and Australian regions (Wallace, 1860). Wallace's Line separated Bali and Lombok, extended north between Borneo and Sulawesi, and finally southeast of the Philippines (Simpson, 1977). Subsequently, the line was redrawn to the west of all Philippine islands except the Palawan group to explain bird distributions and was named Huxley's Line (Simpson, 1977). Huxley's Line was supported by Merrill (Dickerson *et al.*, 1928), due to the significant number of Australian plant genera (43 genera) with their western limits in the Philippines. Nonetheless, a greater number of Asian plant genera (181) reach their eastern limits in the Philippines (van Steenis, 1950; Ashton, 1993) and reflect the greater influence of Bornean taxa. Hence, Wallace's Line best demarcates the floristic region where the Philippine Islands belong.

The Eocene fossil record of Java includes pollen types found in older deposits in India (Morley, 2000, 2003), suggesting the eastward dispersal of Indian taxa via a dispersal corridor through Indochina (Harley & Morley, 1995). Phylogenetic and biogeographic studies corroborate this trend of dispersal from India to Southeast Asia, including the Philippine Islands (*Aglaia* (Muellner *et al.*, 2008); *Caryota* (Hahn & Systsma, 1999); *Leea* (Molina, 2009); *Spatholobus* (Ridder-Numan, 1998); *Vitex* (Bramley *et al.*, 2009)). In some cases, introductions from India resulted in a shift of centers of diversity to Southeast Asia via radiations of taxa with distributions currently limited to Malesia (Calamoideae, Baker *et al.*, 2000; Dipterocarpaceae, Dayanandan *et al.*, 1999). Further, the Philippines may have served as a source or simply a conduit for plant dispersal to the islands of New Guinea and the South Pacific (*Aporosa*, Schot, 1998; *Aglaia, Cycas, Heterospathe,* and *Syzygium*, Keppel *et al.*, 2009). In contrast, contribution of the Australian taxa to the Philippine flora is observed in the range expansion of *Eucalyptus* subgenus *Symphyomyrtus* from the Australian continent to Sulawesi and Mindanao Island, Philippines (Ladiges *et al.*, 2003). The low number of Australian taxa in the Philippine flora, as well as in the Western Malesian flora in general, has been explained as a result of the adaptation of Australian taxa to poor soils and open habitats, thereby making it difficult to establish successfully in the already rich and exuberant rainforest vegetation in Malesia (van Steenis, 1979).

Despite generic similarities with both Asian and Australasian flora, the Philippine flora is distinct at the species level (Ashton, 1993). Endemic species make up 76.5% (5,832 species) of all plant taxa in the Philippine Islands (Myers *et al.*, 2000), many of which are widespread in their distribution. However, the local floras of Luzon, Mindanao, and Palawan, include many species endemic only to each of these islands and taxa only shared with Taiwan, Moluccas, and Borneo, respectively (Merrill, 1926; Ashton, 1993). In contrast, the centers of endemism documented for non-volant mammals and birds correspond to six PAICs (Peterson *et al.*, 2000; Heaney *et al.,* 2005). Preliminary analysis of the highly endemic and speciose genus *Cyrtandra* (Gesneriaceae) indicates two dispersal phases that demonstrate the Palawan-Borneo connection and subsequent development of endemic species in Luzon and Palawan (Atkins *et al.*, 2001). The first phase occurred before the Quaternary, documented by a divergence into two monophyletic clades: Palawan versus Luzon+Mindoro. Both clades are represented by five to six locally endemic species, indicating rapid diversification within the Archipelago. *Cyrtandra* seem to demonstrate rapid diversification following a single dispersal event to oceanic islands, as seen in the Pacific and Hawaiian clades (Cronk *et al.*, 2005). It appears as though a similar radiation occurred after the first dispersal into the Philippines. The second phase of dispersal involved several events attributed to the close proximity of Borneo, particularly during the LGM when Palawan was separated from Borneo by only 12 km (Voris, 2000; Atkins *et al.*, 2001; Meijaard & van der Zon, 2003).

An interesting pattern identified by Merrill (1926) highlights taxa that are found only in the eastern portion of the Archipelago, from Mindanao to Luzon, including areas with Types II and IV current climate. This area coincides with the proposed Pleistocene distribution of rainforest habitat by Heaney (1991). The presence of local rainforest endemic taxa in Palawan, Mindoro, Negros, and Panay, however, points to the maintenance of fragmented forest refugia, even in the drier western islands.

Phylogenetic or phylogeographic data on Philippine plants illustrating vegetation history through the glacial cycles is mostly lacking. While several genetic diversity studies have been performed, yielding information that could be used to interpret plant population dynamics, the taxa investigated were non-native, introduced, and cultivated species that would not represent Pleistocene populations (*Anacardium occidentale* (cashew), Maranan and Mendioro, 2008; *Capsicum frutescens* (chili pepper), Yamamoto & Nawata, 2005); *Colocasia esculenta* (taro), Lebot & Aradhya, 1991; Lebot *et al.,* 2004). A study of the genetic differentiation of natural populations of *Rubus moluccanus* is an exception (Busemeyer *et al.*, 1997). However, only four populations were sampled, one in Luzon and three in Mindanao. Not surprisingly, the Luzon population was found to be genetically distinct from the Mindanao populations. This is evidence that plants across the Archipelago are not genetically homogeneous and that gene flow can be limited. Intra-island gene flow in Mindanao was found to be relatively high, but the easternmost population, separated from the two western populations by 130-245 km, was significantly different suggesting that even short distances can result in population divergence (Busemeyer *et al.*, 1997). In that case, the role of water as a barrier could not be tested because geographic distance was a confounding factor.

In contrast to plants, research on the phylogeny and biogeography in several animal groups has been documented since 1985: birds (Jones & Kennedy, 2008; Outlaw & Voelker, 2008; Sheldon *et al.*, 2009), fruit bats (Heaney *et al.*, 2005; Roberts, 2006), rodents (*Apomys*, Steppan *et al.*, 2003); *Rattus*, Heaney *et al.*, 2005; most genera, Jansa *et al.*, 2006), and shrews (Esselstyn & Brown, 2009; Esselstyn *et al.,* 2009). The general trend recovered is of pre-Pliocene dispersal and diversification events (Steppan *et al.*, 2003, Outlaw & Voelker, 2008; Esselstyn *et al.*, 2009). Speciation was likely driven by dispersal into new habitats subsequently isolated by the insular setting. Pleistocene glaciation effects are varied across the animal taxa. In shrews, genetic divergence is affected by geographic isolation and genetic diversity can be explained by either modern or Pleistocene island boundaries (Esselstyn & Brown, 2009). In fruit bats and in *Rattus everitti*, genetic structure is clearly correlated with PAIC boundaries (Heaney *et al.*, 2005; but see Roberts, 2006). In contrast, the distribution of genetic variation in birds extends outside some of the PAIC boundaries, suggesting that genetic interchange was not significantly increased by Pleistocene landbridges (Jones & Kennedy, 2008).

The assembly of plants in the Philippines resulted from a combination of colonization events from multiple sources and high rates of local diversification, accounting for the high proportion of endemic taxa. Given that endemicity is lower in vertebrate animals (57%, Heaney & Regalado, 1998) than in plants (76.5%), and diversification rates are, on average similar in plants and animals (McPeek & Brown, 2007), it can be inferred that the process of colonization and diversification in plants began, if not prior to, then at least simultaneously with animals. Estimates of divergence times, however, require significant phylogenetic reconstructions (Ricklefs, 2007), which have yet to be compiled for Philippine plants. In addition to testing and timing broad-scale phylogenetic hypotheses, direct evidence of lineage divergence can be determined from population genetics studies (Ricklefs, 2007). The phylogenetic approach in conjunction with genetic and geographic information of populations can be used to document the response of the flora to strong environmental stimuli, like climate change. Faunal response to Pleistocene glaciations has been varied (see above) suggesting the same could be true for plants. Research in this area is necessary to understand past events and potentially allow the approximation of the effects of future climate change.

Future of the Philippine Flora

Tropical forests covered at least 95% of the land area in the Philippine Archipelago before human civilization established in Palawan ~40,000 years ago (Heaney & Regalado, 1998; Bankoff, 2007). Today, only 7% of primary rainforests remain and most are still being threatened with the highest relative rates of deforestation in the world, even if classified as a protected area (1.4% yr-1 in Southeast Asia vs. 1.2% in Central America or 0.5% in South America; Sodhi *et al.*, 2004). The high diversity, high endemicity, and high habitat loss have earned the country a not-to-be-coveted top spot in the world's biodiversity hotspots list (Myers *et al.*, 2000). Increasing population size combined with slow economic growth (Sodhi *et al.,* 2004) is not conducive to the success of conservation efforts.

Current floristic research and conservation initiatives include botanical inventories (Hamann *et al.*, 1999; Langenberger *et al.,* 2006), creation of protected areas (DENR, 2009), establishment of seed banks (IRRI, 2009), in-situ conservation of food crops (Coronel, 2002; Carpenter, 2005), and numerous interests in the development of sustainable agriculture and the preservation of agrobiodiversity (DENR, 2009).

Plant surveys conducted in recent years have recorded several new species. The most amazing discoveries have been of the genus *Rafflesia* (Rafflesiaceae). Since the 1980s, Borneo and Sumatra have been identified as the centers of diversity with 8 and 7 species, respectively (Barcelona *et al.*, 2009). A thriving ecotourism industry in Malaysia is built on viewing these parasitic plants. Prior to 2002, only two species were known to occur in the Philippines. Since then, eight (maybe nine) new species have been discovered (Barcelona *et al.*, 2006, 2009). This is exciting because some of the species have been discovered in disturbed, or even degraded forests (Barcelona *et al.*, 2009). Another newly recorded species is *Nepenthes attenboroughii*, collected in Palawan, which bears pitchers at the tip of leaves approximately 30 cm in size (Robinson *et al.*, 2009). Both *Rafflesia* and *Nepenthes* are large and striking, and were collected in areas previously visited by other botanists. The potential for other species, less conspicuous than the *Rafflesia* or *Nepenthes*, to be discovered is thus very high and floristic inventories are necessary to address this. I recommend the mountains of the Sierra Madre as well as the islands of Palawan as sites for future surveys because the majority of remaining forests are located in these areas.

Approximately 11% of the total land area of the Philippines is designated as Protected areas (PA) (PAWB, 2007). All the primary forests that remain have been mandated to be ‘no-use zones’ within a protected area. Theoretically, these forests are not accessible to any form of extraction of any forest product except by indigenous people inhabiting the park. In practice, illegal logging and the collection of many non-timber and animal goods are carried out in most of these PAs (DENR, 2009). Members of communities near a PA, usually poverty-stricken, find the exploitation of resources within the PA essential for survival. Even the addition of buffer zones, regions surrounding protected areas allocated for traditional agricultural use, has not curtailed the exploitation of the parks (Lynagh & Urich, 2002). Unfortunately, implementation of the policies regarding the protection of PAs is not strict due to the limited resources of the responsible agencies. Thus, the threat of habitat and biodiversity loss continues in the Philippines.

Conservation of fruit-bearing trees and other crops is a national priority supported by the Philippine government, NGOs, and external government agencies (Dillaha *et al.*, 2008; DENR, 2009). Several national institutes have been tasked to establish gene banks, in the form of seed or living specimens in gardens (Coronel, 2002). Ex-situ and in-situ conservation programs have been designed, particularly for rice, to preserve the many traditional varieties (Carpenter, 2005). Timber species, especially native hardwood species like *Pterocarpus indicus* (Fabacaeae), *Shorea contorta* (Dipterocarpaceae), and *Vitex parviflora* (Verbenaceae), are also targeted for conservation (Baja-Lapis, *pers. comm.*; Martin, 2007; Snelder & Lasc, 2008). Even non-timber forest products such as rattans (Arecaceae) are being preserved because of their economic importance (Dransfield *et al.*, 2002).

Currently, the future of Philippine forests appears dismal. However, intensive research and proper implementation of conservation programs can help to preserve the remaining forests and possibly even restore some habitats. I recommend that research be focused on species that still have a widespread distribution in many islands as the understanding of their metapopulation dynamics could provide insight into the interaction of anthropogenically-fragmented habitats. This research needs to be conducted immediately before further habitat loss makes it impossible. In addition, species with limited distributions that have persisted through geological time, could also serve as a model for the maintenance of small populations. Both of these approaches require replication across various taxa before generalized conclusions can be made. The immediacy in starting this considerably large task is imperative.

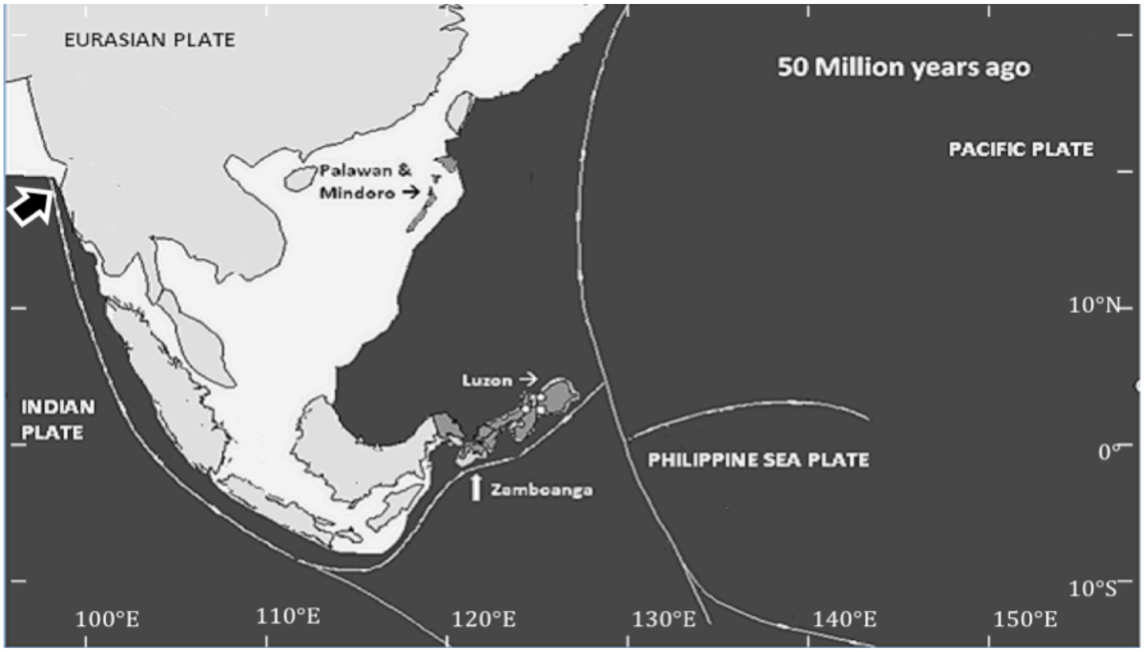

Figure 1.1. Reconstruction of Southeast Asian geology at 50 Million years B.P. with the first appearance of the volcanic island, Luzon, and the continental islands of Palawan, Mindoro, and Zamboanga (shaded dark gray). Philippine Islands remained under shallow water (Hall 1998). Areas outlined in black (outside of the Philippine Islands) are above sea level and light gray areas represent the continental crust below sea level. The arrow at top left indicates the movement of the Indian Plate towards the Eurasian Plate (modified from Hall 2002).

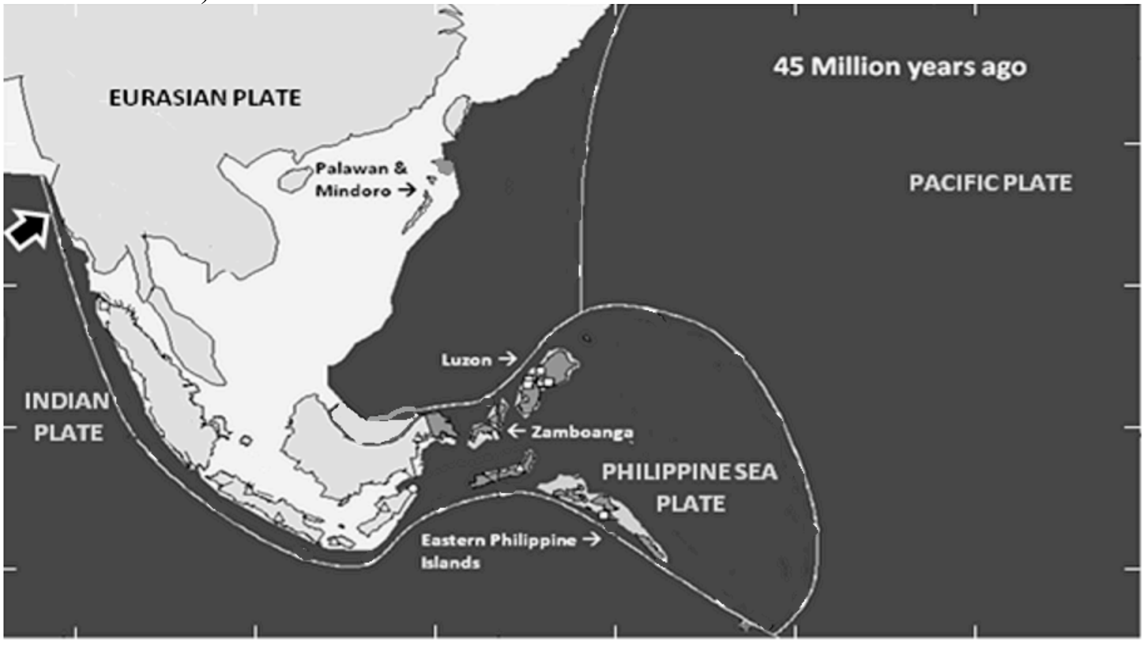

Figure 1.2. Reconstruction of Southeast Asian geology at 45 Million years B.P. with the first appearance of the eastern Philippine islands. A small area in central Luzon appears above water (modified from Hall 1998, 2002).

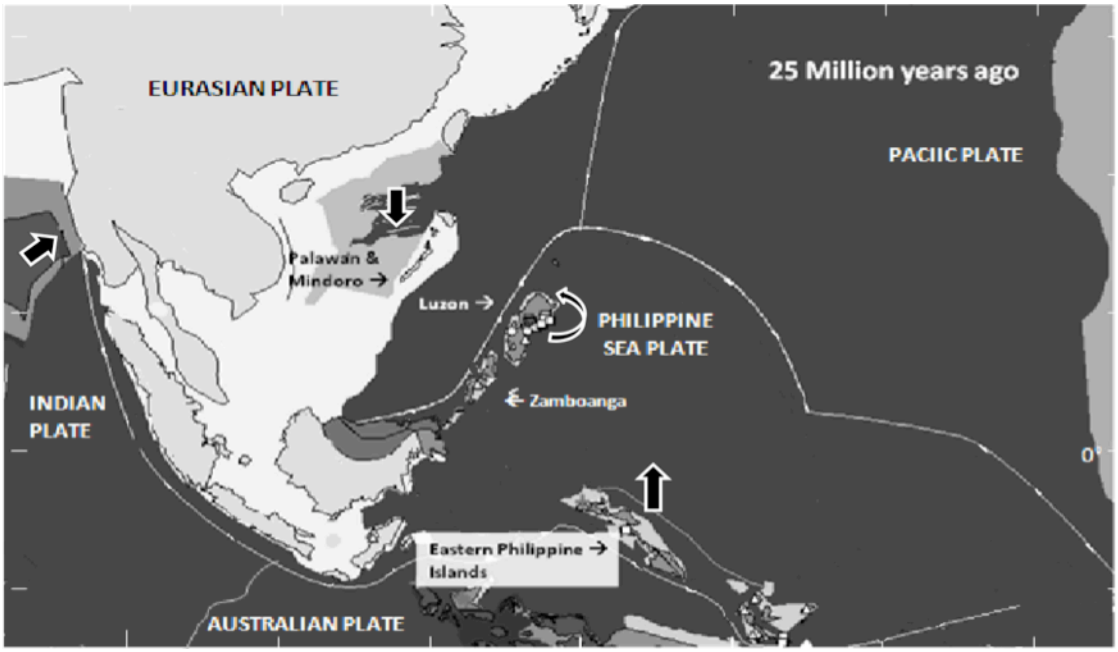

Figure 1.3. Reconstruction of Southeast Asian geology at 25 Million years B.P. showing the southward movement of Palawan and Mindoro, the rotation and northward movement of Luzon, and northward movement of the eastern Philippine Islands. Most Philippine islands remain under shallow water (modified from Hall 1998, 2002).

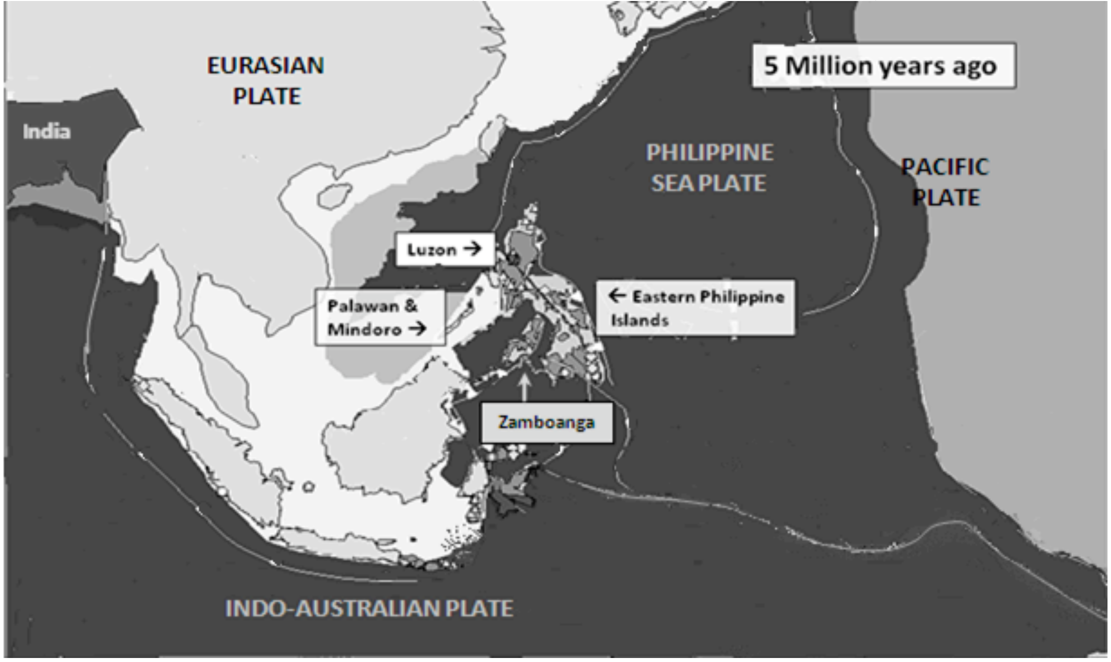

Figure 1.4. Reconstruction of Southeast Asian geology at 5 Million years B.P. showing Palawan and Mindoro north of Borneo and south of Luzon island. The eastern Philippine islands are at a northern latitude. Majority of the islands appear above water (modified from Hall 1998, 2002).

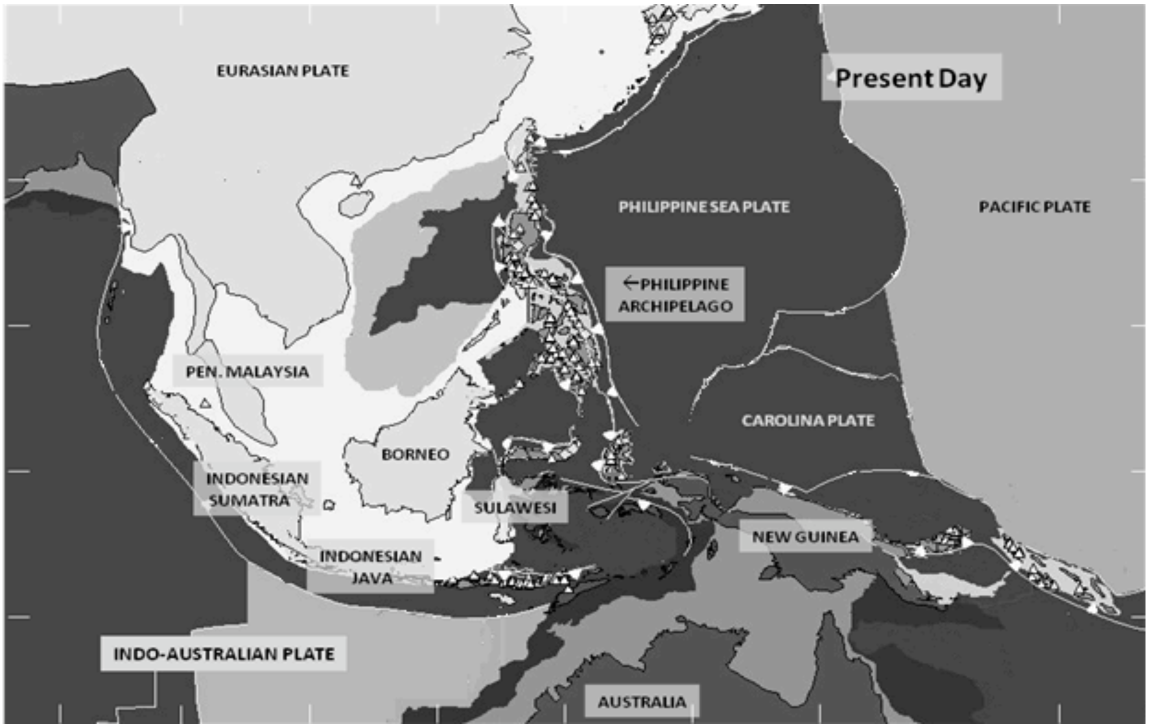

Figure 1.5. Present Day Southeast Asian geography. This resulted from the tectonic activity of the Carolina, Eurasian, Indo-Australian, Pacific, and Philippine Sea Plates (modified from Hall 2002).

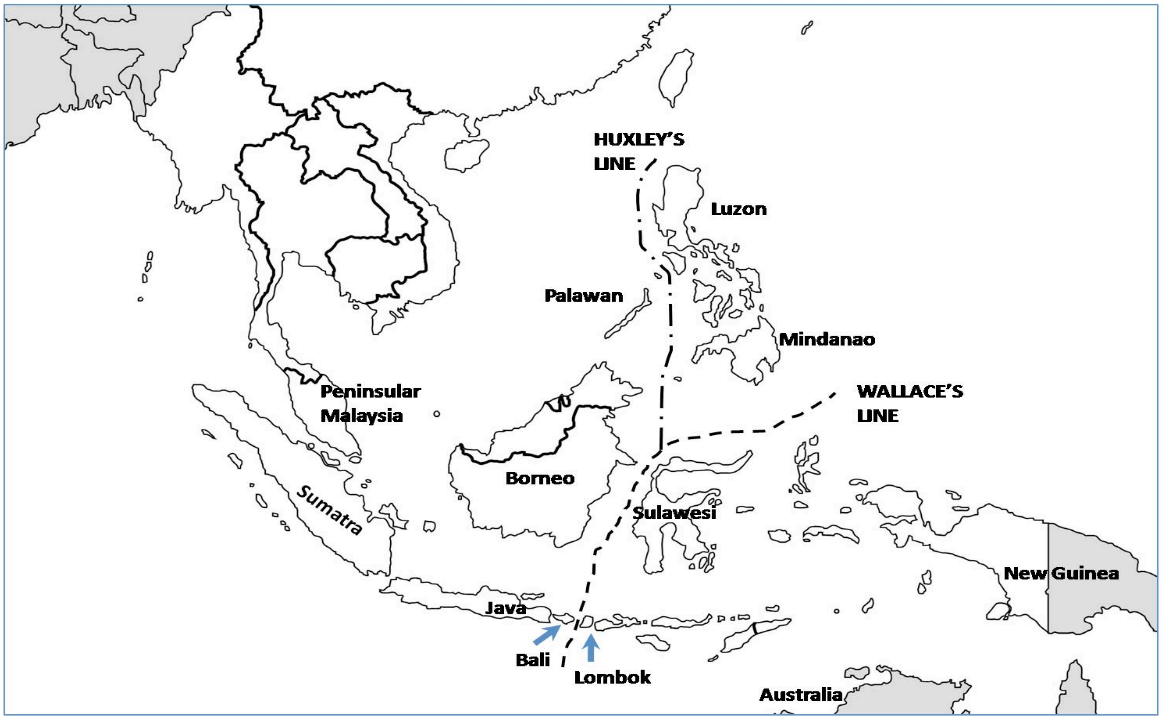

Figure 1.6. Wallace's and Huxley's Line.

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Chapter 2

Population genetics of endemic Philippine plants – patterns in *Daemonorops mollis* (Arecaceae) and *Macaranga bicolor* (Euphorbiaceae)

Abstract

The biogeographic history of endemic plant populations from the Philippine Archipelago was addressed using 97 *Daemonorops mollis* (Arecaeceae) lianas and 71 *Macaranga bicolor* (Euphorbiaceae) trees. DNA sequences were collected from the chloroplast region, rpl16, in *D. mollis*, and used to identify five haplotypes. In *M. bicolor*, the nuclear ITS region and chloroplast trnL-f region were sequenced, recovering 7 and 6 haplotypes, respectively. Phylogeographic structure is recovered only in *M. bicolor* and shows a potential route of colonization in the south- and west- ward direction from populations in northeast Luzon. Water barriers are more easily crossed by *D. mollis*, although for both species, AMOVA tests showed no effect on the observed genetic structure of present-day boundaries and Pleistocene island boundaries. In contrast, high F_{ST} values (0.72 in *D. mollis* and 0.97 in *M. bicolor*) imply that dispersal among populations is restricted, both within and among islands. Genetic discontinuities corresponding to the isolation of islands and a topographic barrier between eastern and western Luzon populations were identified in SAMOVA and help explain the distribution of genetic diversity.

Introduction

Active tectonic history in the Southeast Asian region throughout the Cenozoic via the collision of the Eurasian, Pacific, and Indo-Australian plates (Hall, 2002) resulted in the mixing of Gondwanan and Laurasian taxa followed by subsequent rapid development of endemic floras in the newly formed island arcs (Morley, 2000). Today, among the 7,107 islands of the Philippine Archipelago, 76% of the flora is endemic (Myers *et al.*, 2000). Sadly, an estimated 3,400 (58%) species of Philippine endemic plants are believed to be extinct primarily due to the effects of habitat loss (Brooks *et al.*, 2002). Today, less than 3% of primary vegetation remains in the Philippine islands (Heaney & Regalado, 1998; Myers *et al.*, 2000) and a total of 21% of the land area has primary or secondary forests (Mendoza, *et al.,* 2010).

Despite the diversity of taxa in this unique archipelagic setting, and the threatened status of most of the species, the flora of the Philippines and the Southeast Asian region as a whole, has been the focus of very few evolutionary studies (Beheregaray, 2008). The application of molecular phylogeographic techniques on Malesian taxa has lagged behind research on plant species from Europe, North America, and tropical South America (Petit *et al.*, 2002; Soltis *et al.*, 2006; Dick & Heuertz, 2008). The majority of phylogeographic research has been on continental species, although recent studies have tackled the history of the Caribbean (Butaud *et al.*, 2005), Hawaiian (Wallace *et al.*, 2009), Canary Archipelagos (Juan *et al.*, 2000), and the Asian islands of Taiwan and the Ryukus (Chiang & Schaal, 2006).

The foremost phylogeographic research on plants in Malesia was conducted on the stone oak genus *Lithocarpus* (Cannon & Manos, 2000). The study addressed the population dynamics of the genus, demonstrating its persistence in rainforest habitats through a series of drying events during the Pleistocene. However, a broader biogeographical history of the Philippines, particularly of endemic plants, is very poorly understood.

The phylogenetic and biogeographic histories of animal taxa in the Philippine Islands have received greater attention, providing a testable framework for plant studies. Widespread continental species that colonized and established in the islands, subsequently speciated and diversified to create a highly endemic fauna (47% of vertebrates) with geographically and genetically isolated populations (Heaney & Regalado, 1998; Outlaw & Voelker, 2008; Sheldon *et al.*, 2009). In the caddisfly genus *Hydropsyche*, adaptive radiation of 12 species occurred in a single river in the island of Luzon (Mey, 2000). In the Asian cobra, *Naja naja,* three distinct forms (currently taxonomically considered subspecies) each inhabit a single island or group of islands connected during the Pleistocene (Wuster & Thorpe, 1990), supporting the hypothesis of a potential opportunity for dispersal among connected islands during periods of lowered sea level.

Using phylogeographic analyses, which determine the genealogical relationships of spatially distributed populations within a species (Avise, 2000), Peterson and Heaney (1993) examined fruit bats and discovered patterns of genetic differentiation associated with Pleistocene island water boundaries. In a subsequent study including five species of bats and one species of murid rodent, phylogeographic structure was correlated with boundaries of Pleistocene islands rather than present-day island boundaries (Heaney *et al.*, 2005). Historical sea level fluctuations, particularly during the Last Glacial Maximum (LGM), are thus presented as influential in the evolutionary history of Philippine fauna. In contrast, this pattern was not evident in the malaria vector *Anopheles flavirostris*

(Foley & Torres, 2006). Inter-island population gene flow was only partially inhibited by water barriers of present-day islands and a south-to-north range expansion was recovered. Further, allozyme analysis of milkfish populations indicated no genetic isolation among marine populations that were separated by landbridges during each glaciation event (Winans, 1980) but see (Lourie *et al.*, 2005). A brief review of comparative phylogeographic studies on Philippine animals tested four major patterns of colonization: (1) north (N) to south (S) via Taiwan; (2) S to N from Borneo via Palawan; (3) S to N from Borneo via Mindanao; and (4) S to N from Sulawesi via Mindanao (see Figure 1 in Jones & Kennedy, 2008). The strongest support was found for south-to-north colonizations from Borneo via both Palawan and Mindanao, accompanied by speciation and within species differentiation on isolated islands (Jones & Kennedy, 2008).

In contrast to the increasing number of phylogeographic studies on animals, research on plant population genetics is limited to a few phylogenetic studies conducted at higher taxonomic levels. Phylogenetic analyses have presented potential colonization routes in both northward and southward directions, along the 1600 km of the archipelago, and indicate the importance of water barriers to facilitating speciation (Atkins *et al.*, 2001; Muellner *et al.*, 2008). Restricted gene flow within and across islands was also documented in a limited sample of *Rubus moluccanus* (Rosaceae), from three populations in Mindanao and a fourth from Luzon (Busemeyer *et al.*, 1997). The genetic structure of Philippine populations has the potential to clarify the evolutionary and ecological history of a highly diverse flora distributed across many islands. The present study is the first range-wide comparative phylogeographic study of Philippine plants.

Here, comparative analyses are performed on *Daemonorops mollis* and *Macaranga bicolor*, two phylogenetically distant species that bear some important similarities. The two species occur in sympatry and share several traits particularly those involving their mechanism of dispersal. Both species inhabit primary and secondary forests, are widespread Philippine endemics, bird-dispersed, and dioecious (Merrill, 1926; Uhl & Dransfield, 1987).

Daemonorops mollis is a spiny, long-lived liana species belonging to the oldest and largest lineage in the Arecaceae, the Calamoideae subfamily (Lewis *et al.*, 2000; Asmussen *et al.*, 2006). The Calamoids are distributed throughout the Old World tropics (Uhl & Dransfield, 1987) and typically comprise nearly half of the palm species in the Malesian region. In the Philippines, four Calamoid genera include 65 of the total 135 palm species (Fernando, 1990). While the Philippine palm flora is not very species-rich, including only 5.8% of all palm species, over 70% of the species that occur in the Philippines are endemic (Fernando, 1990), suggesting a high speciation rate within the Philippine islands. The palm flora of nearby Celebes, Malay Peninsula, and Borneo, share the largest number of species with the Philippine flora, suggesting that the introduction of palms into the volcanic islands of the Philippines came from these areas (Fernando, 1990). The southern locations of these probable sources indicate a south to north colonization route into the Philippine islands.

Macaranga bicolor is a short-lived pioneer tree species in the Euphorbiaceae. The genus *Macaranga* is comprised of approximately 250 species, distributed in the paleotropics (Govaerts *et al.*, 2000). Like the Calamoid palms, *Macaranga* is most diverse in the Malesian region including 133 of 250 (53.2%) species (Govaerts *et al.*, 2000). Twenty-three (9.2%) species are found in the Philippines, 17 (74%) of which are endemic (Merrill, 1926; but see Whitmore, 2008). The high number of endemic *Macaranga* species in the Philippines also attests to the fast pace of evolution in the islands, given that the oldest island in the Philippine archipelago is only 50 Million years old (Hall, 2002). Furthermore, the restricted distribution of some species like *M. amplifolia, M. balabacensis*, and *M. leytensis* to a single or a few islands indicates that dispersal across islands is limited, potentially contributing to population or species divergence. Local and widespread endemism is also exhibited in *Daemonorops* and thus, analysis of both *D. mollis* and *M. bicolor*, could reveal a comparable account of the evolutionary history of the Philippine flora.

The following hypotheses are tested here: (1) Colonization events among islands proceeded from south to north resulting in ancestral haplotypes found in Mindanao, and more derived haplotypes in Luzon. (2) Increased geographic distance between populations reduced gene flow producing a correlation between geographic and genetic distance. (3) Water barriers isolated island populations and thus the distribution of genetic variation is predicted to be among rather than within islands. (4) Lower sea levels during the Pleistocene facilitated gene flow between currently isolated island populations within a larger Pleistocene island. It is expected that genetic differentiation among populations will be correlated with the Pleistocene grouping of present-day islands (Figure 2.1.a).

Methods

Sampling

Leaves from 4-16 individuals of *Daemonorops mollis* and *Macaranga bicolor* were collected from 9 and 8 sites, respectively (Figures 2.2.a, 2.3.a, 2.4.a, and 2.5.a; Table 2.1). Sites were chosen based on forest quality and including as much as possible of each species' known distribution. Leaf samples were preserved in silica gel immediately after collection. Outgroup species were selected and used to determine if the target species were monophyletic or comprised of a species complex. For *Macaranga,* five outgroup species included (1) *M. triloba*, which belongs in the same clade as *M. bicolor* based on the phylogeny constructed by Kulju *et al.* (2007), (2, 3) two species (*M. hispida* and *M. tanarius*) from the only other clade with Philippine representatives, and (4, 5) two endemic species (*M. dipterocarpifolia* and *M. ovatifolia*) of unknown position in the phylogeny. No proposed phylogeny exists for *Daemonorops,* so two endemic sympatric species, *D. loheriana* and *D. ochrolepis*, were selected as outgroup species.

DNA extraction, amplification, and sequencing

DNA extraction – Twenty milligrams of dried leaf material were ground in a Retsch MM 301 mixer mill (Retsch, Haan, Germany) from which DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Valencia, California). The manufacturer's protocol was followed with an additional incubation step to digest proteases using 5µl of Proteinase K for five minutes at room temperature.

PCR amplification – Nine notably variable regions, including the barcode region psbA-trnH (Table 2), were initially tested for genetic variation but only two regions showed nucleotide differences among test samples. Two gene regions, one nuclear and one noncoding chloroplast, were amplified via polymerase chain reaction (PCR) for all samples of *Macaranga bicolor*. A ~900 bp segment of the nuclear internal transcribed spacer (ITS) was amplified with the primers 17SE (5’-ACGAATTCATGGTCCGGTGAAGTGTTCG-3’) and ITS4 (5’-TC$_{CT}$CCG$_{CT}$TATTGATATGC-3’) following Baker *et al.* (2000). The primer sequences trnQ (5’-GCGTGGCCAAGYGGTAAGGC-3’) and rps16 (5’-GTTG$_{CT}$TTYTACCACATCGTTT-3’) were used to amplify the plastid genetic marker, trnQ (Shaw *et al.*, 2007). Amplification reactions were performed in 25µl volumes containing 2.5µl of 10X Buffer, 2.5µl of 2mM dNTPs, 1µl of each primer at 10 pmol/µl dilution, 0.1µl of Qiagen HotStar Taq polymerase, and 1µl of DNA template, which was prepared by diluting the total genomic extracts 1:50. PCR was performed with a Touchdown PCR protocol (Qiagen) with an initial heating at 95ºC for 15 min; each of 35 subsequent cycles used the following annealing temperatures: 60ºC, 59ºC, 58ºC, 57ºC, 55ºC, 52ºC, and 50ºC; and elongation was set at 72ºC for 45 seconds. A final extension at 72ºC was run for 15 min. The noncoding region, rpl16, was sequenced for all *D. mollis* samples using the primers rpLF71 (5’ – G$_{CT}$ATG$_{CT}$TAGTGTGTGA$_{CT}$CGTTG-3’) and rpL1516 (5’-CC$_{CT}$TCATT$_{CT}$TC$_{CTCT}$ATGTTG-3’) from Shaw *et al.* (2005). Amplification reactions comprised of 2.5µl of 10X Buffer, 2.5µl of 2mM dNTPs, 1.5µl of each primer at 10 pmol/µl dilution, 0.1µl of Qiagen HotStar Taq polymerase, 2µl of DNA template, and 15 µl of ddH2O. PCR followed the protocol used for *M. bicolor*. PCR amplification quality was assessed by visualizing 3µl of the product in 1% agarose gel with ethidium bromide.

DNA Sequencing - PCR products from successful reactions were cleaned using ExoSAP-IT® (USB Corp., Cleveland, Ohio) following manufacturer’s specifications, and then submitted to the University of Michigan DNA Sequencing Core Facility for sequencing using Applied Biosystems DNA Sequencers (Model 3730 XL sequencer). Each DNA fragment was sequenced in both forward and reverse directions.

Sequence Alignment and Data Analysis

Sequence Alignment – DNA sequences were manually edited in Sequencher ver. 4.6 (Gene Codes Corp.) and initially aligned with ClustalW (European Bioinformatics Inst.) using default parameters. Minor adjustments were made in MacClade 4.0 (Maddison & Maddison, 2005). The two regions, ITS and trnQ, sequenced for *M. bicolor* were concatenated in MacClade 4.0.

Data Analysis - The alignment was converted into a NEXUS file and was used to perform maximum parsimony (MP) analyses in PAUP* v4.0 (Swofford, 2003). Heuristic searches were performed with 100 random addition-sequence replicates and tree-bisection reconnection branch swapping, saving all most parsimonious trees. A 50% majority-rule consensus tree was reconstructed from all saved MP trees. A MP bootstrap analysis (Felsenstein, 1985) was performed with 1000 bootstrap pseudoreplicates. Partition homogeneity was tested for the *M. bicolor* concatenated data with the incongruence-length difference (ILD) test (Farris *et al.*, 1994) in PAUP.

The program PERMUT (Pons & Petit, 1996) was used to assess phylogeographic structure by testing for significant differences between measures of population differentiation based on either haplotype frequencies only (G_{ST}) or haplotype frequencies and divergence (N_{ST}). Population pairwise F_{ST} values were determined in Arlequin ver.3.1 (Excoffier *et al.*, 2005) and used to conduct analyses of molecular variance (AMOVA) in order to partition molecular variance into among and within populations at three hierarchical levels: among populations, among present-day islands, and among

Pleistocene islands. To define groups of populations that are geographically homogeneous with maximum genetic differentiation (based on total genetic variance), a spatial analysis of molecular variance (SAMOVA) was performed. The test is used to identify the number of groups (K) that would result in the largest F_{CT} value (proportion of total genetic variance due to differences between groups of populations) (Dupanloup *et al.*, 2002). K was set between two and eight, with 100 simulated annealing processes. Isolation by distance (IBD) was tested with a Mantel test in GenAlEx ver. 6.0 (Peakall & Smouse, 2006) between geographic distance and Slatkin-transformed genetic distance, $F_{ST}/(1-F_{ST})$. Significance was assessed using 9999 permutations. Geographic locations used were collected on-site with a Garmin e-Trex Legend GPS unit. Haplotype relationships of *D. mollis* and *M. bicolor* were inferred using statistical parsimony methods in TCS v.1.21 (Clement *et al.*, 2000) represented by a haplotype network.

Results

DNA sequence data was obtained for 71 individuals of *M. bicolor* and 97 individuals of *D. mollis* (Table 2.1, Figure 2.1.b). The *D. mollis* samples were collected from six islands, with a mean sample size of 10.8 individuals. Five islands are represented in the *M. bicolor* data with a mean sample size of 8.9 individuals.

Daemonorops mollis

Within *D. mollis*, rpl16 sequences amplified were comprised of 906 nucleotides. There were only four variable sites, three of which were parsimony-informative. Five polytomous clades were recovered, corresponding to the five haplotypes recognized in the statistical parsimony analysis conducted. Four *D. mollis* haplotypes were different from haplotype h1 by a single base pair substitution. Parsimony analysis shows four of five equally likely trees of 20 steps with a consistency index of 1.0 and retention index of 1.0. The strict consensus tree with bootstrap support values is presented in Figure 2.2.b. The haplotype network (Figure 2.2.c) depicts the same phylogenetic relationships. Nevertheless, when combined with sequences from the outgroup species, all the *D. mollis* individuals still formed a moderately supported (63%) monophyletic group. The outgroup species, *D. ochrolepis*, is different from the most common and ancestral *D. mollis* haplotype, h1, by only one base substitution. *D. loheriana*, however, is 12 mutational steps from *D. ochrolepis*, 9 of which are base substitutions and 4 are single-base deletions.

One haplotype, h1, is very common and found in 59 of 97 (61%) individuals and from eight of nine sites (Figure 2.2.a and 2.2.c). Two haplotypes, h2 and h3, are shared by two and three populations, respectively. The two remaining haplotypes, h4 and h5, are rare and each restricted to one population. Three populations, S4, S10, and S11, are fixed with only one haplotype.

The comparison between N_{ST} and G_{ST} (N_{ST}= 0.718, G_{ST}=0.669, p>0.05) shows a higher N_{ST} but is not significantly different from G_{ST} indicating that haplotype distribution is not phylogeographically structured. However, F_{ST} analyses reveal some genetic structure across populations, with significant F_{ST} values observed in a majority of the population pairwise comparisons (Table 2.3). The AMOVA presents similar findings with F_{ST} of 0.720 (p<0.001) (Table 2.5). Significant genetic variation is found among populations (76%) and within populations (24%). The significantly higher proportion of variance among populations indicates that the genetic diversity is distributed at larger spatial scales rather than within sampling sites. Islands, however, do not form natural groups of populations that explain the distribution of genetic variation. The negative F_{CT} result indicates the absence of genetic structure based on island boundaries. When considering Pleistocene island groups, genetic variation attributed to this hierarchical structuring is also insignificant (2.58%, $p<0.32$). The Mantel test conducted on the geographic distance between each pair of populations and the linearized F_{ST} shows no correlation between genetic and geographic distance ($R^2=0.0082$, $p<0.357$). However, according to the SAMOVA with the highest F_{CT} value ($K=3$, $F_{CT}=0.811$, $p<0.001$), genetic discontinuities were identified that separate the sampled populations into three genetically and geographically homogeneous groups of populations. The first group is comprised of S7 and S8, the second of S4, and the third group includes all other populations (Table 2.1 and Figure 2.2.a).

Macaranga bicolor

In *Macaranga bicolor*, nuclear and non-coding chloroplast regions were 749 and 982 bases long, respectively. The ITS sequences included 55 variable sites, 30 of which were parsimony informative (4%). The best of the 100 saved trees was of 149 steps with a consistency index (CI) of 0.658 and a retention index (RI) of 0.745. The chloroplast region had 27 parsimony informative characters (2.7%) and four equally likely trees were recovered with 25 steps, CI = 0.960 and RI=0.992. The data partition homogeneity test failed to detect significant heterogeneity between the two regions ($p\leq1.000$), so the combined ITS+trnQ sequence for *M. bicolor* is also analyzed. A maximum parsimony tree of 165 steps (CI=0.891, RI=0.959) was constructed using the 57 parsimony-informative characters from the combined sequence length of 1731 bases. The MP majority rule tree from the ITS, trnQ, and combined ITS+trnQ analyses are presented in

Figures 2.3.b, 2.4.b, and 2.5.b, respectively, with bootstrap values (> 50%) indicated on the supported node.

Results from separate analyses of the nuclear and chloroplast data show a marked difference in tree topologies (Figures 2.3.b and 2.4.b) and resolution of haplotype relationships (Figures 2.3.c and 2.4.c). The ITS sequence data presents ambiguous relationships between clades and haplotypes, whereas the chloroplast data recovered no polytomies with one less clade and haplotype. Both DNA regions show the monophyly of *M. bicolor* with strong support for some of the nodes (59-100%). Nevertheless, in both datasets, the h1 haplotype from S1 and S11 (Figures 2.3 and 2.4) is clearly the basal clade. Haplotypes h2 and h3 form sister clades and the remaining clades (four from the ITS dataset and three from trnQ dataset) form a group sister to the h2+h3 clade.

In the combined ITS+trnQ analysis, phylogenetic relationships are more clearly resolved. Seven clades were recognized, each representing one of the eight haplotypes recovered in the TCS haplotype network (Figure 2.5), except the clade of S6 individuals containing both h4 and h5 haplotypes. Monophyly of *M. bicolor* has 100% bootstrap support and most other nodes are moderately to highly supported (55-99%). The outgroup species *M. triloba* was recovered as sister to *M. bicolor* with a net sequence divergence of 1.5% (26/1731) from *M. bicolor*.

Phylogenetic relationships from the MP tree indicate S6 individuals (h4 and h5) diverged from the S5 population (h2 and h3). Populations S7 (h8) and S8 (h7) are sister to S9 and S10 (both h6). Collectively, all other populations are sister to S1 and S11 (h1). In most populations, only one haplotype was found (six of eight) and in two cases, two populations shared one haplotype (S1 and S11, S9 and S10). On the other hand, only populations S5 and S6 had more than one haplotype, and both haplotypes found in each population were unique.

Phylogeographic structure in *M. bicolor* haplotype distributions is reflected in the significant difference between N_{ST} and G_{ST} (N_{ST}=0.889, G_{ST}=0.673, $p<0.05$). F_{ST} analyses corroborate this finding with the majority of population pair-wise comparisons showing significant F_{ST} values (Table 2.3). F_{ST} values range from 0.776 to 1.000, except in two cases, between populations S1 and S11, and populations S9 and S10, both of which share the same haplotype resulting in an F_{ST} value of 0.00.

The AMOVA also showed significant structuring of genetic variation (Table 2.4). Considering only among and within population differentiation, almost all of the genetic variation is distributed among populations (96.8%) and very little within populations (3.2%). Even more than in *D. mollis*, genetic diversity in *M. bicolor* is distributed among populations and beyond the limits of a single collecting area. Furthermore, the negative F_{CT} value in the among-island grouping indicates that island barriers do not delineate populations in *M. bicolor*. Based on the assignment of populations to their respective Pleistocene island groups (Table 2.1 and Figsures 2.1.b and 2.5.a), some genetic variation (15.98%) is attributed to this hierarchical structuring, but is not significant ($p<0.18$). This is likely caused by the distribution of six of seven haplotypes in two Pleistocene island groups (G. Luzon and G. Mindanao) and the seventh haplotype shared in the other two island groups (G. Negros and G. Mindoro PI), Additional samples particularly from G. Negros and G. Mindoro are needed to obtain stronger statistical results from this test. Six groups of populations identified in the SAMOVA (K=6, F_{CT}=0.974, $p<0.001$), indicate where gene flow occurs among populations, and locations of barriers to gene flow (Table

2.8). According to the Mantel test conducted on the geographic distance between any two populations and the linearized F_{ST}, there is a slight ($R^2=0.223$, $p<0.05$) negative correlation between genetic and geographic distance.

Discussion

Analyzing phylogeographic patterns for both *Daemonorops mollis* and *Macaranga bicolor* presents an opportunity to find congruent or contrasting patterns of lineage sorting of plant populations within the Philippine Archipelago. This has provided information on the genetic characteristics of these two species, and given the paucity of phylogeographic information for Philippine plant species, provides a preliminary view of plant migration and diversification within the islands.

Daemonorops mollis

Genetic differentiation recognized among *D. mollis* populations is attributed to only five haplotypes with little nucleotide divergence. Low genetic variation is not unexpected in palm species, as prior studies have indicated that palm DNA is relatively slow in accumulation of base-pair changes (2.5- to 13- fold slower than grasses, Baker *et al.*, 2000). The polytomous phylogenetic relationship among the *D. mollis* haplotypes clearly presents no sign of a distinct island colonization route. Stepwise island colonization is also not recovered in the isolation by distance test, which shows no correlation between genetic similarities and proximity of populations.

AMOVA results show that population differentiation is not consistent with island boundaries. Furthermore, the presence of a widespread haplotype (h1) in almost all populations and a second haplotype (h2) in three separate island populations is evidence that water surrounding each island is not a strong barrier to gene flow via seeds. Although neither *D. mollis* seeds nor fruits are adapted to water flotation, seeds have an 8% chance of germination after a single day of immersion in salt water, which may be sufficiently good odds for successful water dispersal across the narrow seas separating some islands (Yap, *unpublished*). Also, birds have been noted to feed on the sarcotesta of the fruit and are proposed to aid in the dispersal of the seeds (Gunawan, 1991). These dispersal mechanisms potentially explain the distribution of the common haplotypes. In contrast, the limited distribution of three haplotypes each on a single island lends support to the potential of water as a genetic barrier.

There is no evidence to support an increase in dispersal across islands that formed land connections during the Pleistocene. The AMOVA test shows that grouping populations according to the Pleistocene island on which they were located, does not help to explain the distribution of genetic variation. Despite the increase in land area during lowered sea levels, gene flow across present-day islands was not facilitated by the appearance of Pleistocene landbridges. This suggests that either the newly opened landmasses were not suitable habitats for *D. mollis* or that they were open for an insufficient time for migration. This pattern is unlike that found in *Schiedea globosa* (Caryophyllaceae), which was proposed to have expanded its population from Molokai to Maui when both islands formed the Pleistocene island, Maui Nui, of the Hawaiian Archipelago (Wallace *et al.*, 2009).

It is possible that the haplotypes represent ancestral polymorphisms with current distributions resulting from population bottlenecks during the LGM or a recent population expansion after the LGM. Climate change in Southeast Asia during the LGM supposedly facilitated the replacement of rainforest habitats with savanna-like vegetation

(Heaney, 1991; Bird *et al.*, 2007). The reduced extent of forest cover supporting smaller populations may have resulted in the rapid loss of genetic variation from increased genetic drift in each island population. Thus, a random set haplotypes would exist after the bottleneck event and phylogeographic structure cannot be recovered ($N_{ST} = G_{ST}$). The dispersal of ancestral haplotypes after the LGM would further contribute to the random distribution of haplotypes in the current populations.

For *D. mollis*, water is a very weak barrier, and water dispersal across long distances is possible. Nonetheless, land barriers can curtail long distance dispersal. Based on the SAMOVA, a genetic discontinuity between the eastern and western halves of Luzon Island isolates populations S1 and S11 from S7 and S8 (Figure 2.2.a). The genetic break corresponds to the Archipelago's two largest plains divided by the combined foothills of the central Cordillera Mountains and the Sierra Madre Mountains in the east. This is the first record of a land barrier resulting in the isolation of plant lineages in Luzon Island, and the Philippines in general.

The importance of the information that can be interpreted from the limited variation in the chosen marker warrants further study of the species using more variable regions or by developing microsatellite markers, and increasing the extent of sampling. Sampling should include more populations from a greater number of islands and areas located at both sides of potential land barriers, like the Cordillera Mountain Range, Compostela Valley, and Kitanglad Mountain Range.

Macaranga bicolor

In *M. bicolor*, there is evidence of phylogeographic structure expressed by the distribution of genetically distinct populations with unique and fixed haplotypes. *M.*

bicolor shows a possible pattern of island colonization but not parallel to the south to north direction, as seen in birds and bats (Jones and Kennedy, 2008). The plant dispersal route includes a south-oriented dispersal from eastern Luzon to the southeastern islands of Samar (S5) and Mindanao (S6), and a concurrent (cpDNA dataset) or subsequent (nuDNA dataset) dispersal event to western Luzon (S7 and S8) and the western islands of Mindoro (S9) and Panay (S10). A similar southward colonization from Luzon was also documented for a genus of rodents, *Apomys* (Steppan *et al.*, 2003). In both *Apomys* and *M. bicolor,* the ancestral lineage is documented in Luzon and derived populations in the southern islands, which is chronologically consistent as Luzon was one of the earliest, if not the first, islands to emerge from beneath sea level after formation from ocean floor volcanic activity (Hall, 2002).

Luzon was initially located just off the northeast tip of Borneo, making Borneo a potential source of *Macaranga* species to the Philippines, before rearrangement of the Pacific and Philippine Sea Plates rotated Luzon and moved it roughly 7 latitudinal degrees north to its present position (Hall, 2002). It is thus possible that *M. bicolor* diverged from its most recent common ancestor in Luzon during this time of tectonic activity, before expanding its range to other recently formed islands south of Luzon. Other Luzon endemics like *Calamus arugda* (Arecaceae) and *Trigonostemon oblongifolius* (Euphorbiaceae; Merrill, 1926), illustrate the development of divergent evolutionary lineages in this island. Another species of *Macaranga*, *M. stonei*, may also have evolved in Luzon based on its restricted distribution to this single island. Two other *Macaranga* species are found only in Luzon and one other island, Leyte or Mindoro (Whitmore, 2008). Luzon also has the largest land area of all the islands in the archipelago which fits with the island biogeography theory (MacArthur & Wilson, 1967), harboring higher species diversity than smaller islands and hosting many of the endemic species of the Philippine flora, like *M. bicolor*.

Range expansion after evolution, however, may not have occurred in a stepwise island colonization manner, as the IBD test does not show a positive correlation between genetic and geographic distance. The IBD test result indicates that distance *per se* does not explain the observed phylogeographic structure. Rather, it points to the possibility of geographic features, such as variable topography or the ocean, serving as barriers between sampled populations. A slight negative relationship is recovered because the eastern Luzon populations are more closely related (based on ITS, trnQ, and combined datasets) to the southeastern populations of Samar (S5) and Mindanao (S6), than to the geographically closer western Luzon populations (S7 and S8).

Gene flow to and from the eastern Luzon populations appears to be restricted by land and water barriers as indicated by the unique haplotypes present in most populations within and among islands. AMOVA results also show high genetic differentiation between any two pairwise population comparisons, except the shared haplotype composition of S1 with S11, and S9 with S10. S1 and S11 are separated by a mountain range including one of the highest peaks in the country (1850m), yet both populations are identical in genetic composition (*N*m = inf). However, the same genetic discontinuity is uncovered in SAMOVA between the Luzon island eastern populations and the western populations as seen in *D. mollis*. In this case, geographic distance and perhaps topography, although not topography alone, may be the more influential factor in the genetic differentiation of these particular populations. In the unique case of S9 and S10, water boundaries between the two islands seem to have not hindered genetic exchange. However, this may not hold and genetic differentiation may be observed between S9 and S10, if additional sampling from multiple localities in each island can be accomplished.

In all other haplotype distributions, water creates a barrier between island populations. Still, island boundaries do not delineate populations (negative or zero contribution to genetic variance). Pleistocene islands also do not provide a significant proportion of genetic variation (16%, p=0.18). This is supported by SAMOVA results (Table 2.8) assigning S5 and S6 populations (both in the Greater Mindanao PI) into two different groups, and combining S9 and S10 (Mindoro and G. Panay PI, respectively) into one group. The sixth genetic discontinuity (Table 2.8 and Figure 2.5.a) is between the two western Luzon populations. Only a short distance separates these two populations and there is no evident topographic barrier between them. It is possible that a contraction of the forests in these two areas during the LGM resulted in the fixation of a single haplotype in each of these two sites. Recolonization events are sometimes accompanied by the introduction of other haplotypes into the area (Petit *et al.*, 2003), but this pattern is not exhibited in my sampling of the *M. bicolor* populations. Extensive habitat loss in the Philippines however, may be a confounding factor erasing this predicted signal.

Climate during the LGM was drier and cooler, as previously mentioned, which led to the hypothesis of savanna-type vegetation dominating the western Philippine islands (Heaney, 1991). However, some forest cover must have remained as fossils of forest-dependent animals were found in the western island of Palawan (Reis & Garong, 2001). This would suggest that small populations of *M. bicolor* could have persisted in both eastern and western islands, with reduced genetic diversity, both during the LGM and during the expansion of forest habitats after the glacial event. This scenario can explain the current genetic structure of *M. bicolor*, largely represented by populations with fixed haplotypes. To test the hypothesis that rainforest species persisted in Pleistocene forest refugia in both the drier western and wetter eastern parts of the Philippines, extensive sampling should be conducted in Luzon and Mindanao island, which experienced the drying phenomenon only in the most western areas in conjunction with the use of fast evolving genetic markers like SSRs. Forest refugia should have been more dominant in the eastern populations and thus a population genetic survey is predicted to demonstrate an east to west post-LGM population expansion. A similar east-west pattern was revealed by IBD tests in 5 Lepidopteran species in New Guinea, which authors suggest reflects the influence of sea level rise during the Holocene (Craft, K.J., *et al.* 2010).

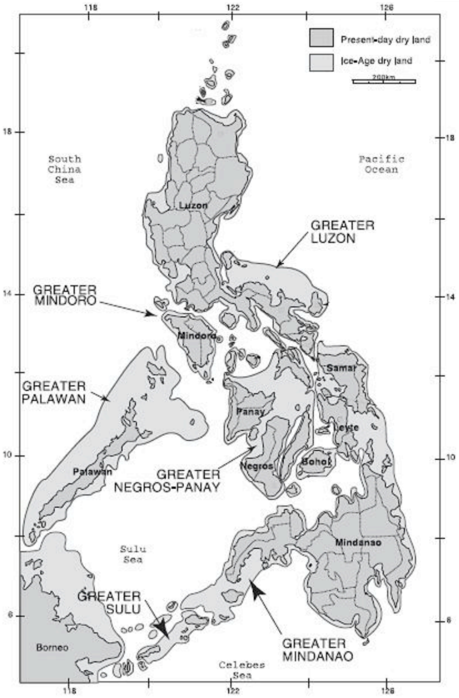
Conclusion

The co-occuring species addressed here, despite having similar habitat preferences and dispersal characteristics, exhibit dissimilar evolutionary histories. First, rates of sequence evolution are not equal in both species. With palm DNA more slowly evolving, less genetic variation is recorded in *D. mollis* than in *M. bicolor*. Phylogeographic relationships are thus more easily resolved in *M. bicolor*. A congruent colonization route cannot be determined, but *M. bicolor* presents support for dispersal in a south- and west-ward direction from the eastern Luzon populations, contrary to the prediction of a northward colonization route. Subsequent isolation of the majority of the populations, from reduced gene flow across water and land barriers, resulted in the recovery of some genetic structure.

The widespread distribution of the two endemic species, *D. mollis* and *M. bicolor*, demonstrates that water does not serve as a barrier to dispersal. However, the presence of phylogeographic structure in *M. bicolor* and haplotypes unique to a single island (also in *D. mollis*) can be argued to support the contention that water serves as a weak barrier to dispersal. A genetic break is evident between eastern and western Luzon populations in both species, which corresponds to a topographic feature in Luzon. There is no evidence that water boundaries of either present-day islands or Pleistocene islands strongly demarcate inter-population gene flow. Persistence of small genetically-depauperate populations in forest fragments, across the larger islands during the LGM, sufficiently explains the current genetic structure in *M. bicolor.*

Future research should expand the range of sampling sites to include replicates from each Pleistocene island and across all potential land barriers. Furthermore, the population genetics of several other species using more variable markers (like SNPs or microsatellites) is important to determine whether the origin and subsequent evolutionary history of a diverse flora follow a common pattern. However, the minimal forest cover left in the Philippine Archipelago and increasing habitat loss will continue to limit the breadth of sampling and recovery of a complete history for Philippine taxa. Nevertheless, every effort to document a piece of complex historical events can only help to assemble a true record of the past.

Effective forest conservation that addresses maintenance of biodiversity as well as potential for climate change mitigation from carbon sequestration (Putz & Redford, 2010) needs the information collected in studies such as this to identify sites with genetically distinct populations that must be prioritized for conservation. The data here, however, indicates many of the sampled sites, six of eight in *M. bicolor* and four of nine in *D. mollis*, qualify as areas that contain different evolutionary lineages. Analyzing the population genetics of additional species may confirm or refute this finding. For the two species in this study, which are widespread and therefore capable of long distance dispersal, limited genetic exchange resulting in fixation of some haplotypes, indicates a need for dispersal corridors to be maintained across island populations. In addition, finding phylogeographic structure in widespread species suggests that species with weaker dispersal abilities such as gravity-dispersal or wind-dispersal, will have greater genetic differentiation among populations. If this is the case, it presents a stronger incentive to preserve as many forest fragments as possible in order to include the greatest proportion of the existing genetic diversity. However, if resources for conservation were limited, I would recommend starting with the Palanan (S1 or S11) and Bislig (S6) forests because these are large forest fragments which also happen to be on the two most diverse islands, Luzon and Mindanao (Merrill 1926), thereby facilitating the preservation of many other species.



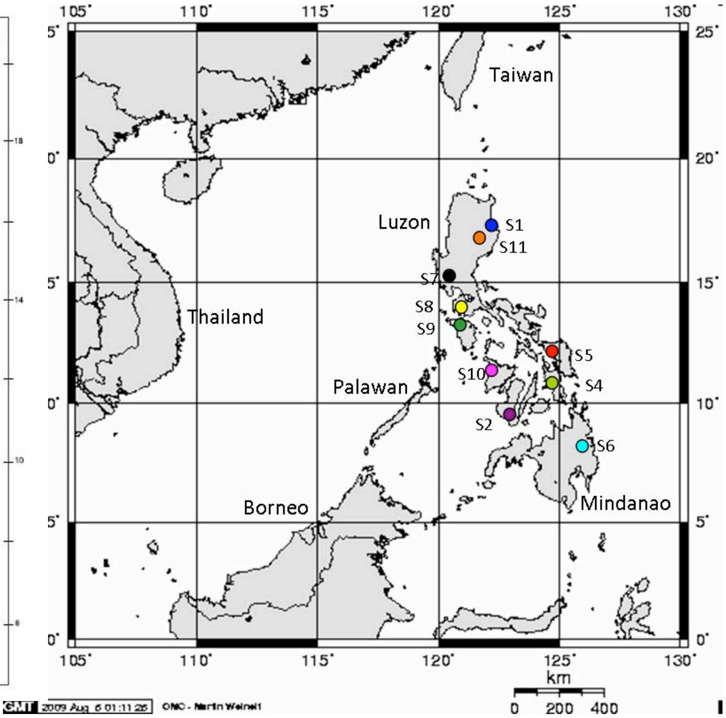


Figure 2.1a. Map of the Philippines.

Figure 2.1.b. Pleistocene island groups formed at the Last Glacial Maximum (Heaney *et al.,* 2005). Collection sites are denoted by dots with corresponding site codes.

Site	Locality	Present-day Island	Pleistocene Island	***M. bicolor***	***D. mollis***
				N	
S1	Eastern Sierra Madre, Palanan	Luzon	G. Luzon	10	16
S2	Valencia	Negros	G. Negros	0	9
S4	Lake Danao	Leyte	G. Mindanao	0	12
S5	Balantac Falls	Samar	G. Mindanao	11	11
S6	Bislig	Mindanao	G. Mindanao	10	12
S7	Bataan	Luzon	G. Luzon	4	9
S8	Mt. Makiling, Los Banos	Luzon	G. Luzon	11	10
S9	Mt. Malasimbo	Mindoro	Mindoro	9	0
S10	Sibaliw	Panay	G. Negros	6	10
S11	Western Sierra Madre, Palanan	Luzon	G. Luzon	10	8
total				71	97

Table 2.1. *Macaranga bicolor* and *Daemonorops mollis* samples. Sites with corresponding locality and island location are listed with the number of individuals collected per site (N) per species.

marker	region	length of region	no. of variable sites
5snts	nu	365	0
ITS	nu	852	16 (both)
M4	cp	740	0
ndhF-rpl32R	cp	800	0
psbA-trnH	cp	800	0
rpl16	cp	915	4 (*D. mollis* only)
rpl32F-trnL	cp	957	0
trnL	cp	870	0
trnQ-rps16	cp	1157	10 (*M. bicolor* only)

Table 2.2. Molecular markers tested for variability with corresponding length of the region amplified and no. of variable sites. Species where variable sites were found is indicated.

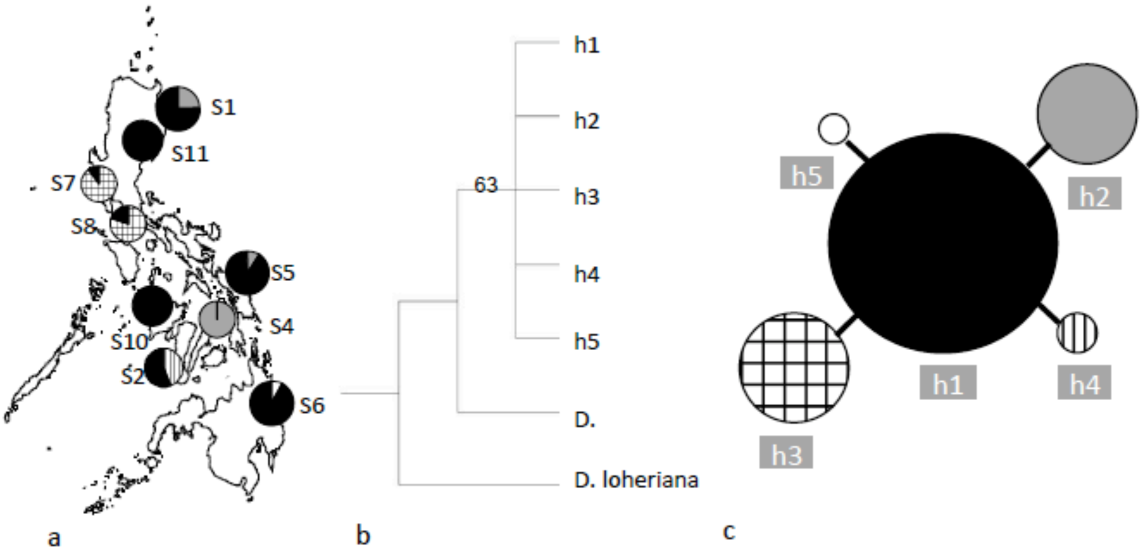


Figure 2.2.a-c. Phylogenetic and phylogeographic relationships of *D. mollis* haplotypes based on cpDNA variation of 906bp from rpl16. Haplotype distributions are mapped in Fig.2.2.a with corresponding site codes. The MP majority rule tree with bootstrap values recovered in the analyses is shown in Fig. 2.2.b, showing the relationship of the 5 *D. mollis* haplotypes, each of which are labeled as h1, h2, h3, h4, and h5. Fig. 2.2.c is the haplotype network constructed from a statistical parsimony analysis. Size of the circles represents haplotype frequency, colors correspond to the collecting sites as labeled in Fig.2.2.a, and each line between haplotypes represents one mutational change.

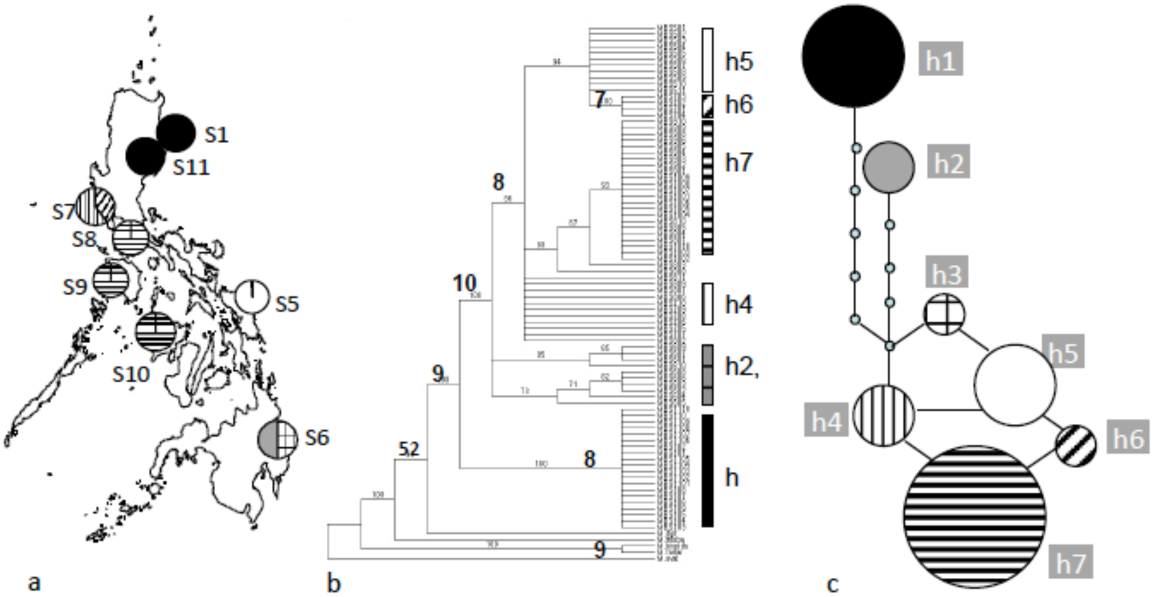


Figure 2.3.a-c. Phylogenetic and phylogeographic relationships of *M. bicolor* haplotypes based the ITS region. The distribution of collection sites is mapped in Fig.2.3.a. The MP majority rule tree with bootstrap is shown in Fig. 2.3.b, showing the relationship of the 7 *D. mollis* haplotypes, each of which is labeled as h1 to h7. Fig. 2.3.c is the haplotype network showing the distribution of each unique and shared haplotype. Small empty circles indicate hypothetical haplotypes not found in the dataset. Size of the circles indicates haplotype frequency, hatch marks correspond to the collecting sites as labeled in Fig.2.3.a, and each line between haplotypes represents one mutational change.

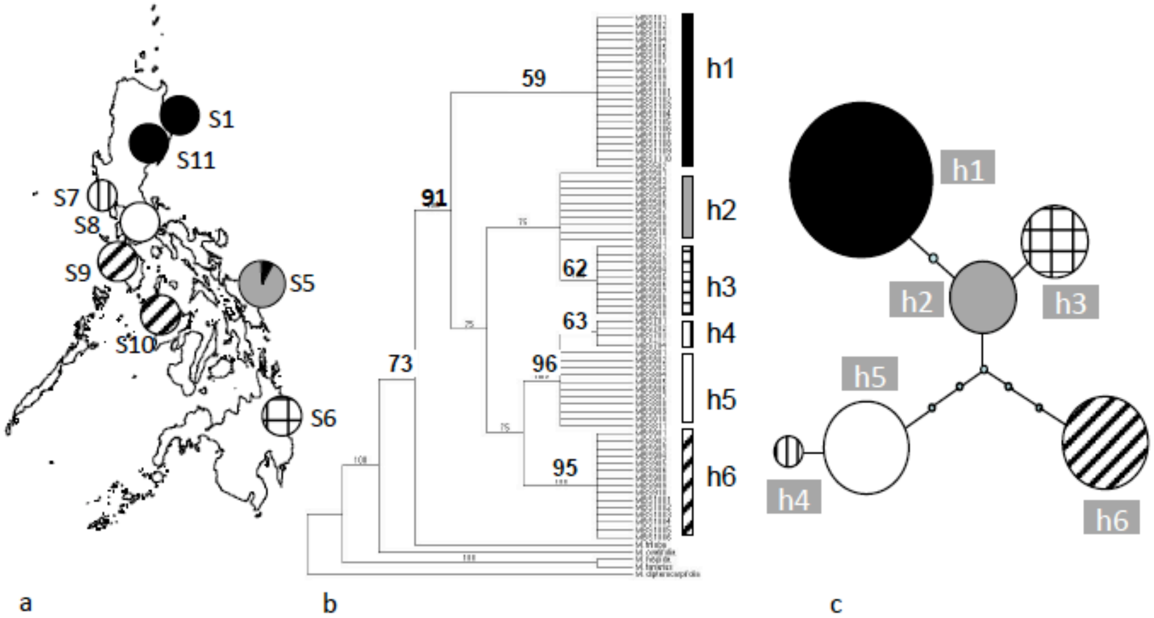


Figure 2.4.a-c. Phylogenetic and phylogeographic relationships of *M. bicolor* haplotypes based on the trnQ region. Collection sites are mapped in Fig. 2.4.a. The MP majority rule tree with bootstrap values is shown in Fig. 2.4.b, and Fig. 2.4.c shows the haplotype network.

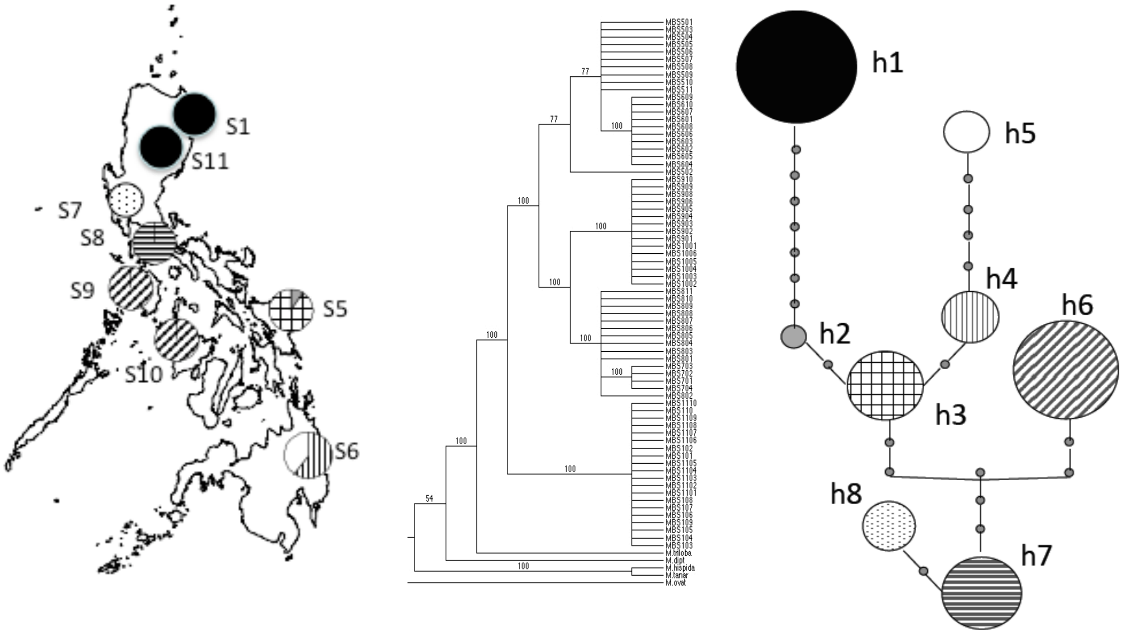


Figure 2.5.a-c. Phylogenetic and phylogeographic relationships of *M. bicolor* haplotypes based on the combined ITS and trnQ regions. Collection sites are mapped in Fig.2.5.a. The MP majority rule tree of the combined ITS and trnQ dataset (PHT p=1.0), with bootstrap values recovered in the analyses is shown in Fig.2.5.b, showing the relationship of the 8 *D. mollis* haplotypes. Fig.2.5.c shows the haplotype network.

Site	h (u)	S1	S2	S4	S5	S6	S7	S8	S10	S11
S1	2	0								
S2	2 (1)	0.267*	0							
S4	1	0.703*	0.903*	0						
S5	2	0.004	0.273*	0.904*	0					
S6	2 (1)	0.136	0.285*	0.923*	0.000	0				
S7	2	0.799*	0.886*	1.000*	0.908*	0.912*	0			
S8	2	0.637*	0.689*	0.910*	0.702*	0.713*	0.097	0		
S10	1	0.144	0.394*	1.000*	-0.009	-0.016	1.000*	0.778*	0	
S11	1	0.119	0.354	1.000*	-0.032	-0.037	1.000*	0.755*	0.0	0

Table 2.3. Pairwise F_{ST} values of *D. mollis* from all sites. Haplotype number, h, is indicated with the number of haplotypes unique to one site, (unique). All significant F_{ST} values ($p<0.05$) are marked with an asterisk (*).

Site	h (u)	S1	S5	S6	S7	S8	S9	S10	S11
S1	1	0							
S5	2 (2)	0.977*	0						
S6	2 (2)	0.924*	0.776*	0					
S7	1 (1)	1.000*	0.955*	0.893*	0				
S8	1 (1)	1.000*	0.963*	0.914*	1.000*	0			
S9	1	1.000*	0.967*	0.914*	1.000*	1.000*	0		
S10	1	1.000*	0.961*	0.897*	1.000*	1.000*	0.000	0	
S11	1	0.000	0.981*	0.934*	1.000*	1.000*	1.000*	1.000*	0

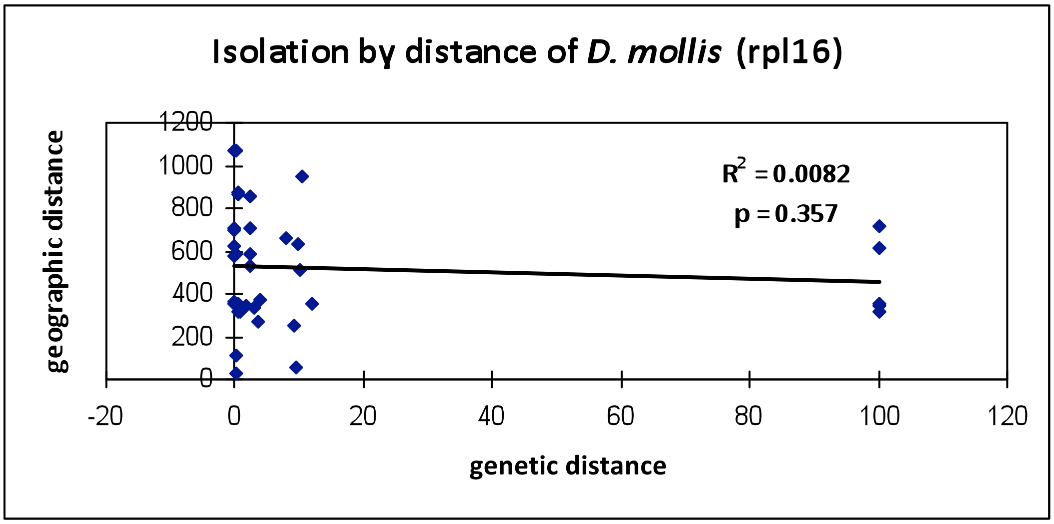
Table 2.4. Pairwise F_{ST} values of *M. bicolor* from all sites. Haplotype number, h, is indicated with the number of haplotypes unique to one site, (unique). All significant F_{ST} values ($p<0.05$) are marked with an asterisk (*).

Groups variation	Source of Variation	df	Φ-statistic	P value	Percent
One	Among populations	8			75.6
	Within populations	88	0.720	<0.001	24.4
Present-day Islands	Among groups	5	-0.020	<0.70	-2.08
	Within groups	3	0.725	<0.001	73.97
	Within populations	88	0.719	<0.001	28.11
Pleistocene Islands	Among groups	3	-0.117	<0.65	-11.75
	Within groups	5	0.742	<0.001	82.88
	Within populations	88	0.711	<0.001	28.87

Table 2.5. AMOVA of the chloroplast DNA sequence, rpl16, in *D. mollis*.

Groups variation	Source of Variation	df	Φ-statistic	P value	Percent
One	Among populations	7			96.8
	Within populations	63	0.968	<0.001	3.2
Present-day Islands	Among groups	4	-0.089	<0.59	-8.91
	Within groups	3	0.970	<0.001	105.66
	Within populations	63	0.967	<0.001	3.25
Pleistocene Islands	Among groups	3	0.160	<0.18	15.98
	Within groups	4	0.963	<0.001	80.96
	Within populations	63	0.969	<0.001	3.07

Table 2.6. AMOVA of the combined ITS and trnQ sequences in *M. bicolor*.



a

Figure 2.6. Isolation by distance in *D. mollis* determined between geographic distance and genetic distance using Slatkin's linearized F_{ST}. Coefficient of determination, R^2, is presented with corresponding p-value.

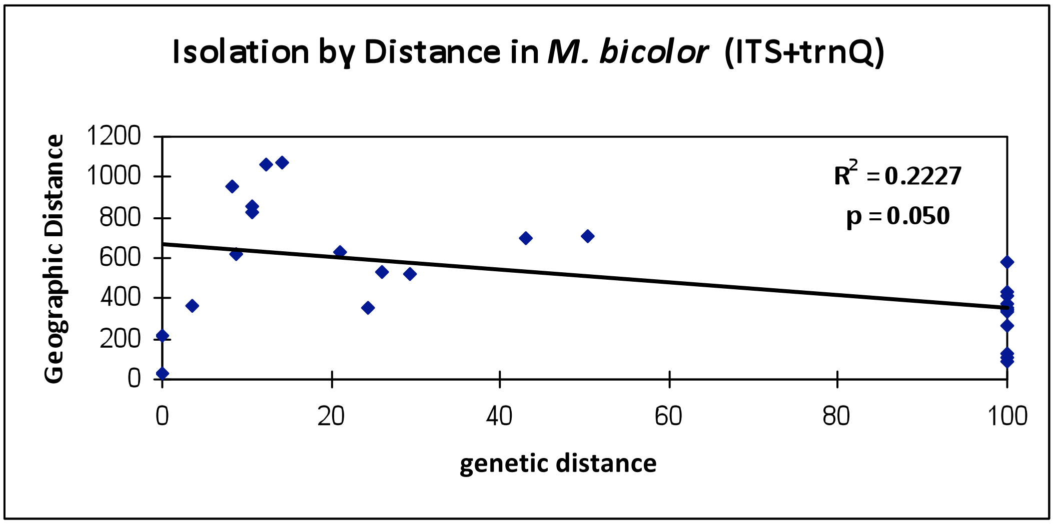


Figure 2.7. Isolation by distance in *M. bicolor* determined between geographic distance and genetic distance using Slatkin's linearized F_{ST}. Coefficient of determination, R^2, is presented with corresponding p-value.

No. groups (K)	Group Composition	F_{SC}	F_{ST}	F_{CT}
Two	Group I: S7, S8 Group II: S1, S2, S4, S5, S6, S10, S11	0.602	0.856	0.638
Three	Group I: S7, S8 Group II: S4 Group III: S1, S2, S5, S6, S10, S11	0.183	0.846	0.811
Four	Group I: S7, S8 Group II: S4 Group III: S2 Group IV: S1, S5, S6, S10, S11	0.093	0.820	0.802
Five	Group I: S7 Group II: S8 Group III: S4 Group IV: S2 Group V: S1, S5, S6, S10, S11	0.089	0.816	0.798
Six	Group I: S7, S8 Group II: S4 Group III: S2 Group IV: S1 Group V: S5, S6, S10 Group VI: S11	0.017	0.776	0.772
Seven	Group I: S7 Group II: S8 Group III: S4 Group IV: S2 Group V: S1 Group VI: S5, S6, S10 Group VII: S11	-0.032	0.772	0.779
Eight	Group I: S7 Group II: S8 Group III: S4 Group IV: S2 Group V: S1 Group VI: S5, S6 Group VII: S11 Group VIII: S10	-0.0496	0.7608	0.772^{NS}

Table 2.7. Group composition and F_{CT} values detected by SAMOVA in 9 populations of *D. mollis* from 6 Philippine Islands based on the chloroplast region, rpl16. F_{SC}, proportion of genetic variation between populations within groups; F_{ST}, proportion of genetic variation across all populations; F_{CT}, proportion of genetic variation among groups. All values are significant ($P<0.05$) unless indicated as not significant (NS).

No. groups (K)	**Group Composition**	**F_{SC}**	**F_{ST}**	**F_{CT}**
Two	Group I: S1, S11 Group II: S5, S6, S7, S8, S9, S10	0.946	0.978	0.597
Three	Group I: S5, S6, S7, S8 Group II: S1, S11 Group III: S9, S10	0.921	0.974	0.673
Four	Group I: S5, S6 Group II: S7, S8 Group III: S1, S11 Group IV: S9, S10	0.819	0.972	0.844
Five	Group I: S5 Group II: S9, S10 Group III: SS6 Group IV: S1, S11 Group V: S7, S8	0.563	0.971	0.933
Six	Group I: S7 Group II: S8 Group III: S6 Group IV: S9, S10 Group V: S1, S11 Group VI: S5	-0.132	0.970	0.974
Seven	Group I: S8 Group II: S5 Group III: S6 Group IV: S9, S10 Group V: S7 Group VI: S11 Group VII: S1	-0.161	0.969	0.973^{NS}

Table 2.8. Group composition and F_{CT} values detected by SAMOVA in 8 populations of *M. bicolor* from 5 Philippine Islands based on chloroplast and nuclear DNA regions. F_{SC}, proportion of genetic variation between populations within groups; F_{ST}, proportion of genetic variation across all populations; F_{CT}, proportion of genetic variation among groups. All values are significant ($P<0.05$) unless indicated as not significant (NS).

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Chapter 3

Hydrologic and topographic associations of a palm community in a lowland dipterocarp rainforest in the Philippines

Abstract

Paleotropical palm species, both climbing and free-standing growth forms, are dominant components of the lowland mixed dipterocarp forest in Palanan, ranking high in importance based on species richness, abundance, and basal area. The distributions of five palm species were recorded and determined to be aggregated at all spatial scales tested ($25m^2$ to $2500m^2$), using Morisita's Index. In *Pinanga maculata* and *Daemonorops mollis*, aggregation is being influenced by associations with patchily distributed microhabitats. Elevation and stream location, but not slope, were correlated with palm abundance and distribution. Torus translation tests showed contrasting positive correlations with elevation and stream microhabitats between *D. mollis* (a climbing species) and three of the four palm tree species, suggesting a potential for niche differentiation among different growth forms. Three palm tree species were significantly positively associated with low elevations unlike *D. mollis*, but *Pinanga insignis* is randomly distributed in the plot with respect to elevation. Stream microhabitats, however, are rich in *P. maculata* trees but rarely are *D. mollis* and *P. insignis* in this microhabitat. Furthermore, the same species-habitat relationships were found in more than one life stage but were not consistent across all three age classes.

Introduction

The Arecaceae includes 2,300 accepted species in 190 genera (Govaerts &

Dransfield, 2005). Palms are largely restricted to the tropics, with the highest concentration of species in the Americas and Asia. Large arborescent palms are prominent in the canopy of Neotropical forests, which easily distinguishes these forests from their counterparts in the Paleotropics, where palms are represented in the canopy layer only by the cirruses (hooked whip at the tips of leaves) of climbers. In the Americas, Central America (southern Mexico to NW Ecuador) and Amazonia have the highest regional species richness with approximately 150 and 189 species, respectively (Henderson *et al.*, 1995; Bjorholm *et al.*, 2005, 2006).

Research on the species diversity and abundance of palms across the Neotropics has provided an insightful approximation of the structure and dynamics of tropical forests because the group is an important and conspicuous component of those forests. Within the Neotropics, palm diversity is more strongly correlated with geographical distance than with environmental variation, suggesting that dispersal limitation promotes beta diversity, at least between local sites in Peru and Ecuador (Vormisto *et al.*, 2004; Normand *et al.*, 2006). However, habitat specialization has also been recognized as important to high beta diversity among palms from *terra firme* forests to floodplains in the Peruvian Amazon (Kahn & Decastro, 1985). Moreover, it has been shown that humidity, specifically total rainfall and the number of wet days, is positively correlated with species richness of palms in the Americas (Bjorholm *et al.*, 2006).

At a smaller spatial scale, alpha diversity and the ecology of Neotropical palms are influenced by the heterogeneity among microhabitats in environmental factors such as light, topography, soil nutrients, and soil moisture (Svenning, 2001). Microhabitat refers to environmental conditions that vary at scales < 1000m, e.g., treefall gaps or local topographic variation (Svenning, 1999). Overall palm community composition and the abundance of eight focal species varied among *terra firme* sites in the Peruvian Amazon wherein differences in abundance were related to the amount of exchangeable cations in the soil and topographic position (Vormisto, 2002). The same environmental factors accounted for the relationship between the densities of five abundant palm species at La Selva Biological Station, Costa Rica (Clark *et al.*, 1995). In Amazonian Ecuador, 14 of the 23 palm taxa studied in a 50-ha plot had distributions correlated with topographic position, and significantly, but less so, with drainage and canopy height (Svenning, 1999). Further, light availability affects palm distribution and abundance as shown in the increasing growth and fecundity of the understorey palm *Geonoma macrostachys* with greater crown illumination (Svenning, 2002).

In contrast to Neotropical palms, less is known about microhabitat specialization in palms from the Paleotropics. Recent research examined the species diversity and abundance of climbing palms across different habitat types in Borneo, Java, and Indonesia finding variable species diversity and abundance among sites, including sites of the same habitat type (Siebert, 2005; Watanabe & Suzuki, 2008). Greater species richness was recorded at higher elevations (1180-1280m) within one study area (830-1330m) in Central Sulawesi, Indonesia but abundance was similar at all elevations (Siebert, 2005). On the other hand, more species were found in lowland mixed dipterocarp forests (<240m) in Borneo than in lower montane forest (1100m) in Java, but palm density was higher in the montane forest (Watanabe & Suzuki, 2008). These studies were limited to palm species of a single growth form, climbers, which only comprise about half of the species in the Paleotropical palm flora. Fruitful investigations on the relationship of microhabitat heterogeneity and palm species richness and abundance should determine the association of all palm species of all growth forms with specific microhabitat features such as elevation, slope, convexity, soil moisture, soil nutrients, and light availability.

The Philippines harbors 135 species of palms, equally represented by tree species and climbing species (Fernando, 1990). *Desmoncus* is the only climbing palm genus in the Neotropics and is species-poor (12 spp.), whereas the Paleotropical climbing genera *Calamus* and *Daemonorops* include 350 and 115 species, respectively (Govaerts & Dransfield, 2005). Climbing palms, commonly known as rattans, are represented worldwide by 650 species belonging to the subfamily Calamoideae. These species have a restricted distribution limited to the Old World from Africa to Southeast Asia, with the center of diversity in Malesia. Rattans are a valuable resource for the region earning as much as US$1.0 billion annually (INBAR, 2007). This is, however, also the cause for the decline in their abundance in the wild. Exploitation and deforestation have resulted in the increasing loss of this resource (Dransfield *et al.*, 2002). Aside from rattans, other palms are important as non-timber forest products, such as species in the genus *Caryota*, a source of the starch *sago* (Whitmore, 1998). It is important to understand the microhabitat preferences and niche differences among palm species, both free-standing and climbing, because these data may be crucial to the conservation and management of palm resources.

Here, I report on the palm community of a 16-ha plot in a lowland rainforest of the Philippines and evaluate the relationship between topography (elevation, slope, and proximity to water) and palm species distribution and abundance. Optimum conditions for growth can vary with age leading Grubb (1977) to posit that all stages in the life history of species are important. Separate analyses on three different age classes (young, middle-age, old) for each palm species are conducted to determine if microhabitat preferences change or are maintained throughout the species' lifetime. A plant's requirements for growth need to be met beginning at the earliest life stages, likely resulting in strong species-habitat associations in young stems. If habitat preferences are consistent across life stages, the same habitat associations are expected in the three age classes, whereas no pattern is expected when habitat preferences are modified with age. Alternatively, the effects of environmental filtering, or the establishment and survival of individuals best suited to a certain set of environmental conditions, could be reflected by the stems reaching the later life stages and thus exhibit the strongest associations in the old age class comprised of large-sized stems (Keddy, 1992; Tuomisto *et al.*, 2003).

Methods

Study Site

Fieldwork was conducted in the 16-hectare Palanan Forest Dynamics Plot (PFDP) (Figure 3.1). The PFDP is a permanent plot monitoring tree demography in a primary lowland mixed dipterocarp forest within the Northern Sierra Madre Natural Park, Palanan, Isabela, Philippines. PFDP is located at 17° 02' 36 N, 122° 22' 58 E, with an elevational range from 76m to 118m a.s.l. Topographic data was recorded during the establishment of the plot in 1994. Two streams, one on each side of a ridge, bisect the plot in a southwesterly direction. The nearest meteorological station in Casiguran, 90km SSW of Palanan, records annual rainfall in this region as 3,200mm. However, Palanan probably receives more annual rainfall, possibly exceeding 5000mm (Co *et al.*, 2006). There is very little seasonality in Palanan: rainfall is more or less evenly distributed throughout the year. Tropical cyclones coincide with Southwest monsoons during the months of June to November. About 10-15 typhoons pass through the Philippines annually and super typhoons with gale force exceeding 200kph occur every five years. More details of the plot are presented in Co *et al.* (2006).

Data collection and Analyses

A census of all trees in the PFDP was conducted in 2004, which included free-standing palms (Co *et al.*, 2006). All palms with a trunk ≥ 1cm above 1.3m were tagged, measured for diameter at breast height (DBH), and identified. Assuming that trees of similar size are of similar age, three age classes were created based on the 33rd and 66th percentile of the diameters measured (including each observed diameter only once), representing three age classes of palm trees. The exact location of each tree in the plot was also recorded using x and y coordinates (Figure 3.2). A voucher specimen for each species was collected and stored at the University of the Philippines Herbarium (PUH). In May 2005, a survey of climbing palms in the plot was made, followed by a complete census of the most abundant species, *Daemonorops mollis*. At any given time, there are a few adult stems of the *D. mollis* population maturing edible fruits, but the species also reproduces vegetatively, forming small (<1m diameter) distinct clusters of genetically identical (genets) stems. All individuals in each cluster of *D. mollis* were counted. Each cluster was tagged, mapped, and measured for diameter at the base. Each individual was then classified as a juvenile, a sub-adult (≥ 3 leaves or appearance of cane), or an adult (≥ 5m long cane).

Using Morisita's index (Krebs, 1989) as a measure of dispersion, the spatial distribution of each species was analyzed for patterns of aggregation or random distribution. Morisita's Index of Dispersion (I_d) values are categorized into the following: <1 (uniform distribution), =1 (random), and >1 (aggregated). Whereas Morista's Index of Dispersion uses counts within a specified area, Ripley's K is a tool which also measures aggregation but uses the location coordinates of each stem (Ripley, 1981). Ripley's K function can describe spatial patterns at multiple distance scales, and this was used to calculate aggregation at five spatial scales (5, 15, 25, 35, and 45m) for three age classes in four palm species (not including *O. decipiens*). To estimate palm biodiversity for the PFDP, Fisher's alpha (Fisher *et al.*, 1943) was calculated using EstimateS (Colwell, 2009).

Within the plot, each of the 400 20 x 20m quadrats was assigned microhabitat types according to three topographical features: elevation, slope, and stream location. The quartiles (from lowest to highest values) of the elevation data were used to assign equal numbers of quadrats for each of four elevation microhabitat types: Low= first quartile (lowest elevation), Mid-low = second quartile (mid-low elevation), Mid-High = third quartile (mid-high elevation), and High = fourth quartile (highest elevation). The same procedure was carried out based on the slope of each quadrat. Stream vs. non-stream microhabitat types were scored based on the presence or absence of a stream of any size in each quadrat.

Three age classes based on stem diameter were assigned for each palm tree species, with the exception of *O. decipiens* due to small sample size, which was only analyzed as a species with all stems combined. The three size classes based on tertiles of the observed range of DBH, for *C. cumingii, P. insignis*, and *P. maculata*, respectively, were as follows: young (≤13.7cm, ≤9.8cm, ≤3.6cm); middle-age (>13.7 & ≤21.5cm, >9.8

& ≤13.8cm, >3.6 & ≤ 5.4cm); old (>21.5cm, >13.8cm, >5.4cm). For *D. mollis*, life stages were as described above.

Using the quartiles from the elevation and slope data, the four elevation microhabitats were defined by the following break points: (Low) <90.50m, (Mid-low) ≥ 90.50 and < 97.75m, (Mid-high) ≥ 97.75 and < 105.01m, and (High) ≥ 105.01m. The slope microhabitats were assigned into the following bins according to the degree of inclination: (Low) <11.96º, (Mid-low) ≥ 11.96º and < 16.94º, (Mid-high) ≥ 16.94º and < 23.57º, and (High) ≥ 23.57º. Three maps show the distribution of microhabitat types according to elevation, slope, and stream locations (Figures 3.4, 3.5, and 3.6).

Torus translation tests, following Harms *et al.* (2001), were conducted to determine the strength and sign of the relationships between palm distributions and habitat characteristics, taking into account spatial autocorrelation. The test compares the observed relative density of a species on the true habitat map with expected relative densities from simulated habitat maps. By shifting the true habitat map in 20-m increments along the x and y coordinates, I created 400 simulated maps. Habitat association is significantly positive or negative if the observed relative density is greater or lesser than 97.5% of expected relative densities (390/400 simulations). Analyses of these data sets were performed using R (R Development Core Team, 2008), and conducted on each of the three life stages for each species, as well as a combined dataset of all individuals per species, hereafter referred to as per-species analysis.

A univariate general linear model was used to conduct ANOVA tests from the results of the torus translation tests. The number of positive associations per microhabitat for each species was used to determine the effects of age class, microhabitat type, and species identity on the species-habitat associations.

Results

Palm community

Fourteen species of palms were present (Table 3.1), and Fisher's α was 1.6 for the PFDP plot. Four palm species were free-standing trees and ten species were climbing palms in the genera *Calamus* and *Daemonorops*. Three of the six subfamilies of palms are represented in the plot: Arecoideae, Calamoideae, and Coryphoideae. *Daemonorops mollis* was the only climbing palm completely censused because this species was extremely common (6,496 clusters) whereas all other species were relatively very rare (Table 3.1). The distribution of the abundant *D. mollis* should have the strongest support for any pattern of habitat association. Of the five palm species censused, *D. mollis* was the most abundant, followed by *Pinanga maculata* (1,371) and *P. insignis* (1,075). *Orania decipiens* was the rarest, represented by only 31 individuals in 19 quadrats, after *Caryota cumingii* with 431 trees.

Spatial Distribution

The distribution of each of the five species was mapped on the elevational contour map (Figure 3.2). The mapped species exhibit heterogeneous distribution patterns, some showing obvious patchiness across the landscape. Tests of dispersion, conducted individually at spatial scales of 25, 100, 400, and 2500 m^2, indicate aggregation of individuals of each of the five species at all spatial scales (Figure 3.3). Aggregation appears to be greatest at the smallest spatial scale tested ($25m^2$), with decreasing aggregation of individuals at larger spatial scales. Morisita's index indicates that *O. decipiens* has the most clustered pattern with $I_d > 7.4$, followed by *C. cumingii* ($I_d >$

1.45), *P. maculata* ($I_d > 1.4$), *D. mollis* ($I_d > 1.22$), and *P. insignis* ($I_d > 1.19$), at the 2500m^2 spatial scale, where aggregation is at its minimum. Ripley's K reveals a similar decreasing intensity in aggregation with increasing scale (after 5m) for all age classes in *C. cumingii* and *P. insignis*, and the opposite trend for *P. maculata* and *D. mollis* (Table 3.2). In all four palm species, old stems are more clustered than young or middle-age stems, at all spatial scales.

Habitat Preferences

Based on both per-species and age-class analyses, three species of free-standing palms, *C. cumingii, O. decipiens,* and *P. maculata,* were significantly positively associated with areas below the median elevation for the plot (<98m) in contrast to the climbing palm, *D. mollis* (Table 3.3), which was found primarily in the highest elevations within the plot. *P. insignis* is most often positively associated with low elevations (347/400 simulations were positive), although the result is not statistically significant.

Significant microhabitat associations also varied within a species among the different age classes (Table 3.3). In *C. cumingii*, only the young trees show a significant preference for the lowest elevations while the old trees exhibit a negative association with the highest elevations, a pattern reflected in the per-species analysis. Both *P. maculata* and *D. mollis* show significant associations in all three age classes, similar to their per-species associations. In *P. maculata*, significant positive associations are with below median elevations with a corresponding negative association with elevations above the median. The opposite is observed in *D. mollis,* where stems are only significantly positively associated with the highest elevations. No relationship is seen in *P. insignis*, in any age class, nor collectively as a species. No comparisons across age classes can be made based on the limited *O. decipiens* dataset, although the per-species data are positively associated with the lowest elevations in the plot.

None of the species exhibited preferences based on the slope of the microhabitat, even in multiple analyses creating bins using different break points to assign slope microhabitat types (results not included here). The only correlation observed was a positive association (p<0.06) of young *C. cumingii* stems with the steepest slopes in the plot.

In stream microhabitats, *P. insignis, P. maculata,* and *D. mollis* showed significant microhabitat preferences (Table 3.3). Results from both per-species and age class analyses showed significantly fewer individuals of *D. mollis* in stream microhabitats, whereas *P. maculata* was positively associated with stream microhabitats. *O. decipiens* also was positively associated with stream habitats, but this was not statistically significant (p<0.075). Only old *P. insignis* trees showed a significant negative association with stream microhabitats, whereas *C. cumingii* showed no demonstrable preference for either stream microhabitat type.

The results of the ANOVA showed no significant effect of age class (p<0.986), elevation (p<0.309), species (p<0.946), or age class x species interaction (p<0.988) on the overall species-elevation associations. When only tree palms are included in the ANOVA, (excluding *D. mollis*), the test reveals that only elevation (p<0.0001), not age class (p<0.925) nor species identity (p<0.936), is correlated with the elevation-microhabitat preferences of palm tree species. A torus translation test performed on a dataset of the three palm tree species also shows a collective positive association with below median elevations (p<0.005) and a negative association with the highest elevations

($p<0.005$). Similarly, with species-stream associations, none of the above-mentioned variables were significant except when only palm trees are included in the ANOVA, stream location is nearly significant ($p<0.058$).

Discussion

The Arecaceae includes many economically valuable species and is an important component of forests in both the Neo- and Paleotropics. A survey of the assemblage of palm species in the PFDP and pattern analysis of species distributions, will aid in understanding the role of palms in forests. For conservation and trade goals, habitat preferences can be a guiding principle when allocating habitats for the preservation of threatened species and in the design of palm plantations that are economically viable. This study describes and reveals the patterns observed, but does not determine the mechanisms causing such patterns to occur.

Palm community

The five genera represented in the PFDP, *Calamus*, *Caryota*, *Daemonorops, Orania*, and *Pinanga*, are restricted to the Paleotropics. Generic endemism is common in the Arecaceae, as noted by Corner (1966), despite the strong pantropical distribution of the family. Seven of the eleven (64%) identified species in the plot are endemic to the Philippines, consistent with the 76.5% endemicity ratio estimate for the whole Philippine vascular flora (Myers *et al.*, 2000).

Palm species diversity is higher in the 16-ha PFDP than in other Neotropical sites, where 2, 6, and 10 species of tree and climbing palms were found (50-ha Barro Colorado Island, 25-ha La Planada, and 16-ha Luquillo plots, respectively), except in comparison with the species-rich 50-ha plot in Yasuní where 24 species occur (Co *et al.*, 2004). High palm species richness in the Yasuní region was previously recorded, with a mean Fisher's α of 5.26 for 11 transects (Vormisto *et al.*, 2004), notably higher than the Fisher's α of 1.6 for the Palanan plot. The Palanan FDP, which is at a similar latitude as the Luquillo FDP, has more palm tree and climber species but is comparable in richness to the Yasuni FDP when taking into account the disparity in the size of the plots.

Palm species diversity decreases with increasing latitude (Appendix 3.1; Bjorholm *et al.* 2006), a pattern demonstrated among the Neotropical plots, with the exception of the Luquillo plot. In the absence of comparable datasets from Paleotropical plots, data from the World Checklist of Arecaceae Database was examined (Appendix 3.1; Govaerts *et al.*, 2006). A clear latitudinal gradient in palm species richness is also present in the Paleotropics. However, a series of palm surveys should be conducted within areas of limited latitudinal range, rather than an entire country, to firmly establish that latitude is correlated with species richness. For example, the surveys can be performed in similar-sized plots among islands in the Philippines, which are located from 5°N to 20°N latitude. At this time, a comparison of palm species diversity within the Philippines cannot be made due to differences in sampling strategies, but floristic lists show that in Mt. Makiling, Laguna (14°N), there are at least 14 palm species (Fernando *et al.*, 2004) and in Mt. Pangasugan, Leyte (10.5°N) there are 67 species (Langenberger *et al.*, 2006), suggesting consistency with a latitudinal gradient.

Tree and climbing species of palms in the Palanan plot rank first in abundance, second in basal area, and seventh in species richness among the 67 families represented. Excluding climbing species, the Arecaceae rank ninth in abundance, fifth in basal area, and 23rd in species richness. In other Asian FDP plots, palm trees have not been censused, but only a few palm tree species are present in the Huai Kha Kheng plot, the Khao Chong plot (Thailand), the Nanjenshan plot (Taiwan), the Bukit Timah plot (Singapore), and the Malaysian Lambir and Pasoh plots (LaFrankie, J. and Sun, I, *personal communication*). Climbing palms may be more abundant in species and number in these plots, but climbing species are not included in plot censuses. It is clear from the Palanan plot that palms are dominant components of the forest, and because palm diversity increases with decreasing latitude, it is expected that palms are even more important in the Southeast Asian region, south of the Philippines, such as in Singapore and Malaysia. It is thus essential to include palms, especially climbers, in future censuses.

Among the palms found in the PFDP, eight of the 11 species (three are yet to be identified to the species level) are widely distributed throughout the Philippines (Govaerts & Dransfield, 2005; Merrill, 1926) and one palm in particular, *D. mollis,* is the most dominant species surpassing the abundance and basal area of all other palm species combined. A complete census of the rattans in the plot is needed to confirm the absolute dominant status of *D. mollis*. Although. *D. mollis* is commonly found in many islands throughout the archipelago, it appears to be most abundant in the PFDP (*pers. obs.*). The dominance of *D. mollis* may have been the natural condition in all lowland dipterocarp forests prior to deforestation, as it is in the pristine forest plot at Palanan. This is similar to the oligarchic dominance of six palm species in the western Amazonian sites of Yasuní and Iquitos-Pebas (Vormisto *et al.,* 2004). The relatively lower numbers of individuals of *D. mollis* in other sites could be due to habitat loss and excessive cane collection. Alternatively, the current abundance pattern may represent the dominance of one species in the Palanan site, while another complementary species dominates in a different locality. Comparative censuses conducted in multiple islands with well-preserved forest cover are necessary to address the question of whether one or a group of palm species is equally dominant across lowland dipterocarp habitats.

Abundance and Spatial Distribution

The five palm species analyzed show varying levels of abundance, from the 31 individuals of *O. decipiens* to the 6,496 clusters of *D. mollis*. The two congeneric *Pinanga* species have almost equal numbers of stems yet exhibit different growth strategies. *P. insignis* develops large diameter stems resulting in its dominance of basal area (13.38 m$^{2)}$, whereas all stems of *P. maculata* have a collective basal area of 2.36 m^2. *Caryota cumingii* individuals show a total basal area of 11.14 m^2, despite representation by a third of the stem abundance of *P. maculata,* a testament to its big, solitary trunk. Taking into account both abundance and basal area, *D. mollis* has the highest importance value (I.V. = 1.5) of the five species, with *P. insignis* (IV. = 0.2) following as a distant second. Among the tree species, there is no one species clearly dominant over the others, although *O. decipiens* includes few individuals and total basal area. On the PFDP, *O. decipiens* is a rare species with few individuals, but could possibly be recently dispersed into the area. Censuses in other protected areas as well as in the PFDP in the future may distinguish between these alternative scenarios. If *O. decipiens* is found to be more abundant and occupying a greater proportion of the PFDP in future censuses than at present, we should expect larger populations in other areas as well.

Aggregation of conspecific trees is well documented in tropical forest species (Condit *et al*., 2000; Harms *et al*., 2001), and is exhibited by all five species of palms studied. Stem distribution of each species is aggregated at all spatial scales analyzed (25

m^2 to 2500 m^2), but the aggregation decreases in intensity with increasing scale, possibly attributable to seed dispersal limitation or patchiness of microhabitat distribution (Condit *et al.*, 2000; Harms *et al.*, 2001; Valencia *et al.*, 2004). Small rodents disperse *Pinanga* fruits (Zona, 2007) and in the Neotropics, small rodent species disperse palm fruits only short distances from the parent tree: 5 - 75 cm in *Attalea,* and 3.6 - 5.2 meters in *Astrocaryum* (de Almeida & Galetti, 2007; Donatti *et al.*, 2009). If dispersal limitation was the sole cause of the distribution pattern, a decrease in aggregation intensity should not be observed with increasing scale beyond five meters ($25m^2$, Figure 3.3). As decreasing aggregation beyond $25m^2$ is found in all five species, the data suggests that seed dispersal limitation does not explain palm distributions. Furthemore, aggregation in the old age class is greater relative to the young and middle-age groups in four palm species, reflecting the collection of adults in the most suitable habitats that are patchily distributed. The disparity in the results of the Morisita's Index and Ripley's K is likely driven by the strong associations of both *P. maculata* and *D mollis* with specific microhabitats that are irregularly distributed in the plot (see below).

Habitat Preferences

A typical lowland dipterocarp forest was differentiated into several microhabitats based on variability in elevation, slope, and location of streams. Microhabitat heterogeneity is correlated with the distribution and abundance in four of the five palm species within the plot. Elevation is the best predictor of abundance, while stream presence affected only *P. maculata* and *D. mollis*. Slope, however, was not found to be associated with any of the species at any age class, contrary to findings of equal effects on tree species distributions by slope, aspect, elevation, and convexity, where 70, 63, 67, and 73 tree species, respectively, were related to each topographic variable in a 20-ha plot in subtropical China (Wang*, et al.,* 2009).

The single species of climbing palm censused, *D. mollis*, was positively associated with areas of higher elevation in the plot, above that of the median elevation of 98m. *D. mollis* is very common in primary forests at low to medium elevation, but this is the first recorded habitat preference based on elevation of *D. mollis*, or of any Philippine rattan. One potential explanation for association with the higher end of the elevation range is a preference by rattans for greater solar radiation (Gale, 2004). In Sarawak and Peninsular Malaysia, rattans are more abundant on ridges than in valleys (Putz & Chai, 1987; Siebert, 1993). To confirm rattan preference for ridges and higher light intensities, photosynthetically active radiation (PAR) could be measured at the PFDP and analyzed for *D. mollis* preference with high elevation and high PAR microhabitats.

In contrast to *D. mollis*, the distributions of palm trees (excluding *P. insignis*) were significantly correlated with a lower elevational range. Preference for low elevations, despite separation of these microhabitats by a ridge (Figure 3.4), indicates that distribution and abundance of the three palm species is more influenced by topography than dispersal. The preference for contrasting elevation microhabitats between a climbing species and three palm tree species suggest a potential for niche differentiation between growth forms. A characteristic shared by the palm tree species is their low stature (*P. maculata*, 5m to *C. cumingii*, 15m), whereas *D. mollis*, and most other rattan species, reach the top of the canopy layer by attaching to trees (Uhl & Dransfield, 1987), including members of the dipterocarp family that attain heights of 50m at maturity. At Palanan, palm tree species occupy the forest understorey, are shade-tolerant, and are adapted to the decreased light intensities in lower elevations or non-ridge microhabitats. In order to validate this as a rattan generality, other rattan species in the plot could be included in future analyses.

The aseasonal forest of Palanan receives at least 100mm of rain every month, thus high soil water content is expected throughout the plot. However, water drainage can create differences in available moisture in an area with heterogeneous topography. Water run-off in streams distinguishes microhabitats with relatively higher moisture, which in Palanan are preferentially occupied by *P. maculata* and avoided by *D. mollis* and adult *P. insignis*. Only one out of five species is significantly positively associated with stream microhabitats, suggesting that habitats with high soil moisture are unsuitable for palms. The survival probability of vegetative stems of *D. mollis* is reduced by five percent after five days immersed in freshwater, and up to 20% after 20 days of immersion (Yap, *unpublished*). *D. mollis* stems rotted from water exposure likely damaging the apical meristem resulting in the death of immersed plants. Constant exposure to water would be a deterrent to the successful establishment of palms. Thus, palms typically do not flourish in flooded habitats, with the exception of examples like *Mauritia flexuosa* swamps in the Neotropics (Henderson *et al.*, 1995), and Paleotropical peat swamps harboring *Calamus caesius*, *C. trachycoleus,* and *C. trachycoleus* (Ali & Barizan, 2002). Presently, *P. maculata,* can be added to the list of exceptions, as it is shown to prefer the most flooded areas in the PFDP.

Liana and tree life forms in palms show contrasting preferences for stream microhabitats. In addition, there is an antagonistic stream microhabitat association between the two understorey *Pinanga* species in the plot, congruent with the results found in eight species pairs of small and medium-sized Neotropical palms (Svenning, 1999). However, no antagonistic relationship based on elevation is exhibited by the four palm tree species in this study. Thus, only partial support is provided for Svenning's hypothesis that the coexistence of palms of the same growth form is promoted by antagonistic patterns of microhabitat specialization. On the other hand, there is substantial evidence that the two different growth forms have opposing microhabitat preferences. Further censuses, including all rattan species in the PFDP, should help determine whether lianas and trees occur in sympatry due to differences in microhabitat specialization.

There is no trend of increasing strength in association across subsequent life stages for any of the species that would indicate increased recruitment in suitable habitats, whether grouped by growth form or not. However, the present data may be insufficient in detecting a gradient in intensity of habitat association because all stems included in the study of palm tree species were at least 1cm in diameter at 1.3m above ground. Palm trees grow in girth before allocating resources to increasing height, thus, all three groups may be considered as belonging to one life stage. The observed preferences for the microhabitats defined in the study are not constant across life stages but the same relationships are found in one or more life stages as found in the per-species analysis. Including all stages of the palm life cycle from seed to maturity would be optimal to gain a better understanding of palm population dynamics.

Increasing our knowledge on the basic biology of palms facilitates every effort to preserve palm diversity and the natural habitats they occupy. This study is particularly important because four of the five species included are endemic to the Philippine Islands and endemic island species are most notably prone to extinction (Frankham, 1998). The climbing palm, *D. mollis*, is currently being collected because of the rarity of other species with better quality cane due to overexploitation. Fortunately, rattan nurseries and plantations have been established, growing the most economically viable species like *Calamus merrilli* and *Calamus ornatus var. philippinensis* (Lapis & Bueser, 2008; Rivera, 1999). Nevertheless, forests must be constantly monitored to maintain sustainable wild populations of other rattan species especially since nine of the ten rattan species in the Palanan plot are rare. The palm tree species, on the other hand, are relatively free from threats except for *O. decipiens* whose population is naturally small and thus more likely to succumb to extinction in the presence of disturbances. The pattern of distribution observed here will serve as a baseline, representing a healthy palm community in comparison with other forests. In the future, it would be advantageous to determine the survivorship of seedlings so seedlings may be collected for nurseries and plantations without negative effects on palm population dynamics.

Conclusion

Paleotropical palm species rank high in importance based on species richness, abundance, and basal area, emphasizing the need to include both tree and climbing species in censuses and forest dynamics studies. The rich palm flora in Palanan should be compared to the palm flora of other sites located at different latitudes across the Philippine archipelago to determine whether the latitudinal gradient in palm diversity exists in the Paleotropics. Confirmation that the gradient is present will allow for predictions of species diversity for understudied areas to be more accurate.

Aggregation is common in palm species distributions. For two palm tree species there is indication of aggregation being influenced by associations with patchily distributed microhabitats. Microhabitat heterogeneity due to elevation and stream location, but not slope, influences palm abundance and distribution. Microhabitat specificity facilitates the occurrence of five palm species in sympatry. Antagonistic microhabitat specialization patterns are exhibited between two palm life forms, trees and lianas. Additional analyses incorporating more liana species and all life stages of the palm is expected to clarify the antagonistic pattern of relationships between different growth forms as well as to provide a better estimate of the contribution of microhabitat specialization (i.e. niche differentiation) to palm species coexistence.

Species Name (Code)	**Subfamily**	**Abundance (16 has.)**	**Basal area, m^2 (16 has.)**
Calamus dimorphocanthos	Calamoideae	1	-
Calamus discolor	Calamoideae	est. < 100	-
Calamus ornatus var. philippinensis	Calamoideae	est. < 100	-
Calamus reyesianus	Calamoideae	est. < 50	-
Calamus siphonospathus	Calamoideae	est. < 10	-
cf. Calamus daemonoropoides	Calamoideae	2	-
Calamus sp. 1	Calamoideae	1	-
Calamus sp. 2	Calamoideae	est. < 10	-
Daemonorops mollis (DAEMMO)	Calamoideae	6,496 (clusters)	128.53
Daemonorops ochrolepis	Calamoideae	est. < 200	-
Caryota cumingii (CARYCM)	Arecoideae	431 (trees)	11.14
Orania decipiens (ORANDE)	Arecoideae	31 (trees)	0.68
Pinanga insignis (PINAIN)	Coryphoideae	1,075 (trees)	13.38
Pinanga maculata (PINAMA)	Coryphoideae	1,371 (trees)	2.36

Table 3.1. Palm species in the PFDP. The species name, subfamily, abundance, and basal area are listed. Abundance is based on individual tree stems and cluster of climbing palms. Estimated abundances of surveyed but non-censused species are also indicated.

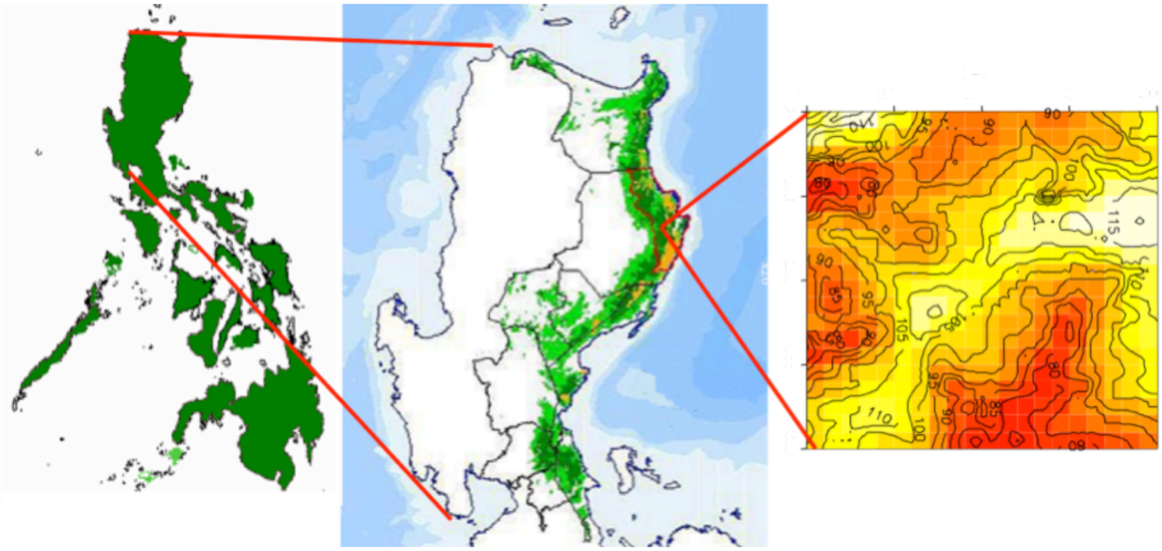

Figure 3.1. Study site. Palanan Forest Dynamics Plot in NE Luzon Island, Philippines. The contour map is shown at the far right.

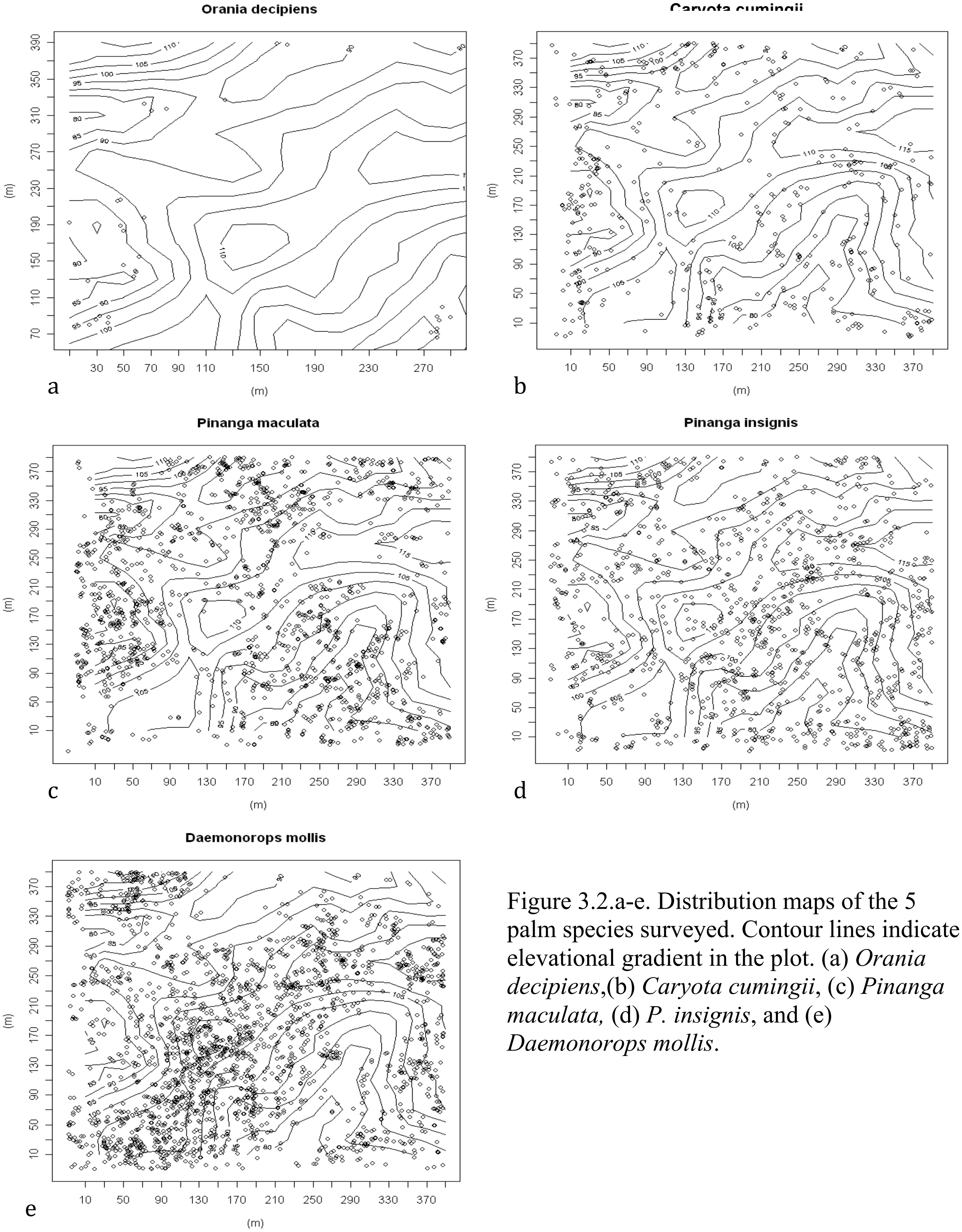

Figure 3.2.a-e. Distribution maps of the 5 palm species surveyed. Contour lines indicate elevational gradient in the plot. (a) *Orania decipiens*,(b) *Caryota cumingii*, (c) *Pinanga maculata,* (d) *P. insignis*, and (e) *Daemonorops mollis*.

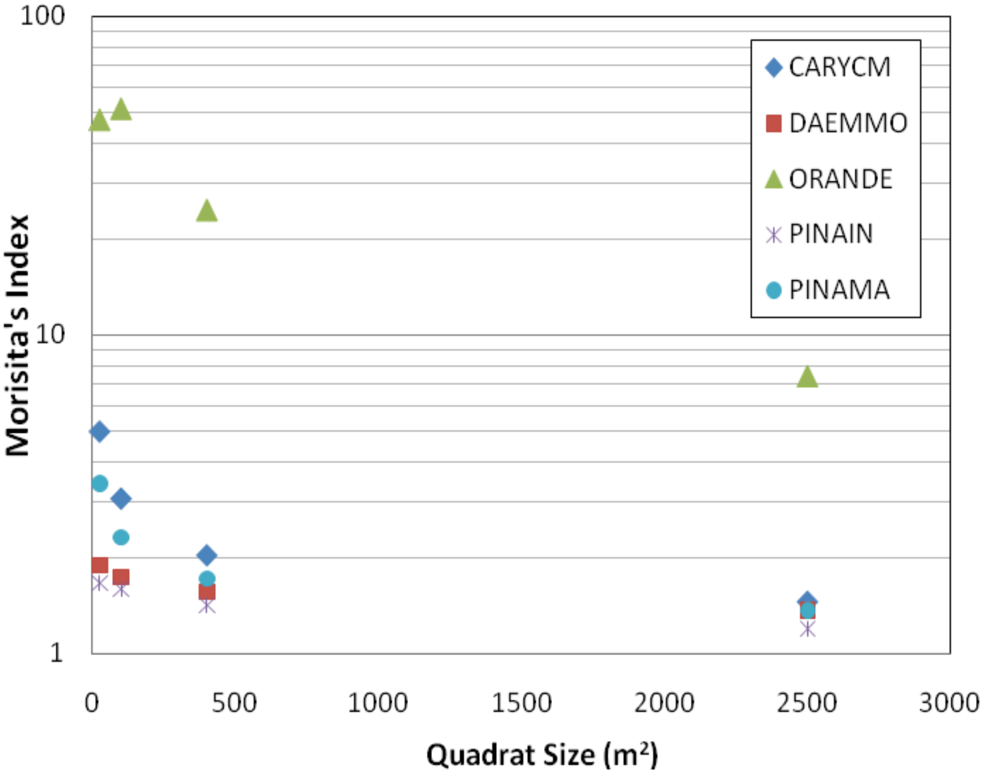

Figure 3.3. Test for dispersion using Morisita’s Index. Test indicates all palms are clustered ($p<0.0001$) at different spatial scales (25, 100, 400, and 2500 m^2).

		Ripley's K (distance in m)				
Species	Age Class	5	15	25	35	45
C. cumingii	young	1.1	4.37	3.95	3.17	0.45
	middle-age	-0.08	2.04	0.97	0.53	-0.99
	old	5.05	10.61	17.37	15.51	12.89
P. insignis	young	1.52	2.95	2.01	0.46	0.13
	middle-age	-0.73	1.04	0.01	-0.85	-1.29
	old	0.94	4.22	4.57	3.13	2.02
P. maculata	young	0.47	1.73	-0.01	-1.1	0.17
	middle-age	0.21	2.76	3.13	3.2	3.36
	old	4.64	7.61	9.6	10.09	8.9
D. mollis	young	-0.41	2.21	2.65	2.88	2.82
	middle-age	-0.5	2.53	2.84	3.39	3.6
	old	0.25	4.37	6.03	8	9.73

Table 3.2. Degree of aggregation in the three age classes of four palm species. Positive values indicate clustering and negative values overdispersion at the 0.05 significance level.

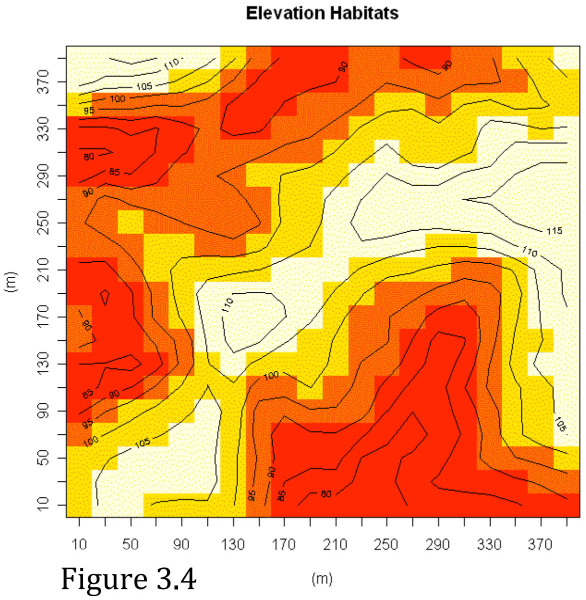

Figure 3.4

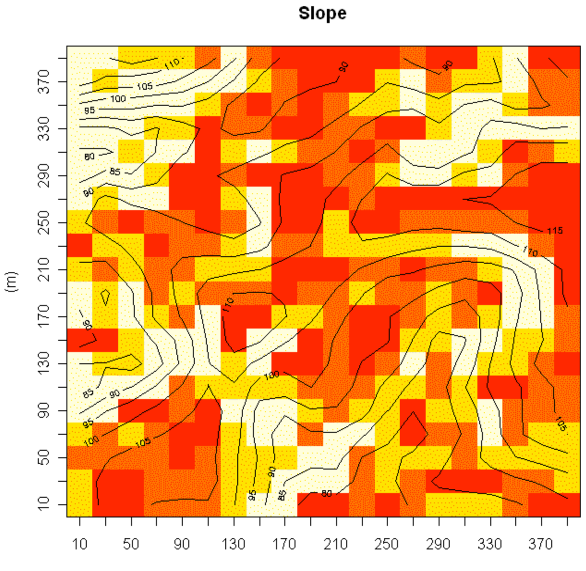

Figure 3.5

Figure 3.4. Distribution map of the four elevation habitats. Increasing elevation is represented by lighter to darker colors.

Figure 3.5. Distribution map of the four slope habitats. Increasing steepness is represented by lighter to darker colors.

Figure 3.6. Distribution map of the two stream habitats. Blue represents stream habitats and green non-stream habitats.

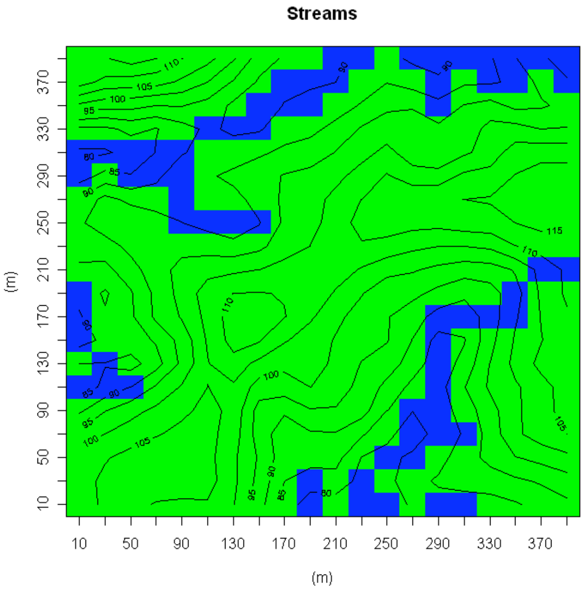

Figure 3.6

		ELEVATION				STREAM	
Species	Life Stage	Low	Mid-low	Mid-high	High	Non-stream	Stream
C. cumingii	per-species	++			---		
	young						
	middle-age	++++			----		
	old				----		
O. decipiens	per-species	++					
P. insignis	per-species						
	young						
	middle-age						
	old						----
P. maculata	per-species	++++	++++		----	----	++++
	young				----		
	middle-age	++++	++++		----	----	++++
	old	++++		----	----		+++
D. mollis	per-species	----	--		++++	++++	----
	young	----			++++	++++	----
	middle-age	--			++++	++++	----
	old		----		++++	++	----

Table 3.3. Habitat associations of five palm species. Elevation habitats: (1) <95.5m; (2)≥95.5 & <97.75; (3) ≥97.75 & <105.01; (4) ≥105.01. Stream habitats: (1) Non-stream; (2) Stream habitats. Positive and negative associations are denoted by ++++/---- (p<0.025) and ++/-- (p<0.05).

Country	Median latitude	No. of palm species	Land area (km^2)	Sp/area (per $10,000km^2$)
Paleotropics				
Taiwan	23°N	11	35,980	3.06
Vietnam	17°N	119	331,690	3.59
Thailand	15°N	196	513,120	3.82
Philippines	10°N	166	299,764	5.54
Malaysia	5°N	278	329,845	8.43
Borneo	1°N	307	743,330	4.13
Sumatra	1°S	177	470,000	3.77
Sulawesi	2°S	67	174,600	3.84
New Guinea	5°S	257	786,000	3.27
New Zealand North Island	38°S	1	113,729	0.09
	Latitude	**No. of palm species per 1°grid ***	**Land area (km^2)**	**Sp/area (per $10,000km^2$)**
Neotropics				
	23°N	6	12,000	5
	17°N	13	12,000	11
	15°N	15	12,000	13
	10°N	26	12,000	22
	5°N	40	12,000	33
	1°N	44	12,000	37
	1°S	44	12,000	37
	2°S	41	12,000	34
	5°S	38	12,000	32

Appendix 3.1. Comparison of palm species diversity in the Paleotropics and the Neotropics. The country is listed along with the median latitude of each country, the number of palm species (including varieties), land area, and no. of sp/area. Data was compiled from Govaerts, *et al.* (2006) for the Paleotropics and from Figure 2 in Bjorholm *et al.* (2005) for the Neotropics.

* 1°grid estimated area is $12,000km^2$ (110km per degree latitude and 109km per degree longitude).

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Chapter 4

Topography and species-habitat associations of dominant tree species in a tropical forest in the Philippines

Abstract

Microhabitat associations based on topographic features including elevation, slope, and stream location, were examined for the 30 most important species in a mixed dipterocarp forest in Palanan, Philippines. Species were also categorized into saplings, juveniles, and adults, and separately analyzed for microhabitat preferences. All species were found to be significantly associated with at least one topographic feature at one or more life stages, but usually varied across life stages. Only four species were consistently associated with the same microhabitat (elevation) across all three life stages, and seven species were consistently associated with one stream microhabitat across all life stages. Among three growth form categories based on height attained at maturity, canopy species were most often associated with high elevations, understory species were most often associated with low or high elevations in similar abundance, and shrub growth-form was associated with low elevations, suggesting a correlation between growth form and elevation as a function of light availability. Habitat heterogeneity, via niche differentiation, is therefore an important factor in the distribution of the dominant tree species within the tropical forest community in the Philippines. Furthermore, differentiation of niches to facilitate species coexistence seems to occur both in space and time.

Introduction

The latitudinal gradient in species diversity peaks in tropical rainforests (Wallace, 1878; Willig *et al.*, 2003). A comparable gradient also exists for rates of deforestation with the fastest rates recorded in tropical rainforest habitats (FAO 2005). Tropical forests host a multitude of coexisting species and the rapid pace of habitat loss increases the threat of extinction to the hyper-diverse biota, making habitat preservation and restoration an immediate global concern. Protocols for effective forest management for species and habitat preservation must be based on sound knowledge of the patterns and mechanisms producing the structure and dynamics of tropical forest habitats.

A comprehensive explanation for the assembly and maintenance of high species diversity in tropical forests has not been generated, but many hypotheses have been offered to explain species coexistence, including the neutral theory proposed by Hubbell (2001). The neutral theory proposes that species are ecologically equivalent, whereas niche theory, proposes that each species is unique and occupies an exclusive specific niche, by way of Gause's competitive exclusion principle (Hardin, 1960; Tilman, 2004). Habitat partitioning, such that a different functionally equivalent species dominates in each habitat, is the end-result of niche differentiation among species. Habitat heterogeneity, therefore, may provide the opportunity for species to coexist (Tilman & Pacala, 1993).

Many studies from the Neotropics have demonstrated the association between single species and environmental factors that define the habitat it occupies (Harms *et al.*, 2001; Nishimura *et al.*, 2008; Potts *et al.*, 2002; Svenning, 2001; Valencia *et al.*, 2004). Important factors for plants include light (Svenning 2001), soil nutrient composition

(Clark *et al.*, 1995; Potts *et al.*, 2002), soil water availability (Kahn & Decastro, 1985), and topographic variation (Harms *et al.*, 2001; Vormisto, 2002). In the last decade, several studies in the Paleotropics have analyzed species-habitat associations in forested communities, also finding that community composition is correlated more with habitat than with geographic distance (Potts *et al.,* 2002) and that light, soil nutrients, and topographic features, including elevation, slope, and convexity influence species-habitat associations (Gunatilleke *et al.*, 2006; Lai *et al.*, 2009; Paoli *et al.*, 2006; Potts *et al.*, 2002; Webb & Peart, 2000). The strength of the relationship between environmental factors and species distributions, however, is not equivalent among forest communities. Observed habitat preferences vary among sites from 44% of the species studied in a Bornean forest (Webb & Peart, 2000), to 80% in a dipterocarp forest in Sri Lanka (Gunatilleke *et al.,* 2006), and to 87% in a subtropical forest in China (Lai *et al.,* 2009).

Habitat associations have also been tested on members of species-rich families that occur in sympatry. Despite close phylogenetic relationships, closely related species are expected to show niche differentiation, demonstrating the role of habitat heterogeneity in facilitating species divergence (Fine *et al.*, 2005) and coexistence (Nishimura *et al.*, 2008). Ten Fagaceae species in West Sumatra (Nishimura *et al.*, 2008), eight Fagaceae and 20 Lauraceae species in Thailand (Noguchi *et al.*, 2007; Sri-Ngernyuang *et al.*, 2003), and ten Sterculiaceae species in Lambir, Malaysia (Itoh *et al.*, 2003; Yamada *et al.*, 2006), were analyzed demonstrating 60%, 100%, 65%, and 80% of species with habitat specialization, respectively. These studies all show the important contribution of heterogeneity in topographic factors in the coexistence of so many species through niche differences (Harms *et al.,* 2001).

Clearly, each life stage from seed to mature adult is important in niche differentiation for the maintenance of species richness (Grubb, 1977). If niche preferences vary through the life history of a species (Lai *et al.,* 2009), more opportunities are provided for promoting coexistence. Previous results of research into habitat specialization, however, have only rarely evaluated life stages independently, most often incorporating all individuals of a species' distribution, including stems 1cm in diameter to those at maximum diameter and maturity. A few studies have addressed the potential error in assuming that stems of all ages are equally suited to the same habitat by separately investigating different life stages and have indeed found habitat associations to vary across life stages (Comita *et al.*, 2007; Lai *et al.*, 2009; Webb & Peart, 2000). Webb & Peart (2000) compared habitat associations of adults (≥10cm dbh) and seedlings (≤ 1cm dbh, >5cm tall) of 22 abundant tropical species in Borneo, finding that trees were more strongly associated with topography than seedlings. Comita *et al.*, (2007) also analyzed habitat association patterns based on elevation, slope, stream, and swamp locations at two life stages: large (≥1cm dbh, diameter at breast height) and small (<1cm dbh, >20cm tall) individuals across 80 neotropical species, finding that although a similar number of species in both small and large size classes were associated with habitat, only 5 of 30 (16%) species were consistent in habitat associations at both stages. Lai *et al.* (2009) subdivided all tree individuals ≥1cm dbh of 60 species in a subtropical forest in China into three life stages: sapling, juvenile, and mature stages. They also subdivided species by mature stage growth form (shrub, understory, or canopy tree). Their research demonstrated more species-habitat associations at the sapling (43) and juvenile (41) stage than the mature (33) stage, and only 31% (16 of 52) of species consistently associated with the same habitat, defined by elevation, slope, convexity, and aspect, across all three stages.

This study evaluates the correlation of elevation, slope, and proximity to streams with species distributions for 30 species from a dipterocarp-dominated forest in Palanan, Philippines. In addition, three life stages (ala Lai *et al.,* 2007) are used to assess the variability in habitat associations throughout the life history of each species. Based on the work of Webb and Peart (2000), it is predicted that saplings and juveniles will have weaker associations than adult trees, suggesting increased mortality at earlier life stages in ‘suboptimal’ habitats. Moreover, weaker associations between habitats and saplings than for habitats and adult trees are anticipated for canopy species because of the high sapling:adult ratio in Old World forests (LaFrankie *et al.*, 2006). There, saplings of canopy species overwhelm the understory and are unlikely to be restricted to specific habitats until they grow to larger sizes.

Methods

Study Site and Data Collection

Data used in this study were collected during a census (2004) of all trees with diameter ≥ 1cm at breast height in the 16-hectare Palanan Forest Dynamics Plot (PFDP, Figure 4.1, see Co *et al.* 2006 for a more detailed plot description). The PFDP is located within the largest remaining tract of primary forest in the Philippines and represents the dominant forest type in the Philippine Islands, Mixed Dipterocarp Forest (MDF). Trees were tagged, dbh recorded, and location of each individual mapped within the 16-ha plot. The PFDP includes a tree flora dominated by members of the Dipterocarpaceae, Meliaceae, and Sapindaceae, a pattern typical of MDF. Dipterocarpaceae species represent 11% of all stems and 50% of the total basal area in the plot. Of the 323 tree species identified in the plot, 30 dominant species based on relative abundance and basal area were selected and used here in the analysis of habitat association.

The 400 x 400m plot was gridded into 400 20x20m quadrats, each of which was assigned two microhabitat types, one based on the quartiles of the recorded elevations and the second based on the quartiles of the slopes measured for all quadrats. Topographic data were collected during plot establishment in 1994, and both elevation and slope for each quadrat are recorded as the calculated mean of the four corners of each quadrat. The plot is divided equally into four microhabitat types (N=100 quadrats per microhabitat type) per topographic feature. Elevation in the plot ranged from 76m to 118m a.s.l. and slopes ranged from 2.44° to 48.5°. The four elevation microhabitats were defined by the following break points: (Low) <90.50m, (Mid-low) ≥ 90.50 and < 97.75m, (Mid-high) ≥ 97.75 and < 105.01m, and (High) ≥ 105.01m. The slope microhabitats were assigned into the following bins according to the degree of inclination: (Low) <11.96º, (Mid-low) ≥ 11.96º and < 16.94º, (Mid-high) ≥ 16.94º and < 23.57º, and (High) ≥ 23.57º. Stream microhabitats were assigned to all quadrats partially or completely occupied by the two streams crossing the plot in a southeasterly direction found on either side of a ridge, and all other quadrats were designated as non-stream microhabitats.

Data Analyses

To select the 30 dominant tree species on the plot, Importance Values (IV = relative basal area + relative abundance) were calculated (Table 4.1). The 30 species with the highest IV were then assigned to one of three growth form categories determined by the maximum height of adult trees: shrub (<5m), understory (≥5m and <15m), or canopy tree (≥15m). Individuals from each species were further classified into three size classes representing three life stage categories: saplings (shrub 1.0-1.5cm dbh, understory 1.0-2.5cm dbh, canopy 1.0-2.5cm); juveniles (shrub ≥1.5-2.5 dbh, understory ≥2.5-5.0cm dbh, canopy ≥2.5-7.5cm dbh); and adults (shrub ≥2.5cm dbh, understory ≥5.0cm dbh, canopy ≥7.5cm dbh).

Microhabitat association tests using torus translation (Harms *et al.*, 2001) were conducted for each species including all individuals, hereafter referred to as per-species, as well as subdividing each species into the three life stages for additional analysis. Taking into account spatial autocorrelation of plant distributions, the test compares the observed relative density of a species to the expected relative densities based on 400 simulated plant distributions under a null model of random distribution. The true habitat map is shifted by 20-m increments in four directions (north, south, east, west) to create the simulated maps. Microhabitat association is recorded as significantly positive or negative, if the observed relative density is greater or less than 97.5% of expected relative densities ($p<0.05$ in two-tailed test). Positive microhabitat associations represent higher occurrences of a species in the specific microhabitat tested whereas negative microhabitat associations represent significantly low numbers of trees in a microhabitat than expected by chance.

Results

Dominant tree species

The 30 dominant species include 16 families and 22 genera (Table 4.1). Three genera are represented by > 1 species: *Shorea* (6 species), *Litsea* (3 species), and *Aglaia* (2 species), belonging to the Dipterocarpaceae, Lauraceae, and Meliaceae families, respectively. The 30 species include 54.2% of the individuals in the plot and 77.03% of the total basal area (BA). The species with the lowest stem count is *Shorea polysperma* with only 256 individuals but it has the third highest basal area (35.37m^2 BA). On the other hand, the most abundant species, *Nephelium ramboutan-ake*, has 14 times more stems than *S. polysperma* but includes smaller diameter trees with only about half the total basal area of *S. polysperma* (19.64m^2 BA). The species with the smallest basal area is *Aglaia edulis* (0.596m^2 BA) but is very abundant (1236 stems). Only three dominant species are shrubs, nine are understory species, and 18 are canopy species (Table 4.1).

Microhabitat Associations: Per-species-microhabitat associations

Significant microhabitat associations ($p<0.05$) were found in 27 of the 30 (90%) per-species analyses based on results from elevation, slope, and stream microhabitat torus translation tests, excluding *N. ramboutan-ake*, *C. pentandrus*, and *C. blancoi*, but only 24 of 30 (80%) if only positive associations are included. For elevation alone, 21 species showed positive habitat associations, only two for slope alone, and 12 species for stream alone (Table 4.2). Positive and negative associations are reported and are both informative, but only positive associations are evaluated unless otherwise stated because negative associations identify habitats that are outside of a species' niche.

Microhabitat Associations: Life stage-microhabitat associations

Based on the three life stages, all species (100%) at one or more life stages are significantly associated with at least one of the elevation, slope, or stream microhabitat categories (Table 4.3). A total of 105 (of 360) significant positive and negative associations were found between the three life stages of the 30 species and the four elevation microhabitats. In the stream microhabitats, there are 79 (of 180) significant associations with the two stream microhabitats, and 21 (of 360) microhabitat associations with four slope microhabitats (Table 4.3). There are equal numbers of positive or negative associations among the three life stages at each topographic feature tested. For example, with elevation, 36, 32, and 37 significant associations are found in the sapling, juvenile, and adult life stages, respectively (Table 4.3).

Of the 23 species that are significantly positively associated with elevation, most are associated with a single elevation microhabitat category. Only four species, *D. paniculatus, D. oppositifolium, D. validus,* and *S. negrosensis* are consistently positively associated with one elevation habitat from saplings to adults. Seven species are found to be consistently positively associated with the same stream microhabitat in all three life stages, including the four species consistently associated with a single elevation microhabitat and *S. palosapis, S. guiso*, and *F. congesta.* Increasing strength of association with age is only recorded for *S. contorta* (stronger negative association of low elevation with age), *H. reticulata* (weaker negative association with age for the highest elevation habitat), and *L. congesta* (increasing abundance with age at the mid-lower elevations).

Microhabitat Associations: Growth form and elevation microhabitat associations

In the three growth forms, canopy species were most often associated with median to high elevations (12 of 18 species). Three understory species were found in low elevations and six species in high elevation while the shrub growth-form was positively associated with low elevations.

Microhabitat Associations: Shared microhabitats

Based on both per-species and life stage analyses, many species are associated with the same microhabitats (Table 4.2). In the four elevation microhabitats, at least 37% (11/30) of the species are found to be positively associated with the highest elevations (as well as negatively associated with the lower elevations). Seven species are positively associated with non-stream habitats and five species are positively associated with streams. There are only eight species positively associated with any slope habitat at any life stage and, not surprisingly, no two species are associated with the same slopes.

Discussion

The forest structure of the Palanan MDF is largely represented by the 30 most important species chosen for this study. The 30 species with the highest IV include less than 10% of the total tree species diversity in the plot, yet comprise more than half the individuals and close to 80% of the total upright plant basal area in the plot. Focusing on only these species incorporates a majority of the stems contributing the most biomass for nutrient cycling (Saatchi *et al.*, 2007), most of the large-diameter host trees for lianas (Homeier *et al.*, 2010), and the trees that define the vertical forest strata influencing recruitment via light dynamics and detritus deposition (Shiels *et al.*, 2010). In hurricane-affected forests, canopy opening after a disturbance increases recruitment of seedlings and pioneer trees that are later replaced by non-pioneer trees, until the next hurricane restarts the process of succession (Shiels *et al.,* 2010), Understanding environmental influences on canopy tree distributions, many species of which are included in this study, is thus particularly important for the Palanan plot because the Philippines is visited by 20 tropical cyclones every year (PAGASA, 2002)

All of the species studied exhibited some preference with respect to slope, elevation, or stream proximity at one or more stages in their life cycle. When considering only positive associations, either 80% (24 of 30) or 87% (26 of 30) of species are microhabitat specialists, based on analyses using all stems or grouping stems according to three life stages. The proportion of species in the PFDP plot with significant positive microhabitat associations, based on separate analyses of three topographic features, is similar to those previously found in Sri Lanka and China (Gunatilleke *et al.*, 2006; Lai *et al.*, 2009) but higher than the reported 64% in Barro Colorado Island (Harms *et al.,* 2001) and 44% in a Bornean forest (Webb & Peart, 2000). In the other studies, microhabitats were defined by combining variables including some of the following: elevation, slope, convexity, aspect, and soil characteristics. Analyzing habitat associations at different life stages only adds few habitat-specific species to those recovered in per-species analyses but the former test gives additional insight into a potential mechanism for sharing a niche through time (see below) as well as the variability among species in habitat fidelity with age.

The environmental feature that most effectively demonstrated niche differences among species is elevation, with only two species, *N. ramboutan-ake* and *S. philippinensis*, showing no significant association with any of the four elevation habitats in either the per-species or life stage analyses. Stream microhabitats also distinguish habitat preferences for 27 of 30 species, with the exception of *N. ramboutan-ake, C. pentandrus,* and *C. blancoi*. Slope, on the other hand, only reveals positive associations for eight species, and only at a single life stage. Previous studies have defined habitats using a combination of two to four topographic features including aspect, convexity, elevation, and slope (Comita *et al.,* 2007; Harms *et al*., 2001; Lai *et al.,* 2009) thus equally attributing to each feature any effect of habitat heterogeneity on species distributions. Here, the effect of elevation, slope, and location of stream is analyzed separately showing the success of using elevation and stream to capture habitat specificity. In a study of 20 Lauraceae species (Sri-Ngernyuang *et al.,* 2003), slope was also found to be less important than elevation in explaining species distributions, which the authors propose is related to distance from streams. Gunatilleke *et al.* (2006) suggests that mid-slopes are more prone to landslides, and therefore gap openings. Constant replacement of trees in gaps within inclined areas could account for the lack of non-random distributions associated with slope among the 30 species studied, because any signal of slope preference by any species would be lost. The distribution of inclined microhabitats in the plot (Figure 4.1) is such that this scenario could be true.

For most species, habitat associations are not consistent across life stages, similar to the pattern found in Indonesia, Panama, and subtropical China (Comita *et al.*, 2007; Lai *et al.,* 2009; Webb & Peart, 2000). However, equal numbers of significant associations are found here for saplings, juveniles, and adults in all 30 species based on elevation, slope, and stream habitats, indicating that there are equal chances for the 30 species to specialize in the attributes of a specific habitat during their life history. Only four species are associated with the same elevational level from saplings until the adult stage, and only seven species are associated with the same stream habitat proximity from saplings until the adult stage. All other species have variable habitat preferences across multiple life stages, likely due to changing ecological preferences resulting from changes in the plant's physiological requirements during growth (Clark & Clark, 1992). Alternatively, negative density-dependent effects that regulate population densities during recruitment could have driven the observed pattern of change in habitat preferences across life stages (Harms *et al.*, 2000; Zhu *et al.*, 2010).

By dividing a species' population into three life stages, we are able to evaluate the changing relationship between a species' ontogenetic phases and it's habitat requirements. More importantly, each life stage illustrates how species partition space through time. For instance, *S. guiso* saplings are usually found in the highest elevations. S. *polysperma* saplings, on the other hand, are randomly distributed in low and high elevations. As *S. polysperma* saplings are recruited into the next life stage, the saplings that were in the highest elevations successfully transition into juveniles, and finally into adults resulting in a positive habitat association of adult *S. polysperma* in the highest elevations. In contrast, *S. guiso* saplings in the high elevations grow into juveniles, but surviving juveniles from low elevations have a higher survivorship into the adult life stage. This results in a randomly distributed adult population of *S. guiso*. This demonstrates how species "time-share" niches.

The varying patterns of species-habitat associations, including those of consistent microhabitat-specificity in all three life stages and "time-sharing", demonstrate several ways that coexisting species respond to microhabitat heterogeneity, suggesting that niche partitioning is an important mechanism assisting species coexistence (Silvertown, 2004).

Shrubs, understory, and canopy tree species are equally associated with habitats at the three life stages, contrary to expectations of adult canopy trees being more strongly associated with habitat than at younger life stages. The species with consistent habitat associations across the three life stages are all canopy species, three of which are most associated with the highest elevations located in ridges. The exception is *D. paniculatus*, which is more abundant at low elevations. Although not statistically supported, based on per-species analyses, the major trends in habitat preference in the three growth forms are as follows: canopy species (12 of 18) are most often associated with ridge areas (high elevations), understory species are split between high abundance in low elevations (3 species) and high elevations (6 species). Shrubs (all 3 species) are positively associated with low elevations. This suggests a correlation between species growth-form and elevation, which may be associated with light availability as the demand for light increases with increasing tree height (Osunkoya *et al.*, 2007; Poorter *et al.*, 2003).

When habitats are defined using a limited set of topographic features, it is to be expected that several species would share patterns of habitat associations, which does not strongly support the hypothesis of niche partitioning as a mechanism for species coexistence. A high proportion of canopy species preferentially inhabit high elevation habitats, and in particular, five of the seven dipterocarp species are positively associated with the highest elevations and two with no specific elevation level. Four *Shorea* and one *Dipterocarpus* species share the ridge habitats, including 7% of all stems and 33% of the total basal area, suggesting other factors in addition to elevation are important in partitioning habitats. Soil nutrients and soil moisture are good candidates for variables that would explain sympatry of the dipterocarp species in Palanan because soil factors have been shown to influence the distributions of *Dryobalanops*, *Hopea, Shorea,* and *Swintonia* species in Borneo (Palmiotto *et al.*, 2004; Potts *et al.*, 2002). In addition, light availability may be influential in delimiting niches of the 30 species studied, in accord with variable demand for light among eleven *Macaranga* species (Davies *et al.*, 1998) and among eleven species of dipterocarps (Brearley *et al.*, 2007).

Species-specific habitat associations provide information on the characteristics of the habitat where each species is most abundant. Reforestation programs can use this data to appropriately select a suitable habitat for a particular species and therefore, maximize the potential for survivorship of each seedling planted. In reforested areas, there must be constant monitoring to assess the status of the planted trees. However, additional data needs to be collected regarding soil nutrients, soil moisture, and light availability so that these may be adjusted accordingly to assist the growth of planted seedlings. Furthermore, research needs to be conducted on the phenology of each species to incorporate into the planting design the frequency of seedling establishment of a species. Some species may produce a cohort every year, while other species every ten years. Lastly, analysis of the different species occupying specific microhabitat types indicates that habitat heterogeneity promotes species coexistence and is therefore a vital component in designating areas for protection.

Conclusion

Habitat heterogeneity defined by three topographic variables: elevation, stream, and slope, demonstrates that the 30 most dominant species in a mixed dipterocarp forest in the Paleotropics show habitat preferences. Habitat specificity for at least one environmental variable, in at least one of the three life stages is recorded here, yet this specificity is rarely consistent across life stages. By studying species-habitat preferences at three life stages, it is shown how species share the same niche but at different life stages. However, because many species share the same preference for a specific habitat, additional factors must be important in facilitating species coexistence, and can be fruitfully investigated. Experimental research, like transplant, reciprocal transplant or controlled greenhouse experiments on phylogenetically related species pairs or same growth-form species, are necessary to test species-habitat associations to infer suitability of specific habitats defined by elevation, slope, proximity to streams, light, and soil nutrient availability.

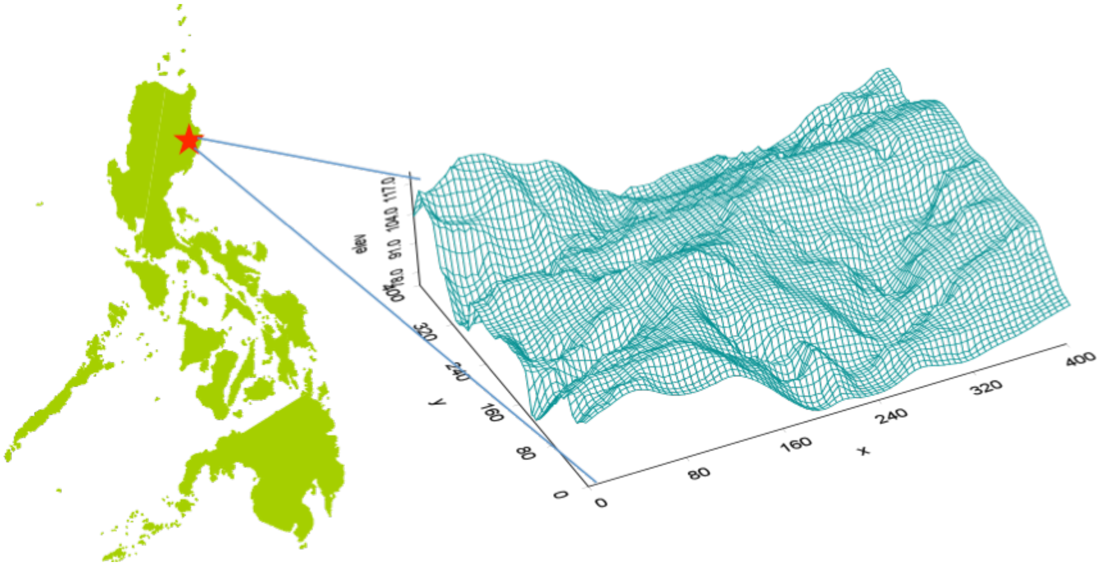

Figure 4.1 Elevational map of the PFDP.

Species	Family	Code	IV	Stem Count				BA (m^2)	Life form Category
				SA	JU	AD	Total		
Shorea negrosensis	Dipterocarpaceae	SHORNE	1	415	459	472	1346	110.28	canopy
Shorea palosapis	Dipterocarpaceae	SHORPA	2	923	815	691	2429	95.17	canopy
Nephelium ramboutan-ake	Sapindaceae	NEPHRA	3	1998	1011	639	3648	19.64	canopy
Shorea contorta	Dipterocarpaceae	SHORCO	4	1364	518	332	2214	29.73	canopy
Drypetes megacarpa	Putranjivaceae	DRYPME	5	743	553	821	2117	23.45	canopy
Diplodiscus paniculatus	Malvaceae	DPLDPA	6	367	353	551	1271	27.44	canopy
Shorea polysperma	Dipterocarpaceae	SHORPO	7	39	38	179	256	35.37	canopy
Strombosia philippinensis	Olacaceae	STROPH	8	622	503	590	1715	15.62	canopy
Dysoxylum oppositifolium	Meliaceae	DYSOOP	9	1295	681	193	2169	10.17	canopy
Chisocheton pentandrus	Meliaceae	CHISPE	10	680	782	309	1771	6.77	canopy
Haplosticanthus reticulata	Annonaceae	HAPLBB	11	1382	809	94	2286	1.39	understory
Leea congesta	Leeaceae	LEEACG	12	539	1139	567	2245	0.97	shrub
Dipterocarpus validus	Dipterocarpaceae	DIPTVA	13	404	403	274	1081	7.85	canopy
Praravinia sablanensis	Rubiaceae	PRARSB	14	475	576	573	1624	0.72	shrub
Leptonychia bahanensis	Malvaceae	LEPTBA	15	424	405	365	1194	2.70	understory
Microcos stylocarpa	Malvaceae	GREWST	16	354	321	210	885	5.00	canopy
Litsea fulva	Lauraceae	LITSFU	17	862	394	68	1324	0.94	understory
Aglaia edulis	Meliaceae	AGLAED	18	549	478	209	1236	0.60	shrub
Shorea philippinensis	Dipterocarpaceae	SHORPH	19	167	111	78	356	8.44	canopy
Aglaia elliptica	Meliaceae	AGLAEL	20	550	220	115	885	3.43	understory
Litsea garciae	Lauraceae	LITSGA	21	441	272	123	836	3.65	understory
Litsea albayana	Lauraceae	LITSAL	22	609	350	149	1108	1.16	understory

Table 4.1. Top 30 species listed in aphabetical order, ranked based on importance value. The species codes are indicated as well as the abundance, basal area, and growth form of each species. Stem count is listed for saplings (SA), Juveniles (JU), and adults (AD).

Species	Family	Code	IV	Stem Count				BA	Life form
				SA	**JU**	**AD**	**Total**	**(m^2)**	**Category**
Shorea guiso	Dipterocarpaceae	SHORGU	23	63	72	93	228	8.98	canopy
Xanthophyllum excelsum	Polygalaceae	XPHLFL	24	246	138	247	631	5.06	understory
Ficus congesta	Moraceae	FICUCO	25	522	183	147	852	2.21	understory
Lepisanthes tetraphylla	Sapindaceae	LEPITE	26	595	276	100	971	0.87	understory
Calophyllum blancoi	Clusiaceae	CALOBL	27	480	128	58	666	3.61	canopy
Palaquium tenuipetiolatum	Sapotaceae	PALATP	28	162	185	75	422	4.66	canopy
Dacryodes rostrata	Burseraceae	DACRRO	29	236	185	56	477	3.90	canopy
Cynometra inaequifolia	Fabaceae	CYNOIN	30	155	149	119	423	4.33	canopy
PROPORTION OF PLOT TOTAL							**54.20%**	**77.03%**	
PLOT TOTAL							**71,419**	**576.555**	

Table 4.1 continued…

		elevation				stream		Slope			
IV	CODE	Low	Mid-Low	Mid-High	High	Non-stream	Stream	Low	Mid-Low	Mid-High	High
1	SHORNE	-	----		++++	++++	----				
2	SHORPA	--	-		++	++++	----	+			
3	NEPHRA										
4	SHORCO	---			++++		----				
5	DRYPME	----	----		++++	++++	----				
6	DPLDPA	++++	++++		----	---	++++				
7	SHORPO	--			++++	+	----				
8	STROPH	---		+++		+	----	----			
9	DYSOOP	----	----		++++	++++	----				
10	CHISPE			+							
11	HAPLBB	++++		--	----	----	++++				
12	LEEACG		++++		----	----	++++				
13	DIPTVA	----			++++	++++	----				
14	PRARSB	++			----			----			
15	LEPTBA	---	----	++++			-			++++	
16	GREWST	-	----	+++			---				
17	LITSFU	+	----						++		
18	AGLAED	+			---	--	++++	--	+++		

Table 4.2. Habitat associations of the 30 dominant species in the PFDP. Codes correspond to Table 1. Elevation habitats: (1) <95.5m; (2) ≥95.5 & <97.75; (3) ≥97.75 & <105.01; (4) ≥105.01. Stream habitats: (1) Non-stream; (2) Stream. Slope habitats: (1) <11.96°; (2) ≥11.96° & < 16.94°; (3) ≥ 16.94° & <23.57°; (4) ≥23.57°. Positive associations are denoted by (+) and negative by (-) corresponding to p values: p<0.1 (+/-); p<0.075 (++/--); p<0.05 (+++/---); p<0.025 (++++/----).

		elevation				stream		slope			
IV	**CODE**	**Low**	**Mid-Low**	**Mid-High**	**High**	**Non-stream**	**Stream**	**Low**	**Mid-Low**	**Mid-High**	**High**
19	SHORPH						----				
20	AGLAEL	---	--		+++						
21	LITSGA		++++								
22	LITSAL	----		++		++++	----				
23	SHORGU	----	----		++++	+	----	+			
24	XPHLFL	----	---		++++		---				
25	FICUCO		+++		----	----	++++				
26	LEPITE			++++	----		---				
27	CALOBL										
28	PALATP	---	---		++++		---				
29	DACRRO	---	----		++++	++++	----	++			
30	CYNOIN	-		++++		++	----				

Table 4.2 continued…

		elevation		stream		slope		total		
	Life stage	+	-	+	-	+	-	+	-	=
All species	sapling	14	22	12	14	3	6	29	42	71
	juvenile	14	18	10	14	2	2	26	34	60
	adult	15	22	14	15	4	4	33	41	74
TOTAL		43	62	36	43	9	12	88	117	205
per-species		22	29	12	21	2	5	36	55	91
canopy (18 sp.)	sapling	8	13	8	10	2	4	18	27	45
	juvenile	9	11	6	8	1	1	16	20	36
	adult	9	15	8	10	2	2	19	27	46
	sub-total	26	39	22	28	5	7	53	74	127
understory (9 sp.)	sapling	4	6	3	3	0	1	7	10	17
	juvenile	4	5	3	5	1	0	8	10	18
	adult	4	6	4	4	1	1	9	11	20
	sub-total	12	17	10	12	2	2	24	31	55
shrub (3 sp.)	sapling	2	3	1	1	1	1	4	5	9
	juvenile	1	2	1	1	0	1	2	4	6
	adult	2	1	2	1	1	1	5	3	8
	sub-total	5	6	4	3	2	3	11	12	23
TOTAL		43	62	36	43	9	12	88	117	205

Table 4.3 Summary of positive (+) & negative (-) association counts for the three topographic features (elevation, stream, and slope) according to the three life stages (saplings, juveniles, adults), per-species, and growth form.

		life	**elevation**				**stream**		**slope**			
IV	**code**	**stag**	**Lo**	**Mid-Low**	**Mid-High**	**High**	**Non-Stream**	**Stream**	**Low**	**Mid-**	**Mid-High**	**High**
1	SHORNE	SA		----		++++	+++	----				
		JU		----		++++	++++	----				
		AD	---	----		++++	+++	----				
2	SHORPA	SA		---			++++	----				
		JU	---				++++	----				
		AD	---				++++	----	+++			----
3	NEPHRA	SA		---								
		JU										
		AD									++++	
4	SHORCO	SA	-			++++		----				
		JU	---									
		AD	----									
5	DRYPME	SA	----	---			++++	----		+++	---	
		JU										
		AD	----	----		++++	++++	----				
6	DPLDPA	SA		++++		----		++++				
		JU	+++	++++	----	----	---	++++				
		AD	+++	++++		----		++++				
7	SHORPO	SA										----
		JU				++++						
		AD	----			++++	+++	----				
8	STROPH	SA		---								
		JU										
		AD	----				++++	----				

Appendix 4.1. Habitat associations of the saplings (SA), juveniles (JU), and adults (AD) of the 30 most important species in the plot. Codes correspond to Table 1. Elevation habitats: (1) <95.5m; (2) ≥95.5 & <97.75; (3) ≥97.75 & <105.01; (4) ≥105.01. Stream habitats: (1) Non-stream; (2) Stream habitats. Slope habitats: (1)<11.96°; (2)≥11.96° & < 16.94°; (3)≥ 16.94° & <23.57°; (4)≥23.57°. Positive and negative associations are denoted according to these p values: $p<0.05$ (+++/---); $p<0.025$ (++++/----).

		life	elevation				stream		slope			
IV	code	stage	Low	Mid-	Mid-High	High	Non-Stream	Stream	Low	Mid-	Mid-High	High
9	DYSOOP	SA	---	----		++++	+++	----				
		JU	---	---		++++	+++	----				
		AD	----	---		++++	+++	----				
10	CHISPE	SA										
		JU			+++							
		AD		+++		----						
11	HAPLBB	SA	++++			----	----	++++				
		JU	+++		----	--		+++				
		AD				-		++++				
12	LEEACG	SA		+		---						---
		JU		+++		---	----	++++				
		AD		++++		----	----	++++				
13	DIPTVA	SA	----			++++	+++	----				
		JU	----			++++	++++	----			+++	
		AD	----			++++	++++	----				
14	PRARSB	SA			++++	----						
		JU							----			
		AD	+++					+++				
15	LEPTBA	SA		---								
		JU	---					---				
		AD	----	----	++++	+++		---			++++	----
16	GREWST	SA										
		JU		----								
		AD			+++			---				
17	LITSFU	SA		----								
		JU		---								
		AD						----				

Appendix 4.1 continued…

		life	elevation				stream		slope			
IV	**code**	**stag**	**Low**	**Mid-**	**Mid-High**	**High**	**Non-Stream**	**Stream**	**Low**	**Mid-**	**Mid-High**	**High**
18	AGLAED	SA	+++			----	---	++++		++++		
		JU				---						
		AD							---		+++	
19	SHORPH	SA										
		JU						---				
		AD										
20	AGLAEL	SA										
		JU	----			++++		----				
		AD										
21	LITSGA	SA								----		
		JU		+++						+++		
		AD		++++		----		++++				
22	LITSAL	SA	----		++++		++++	----				
		JU					++++	----				
		AD										
23	SHORGU	SA		----		++++		---				
		JU		----		++++		----			----	
		AD	----					---				
24	XPHLFL	SA										
		JU				++++						
		AD	----			++++	+++	----				
25	FICUCO	SA		+++		----	----	++++				
		JU				----	----	++++				
		AD				----	----	++++				

Appendix 4.1 continued…

IV	code	life stag	elevation				stream		slope			
			Low	Mid-	Mid-High	High	Non-Stream	Stream	Low	Mid-	Mid-High	High
26	LEPITE	SA			++++	---						
		JU						----				
		AD				---						
27	CALOBL	SA										----
		JU										
		AD		----								
28	PALATP	SA		---		++++	+++	----				
		JU	----			+++						
		AD							---			
29	DACRRO	SA		----		++++	+++	----	+++			
		JU					++++	----				
		AD										
30	CYNOIN	SA						---				---
		JU										
		AD						----				

Appendix 4.1 continued

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Chapter 5

Negative density dependence and dispersal limitation in dominant Philippine tree species

Abstract

Spatial point pattern analysis is used to measure aggregation in 30 dominant tree species from the tropical Palanan Forest Dynamics Plot, Philippines. Aggregation is calculated at multiple spatial scales from 5m^2 to 185m^2 for each species at each of three life stages: saplings, juveniles, and adults. All species exhibit clustering with one exception (adult *Dacryodes rostrata*). Clustering commonly peaks at the scale of 45m^2 (42 of the 90 individual measures), occurring equally among the three life stages, and is the predominant scale of greatest clustering in the 15 most abundant species. Clustering at a smaller spatial scale (25m^2) is more frequently exhibited in the 15 less-abundant species of the 30 dominants, particularly within the adult life stage. A second peak of clustering at the largest scale tested (185m^2) in nine species indicates multi-scale effects of spatial processes driving species distributions. Two independent correlation tests show greater clustering of saplings than juveniles around adult trees in three species that is attributed to negative density-dependent effects. Moreover, ten species exhibit greater clustering of juveniles around adults, which indicates that saplings experienced negative density dependent effects while successful recruitment of juveniles is promoted with proximity to adult trees. Based on results, seed dispersal, negative density dependence, and species-habitat associations contribute to the spatial pattern in dominant tropical

trees.

Introduction

Species-rich communities in the tropics have fueled research into understanding the ecological processes facilitating species coexistence. Two contrasting hypotheses challenge ecologists: ‘niche partitioning’ and ‘neutral theory’ (Hutchinson, 1957; Hubbell, 2001; Leibold, 2008). The traditional explanation requires differences between species in their ecological requirements including details of resources, interspecific interactions, time, and space (i.e. their niche, Chesson, 2000). The alternative view posits that stochastic processes of dispersal and demography allow the coexistence of functionally equivalent species (i.e., species have identical niches, Hubbell 2001, 2006). Niche differentiation has been demonstrated in a variety of taxa, but does not fully explain the distribution and abundance for all species within a diverse tropical community (Harms *et al.*, 2001; Silvertown, 2004; Valencia *et al.*, 2004). Neutral models, although able to accurately predict patterns of relative abundance for some species (Hubbell, 2001; Volkov *et al.,* 2003), also fail to support neutral theory when re-evaluated due to model limitations (Chase 2005; McGill, 2003; McGill *et al.,* 2006). Clearly, neither perspective alone satisfactorily explains the maintenance of complex species assemblages. As the two hypotheses are not mutually exclusive, both niche-based deterministic and neutral stochastic processes probably structure communities. Thus, current approaches used in analyzing tree community structure combine both perspectives (Leibold & McPeek, 2006; Stokes & Archer, 2010).

Negative density-dependence is one of the important deterministic mechanisms that facilitate species coexistence (Wright, 2002). Distinguishing the relative importance of negative density-dependence and other mechanisms that promote coexistence, such as habitat divergence (Ashton, 1969) and intermediate disturbance (Sheil & Burslem, 2003), is as much a challenge as identifying the mechanisms. Numerous studies have shown negative density-dependence effects on plant survival (Harms *et al.*, 2000; Wyatt & Silman, 2004; Wills *et al.,* 2006), such as increased pests and pathogens (Bell *et al.*, 2006; Ruiz *et al.*, 2009), congruent with the Janzen-Connell hypothesis (Janzen, 1970; Connell, 1971). For this mechanism, the probability of survivorship of a seed is negatively correlated with the density of conspecific seeds in the neighborhood allowing seeds of other species to establish, thereby increasing species diversity (Harms *et al.,* 2000).

A commonly used method for determining density-dependence is analyzing spatial patterns in species distributions and abundances (Wiegand *et al.*, 2007b). Point pattern analysis provides characteristics of spatial patterns resulting from recruitment, and when combined with knowledge of species traits, can be used to infer what processes control the pattern observed (Wiegand *et al.,* 2009; Webber *et al.,* 2010). Repeated censuses provide data on the recruitment of several cohorts, directly measuring the effects of density on plant mortality (Wright, 2002; Wiegand *et al.,* 2009), but multiple cohorts also can be represented by dividing a population into several groups using size as a proxy for age in the absence of long-term census data (Zhu *et al.*, 2010).

In this study, the spatial distribution of 30 dominant tree species from a tropical forest in the Paleotropics are evaluated. The objectives of the analyses are: (1) to investigate changes in spatial patterns among species at different spatial scales and, (2) to determine if recruitment is negatively density dependent. The roles of dispersal limitation, species abundance, and dispersal mechanism in structuring species distributions are also discussed.

Methods

Study Site and Study Species

The spatial distribution of tree species was determined from a 2004 census of the 16-hectare Palanan Forest Dynamics Plot (PFDP) in Palanan, Isabela, Philippines. The PFDP is part of a network of large-scale permanent plots coordinated by the Center for Tropical Forest Science and designed to study population-level processes that drive species diversity and distribution (Co *et al.,* 2006). A uniform methodology is applied to all plots, where all stems with diameter ≥ 1cm at breast height (DBH) are identified, tagged, measured, and mapped relative to their position within a 5m x 5m subquadrat and within the 16-ha plot. The Importance Value (IV= relative abundance + relative basal area) was calculated to determine the 30 dominant species. The population of each species was divided into three size classes representing three life stages: sapling (SA), juvenile (JU), and adult (AD), based on the maximum DBH reached at maturity and recorded DBH of reproductive plants from the literature (Table 5.1).

Data Analyses

The distribution at each size class per species was analyzed for patterns of clustering, randomness, or over-dispersion using a Multi-Distance Spatial Cluster Analysis based on the Ripley's K function (Ripley, 1981) in ArcGis 9.0. Ripley's K is used to determine the threshold distance from which to calculate the size of the area where spatial processes promoting the overall species distribution pattern is most pronounced. Ten distances in 20-meter increments from five meters to 185 meters were included in this study. Clustering or dispersion is statistically significant if the observed K is greater than, or less than, the higher confidence envelope and lower confidence envelope, respectively (Figure 5.1). To calculate the confidence envelope, 99 permutations were run for each distance increment (0.01 significance level).

Individual points (representing a single plant) were combined in 5x5m gridcells, and a count of the number of stems per cell was completed for each of 6,400 gridcells within the 16-ha plot. Hot Spot Analysis was conducted using the gridcell counts, identifying local areas within the plot where a species was highly clustered (Figure 5.2). A corresponding Hot Spot Z score is assigned to each grid cell, where a statistically significant hotspot is a gridcell with a high stem count surrounded by other gridcells with high stem counts. Clustering is indicated by statistically significant Z scores that are ≥1.96 (0.05 significance level). The Hot Spot Analysis was conducted using the Zone of Indifference option, combining the threshold distance band determined in Ripley's K and Inverse Distance. Inverse Distance reflects the decreasing influence of two individuals on each other the farther apart they are in space.

Z scores were used to perform two independent correlation analyses. First, correlation was analyzed using Z scores between the clusters of saplings and adults, and between clusters of juveniles and adults. A second test calculated the correlation between Z scores representing clusters of saplings or clusters of juveniles with distance to the nearest conspecific adult (point-to-point distance in meters). The first test I will hereafter refer to as the CC test to represent the cluster to cluster relationship whereas the second, I will refer to as the CD test to indicate a cluster to distance relationship. For each species in each test, 95% confidence intervals were calculated to determine significant differences between the correlation coefficients obtained.

Results

Ripley's K

Clustering of individuals was exhibited by all 30 species tested, ranging in scale from $25m^2$ to $185m^2$ (Table 5.2). All species formed clusters of trees in at least one spatial scale for each of the three size classes with one exception: adult *Dacryodes rostrata* did not show aggregation, rather, overdispersion was observed in all spatial scales but was least overdispersed at the scale of $25m^2$. No species, at any life stage, presented a random distribution.

Clustering was strongest at the scale of $45m^2$ for majority of species (23 of 30 species, 42 of 90 possible outcomes), and predominant among the 15 most abundant species (30 of 42 occurrences, Table 5.1 and 5.2, and Appendix 5.1). The 15 less abundant species showed greater variability in the scale of clustering patterns and a higher frequency of clustering at $25m^2$ (14 here vs. 3 in the 15 abundant species). In nine species, aggregation intensity is seen to increase again following the first peak in clustering patterns, until finally at $185m^2$, values of K are at its highest (Table 5.2, Appendix 5.1).

The highest degree of aggregation (K= 44.1) at any spatial scale was recorded in the saplings of *Shorea guiso*, followed by *S. polysperma*, *S. philippinensis*, *P. tenuipetiolatum, S. negrosensis, F. congesta,* and *S. contorta*. Incidences of intense aggregation mostly correspond with species of low abundance (Table 5.1 and Appendix

5.1). Aggregation patterns among different size classes at the same spatial scale show no overall trend of increasing or decreasing aggregation with age.

Correlation Analysis

In the CC test, 13 species have clusters of juveniles that are more strongly correlated with clusters of adults than are the sapling clusters (Table 5.3). Conversely, five species show greater correlation between adult and sapling clusters than adult and juvenile clusters. In one species, *Lepisanthes tetraphylla*, sapling and juvenile clusters are equally correlated with adult clusters. Results of the CD test indicate that 12 species include juveniles that are more negatively correlated with distance to the nearest adult. In other words, clustering of juveniles increases with decreasing distance to a conspecific adult for those 12 species. Three species, on the other hand, have saplings increasing in clustering the closer to a conspecific adult.

Only in 13 of the 30 species are the same relationships reported from both correlation analyses. Of these, ten species have stronger juvenile-adult clustering and three species have more saplings the closer to a conspecific adult.

Discussion

Analysis of the spatial patterns in different life-stages of the dominant tree species in Palanan gives insight into the processes responsible for the distribution and abundance of species within a tropical forest habitat. In earlier spatial analysis studies, little could be inferred from the characteristics of clustering or dispersion patterns because tests were performed at a single scale or as a static observation of the entire population (Condit *et al.,* 2000; Siedler & Plotkin, 2006). Here, several spatial scales are incorporated and tested for patterns of aggregation at three life stages: saplings, juveniles, and adults (Wiegand *et al.,* 2007b; Zhu *et al.,* 2010).

Clumped distributions are common among tropical forest tree species (Condit *et al.*, 2000) and this was evident in all 30 species included in the study. Aggregated distributions reflect seed dispersal limitation resulting in clustered recruits from seeds dispersed in clumps, typically deposited by animal vectors (Russo & Augspurger, 2004). Also, in many tree species, the majority of seeds fall beneath the canopy of the parent tree, with a small number of seeds experiencing long distance dispersal (Clark *et al.,* 2005). In some cases, seeds are first dispersed by gravity and undergo secondary dispersal by rodents that cache seeds (deAlmeida *et al.,* 2006).

Among the 30 species in this study, clustering is highest at scales ranging from 25m^2 to 185m^2, illustrating differences among and within species in effective dispersal distances and responses to processes with a spatial component. Wind dispersed seeds travel shorter distances relative to animal-dispersed seeds (Condit *et al.,* 2000) and this is expected to result in greater clustering of wind-dispersed species than animal-dispersed at the same spatial scale. Among the Palanan dominant species, seven dipterocarp species employ wind to disperse winged seeds, and are shown to have more intense clustering patterns than all other species in the plot that are animal dispersed (Appendix 5.1). For example, at 45m, *Chisocheton pentandrus* saplings with seeds dispersed by birds (Velho, *et al.,* 2009), has K=1.1 in Ripley's index whereas, *S. negrosensis* saplings have a K=21.5.

Still, species with the same dispersal mechanism have different aggregation patterns. *Shorea polysperma* saplings cluster within 25 m^2*,* while *S. contorta* juveniles are most intensely aggregated within 105 m^2, but the estimated distance traveled by at least 90% of bird-, monkey-, and wind- dispersed seeds is <60 m (Clark *et al.*, 2005). The small proportion of seeds that undergo long distance dispersal (>60m) could potentially be important in developing large cluster sizes in dipterocarps. Furthermore, contrasting growth strategies in dipterocarp species from Malaysia showed high-growth and high-mortality species aggregating at smaller distances (<100m) in small trees, whereas slow-growth and low-mortality species formed larger clusters (>200m; Suzuki *et al.,* 2009). The dipterocarp species in the Palanan plot may be differentiated like the Malaysian species hence the greatest clustering at small (25m^2) and large (105m^2) spatial scales. Further investigation into the dipterocarp species in the Palanan plot is warranted to confirm physiological divergence as a mechanism for increasing species coexistence (Ashton, 1969).

Clustering most commonly peaks at 45 m^2, occurring equally among the three size classes, but predominantly in the 15 most abundant species. On the other hand, clustering at a smaller scale, 25 m^2, is more frequently observed in the 15 less abundant species. Greater aggregation in rarer species was also documented among the 1768 species analyzed in Condit *et al.* (2000). In addition, the most intense aggregation recorded at any spatial scale for any of the 30 species occurred in saplings of a dipterocarp species, *S. guiso*. This result was also expected based on previous findings of greater aggregation in dipterocarps than non-dipterocarps (Condit *et al.,* 2000). All dipterocarp species follow this pattern of very intense clustering of individuals, including both most and least abundant species among the species studied (*S. guiso*, ranked 30th in relative abundance, *S. polysperma,* ranked 29th, *S. palosapis*, ranked second most abundant species in the plot). The aggregation observed in dipterocarps is likely driven by habitat specificity, as it has been shown that most of these large canopy trees proliferate in high elevation ridge habitats (Figure 5.2; Yap, *Chapter 4*). This result contradicts the claim of Plotkin, *et al.* (2000) that dispersal and gap recruitment are more important to the 817 species in Pasoh, Malaysia than habitat specialization with respect to topography.

A second peak in clustering for some species is reminiscent of the results of Weigand *et al.* (2009) showing multi-scale complex clustering, which the authors attribute to two methods of dispersal. For the species in the Palanan study manifesting this pattern, it is difficult to acknowledge the two-dispersal method scenario, as it does not appropriately fit all the species with this pattern. For example, *S. contorta* has winged seeds, which are dispersed by wind with no known secondary dispersal agent (Osada *et al.,* 2001). Also, in *Leea*, dispersal of the small <20mm seeds by ground-welling secondary dispersers would certainly not add 140m (from first peak at 45m^2 to second peak at ≥185m^2) to the total dispersal distance. Inferring from known habitat association in *Leea congesta* with mid-low elevation habitats that are mostly distributed alongside the main ridge bisecting the plot (Figure 5.2), large scale effects from topography and habitat heterogeneity are responsible for complex spatial patterns.

Analyzing and comparing the spatial patterns between cohorts relative to the aggregation pattern of adults (CC test) and proximity to adult trees (CD test), shows the recruitment of three species to be potentially controlled by negative density dependence. *D. validus, D. paniculatus*, and *S. philippinensis* saplings cluster near adult trees (potential parents) whereas the cohort of juveniles are less associated with adults (Table

5.3). Negative density dependence affects populations by decreasing the density of individuals in a cohort in a given area near a parent tree (Janzen, 1970; Connell, 1971). As a consequence, the affected cohort will be less aggregated, as is demonstrated by the juveniles.

In contrast, ten species exhibited more intense clustering of juveniles around adults than saplings. This pattern points to dispersal not strongly limiting species distribution. It also suggests that at an earlier life stage, seedlings were subjected to negative density dependent effects resulting in a weak correlation between clusters of saplings and adults (Queensborough *et al.,* 2007). Finally, this positive correlation between clusters of juveniles and adults shows that juveniles are recruiting in areas that are close to established adult trees. Adult trees are likely collecting in habitats that are most suitable for the longevity of the species and mortality of juvenile individuals is lower in or near these habitats.

In conclusion, this study finds aggregation in all species at multiple spatial scales. Aggregation intensity is decreased by species abundance and long-distance dispersal mechanisms. Recruitment is shown in some species to be due primarily to negative density dependence and in other species in combination with habitat preference. In order to fully understand these processes and how they generate the observed spatial patterns, field experiments directly testing the effects of density on mortality or multi-year censuses should be conducted.

The approach taken in this study to describe distribution patterns in relation to the abundance of saplings or juveniles near adult trees assesses not only the suitable habitat conditions for each life stage of each species but also the roles of seed dispersal and negative density dependence that result in the distribution of adult trees. Aggregation in tropical trees is tempered by differential survival due to negative density dependent effects. Having prior knowledge of the distribution of a species at different life stages can guide conservationists to selectively collect seeds and seedlings from forest sources without undue effects on the plant population. Moreover, identity of neighboring species can be taken into account to minimize mortality in addition to proper site selection based on environmental factors, to boost the project's potential success rate while effectively applying limited resources.

			Stem Count				Max DBH
Species	**Code**	**IV**	**Total**	**SA**	**JU**	**AD**	**(cm^2)**
Shorea negrosensis	SHORNE	1	1346	721	418	207	190
Shorea palosapis	SHORPA	2	2429	1522	609	296	122
Nephelium ramboutan-ake	NEPHRA	3	3648	1998	1011	639	46.6
Shorea contorta	SHORCO	4	2214	1767	346	101	120
Drypetes megacarpa	DRYPME	5	2117	743	679	695	45.3
Diplodiscus paniculatus	DPLDPA	6	1271	367	654	250	70.4
Shorea polysperma	SHORPO	7	256	66	99	91	145
Strombosia philippinensis	STROPH	8	1715	622	614	479	61.8
Dysoxylum oppositifolium	DYSOOP	9	2169	1295	714	160	76.4
Chisocheton pentandrus	CHISPE	10	1771	680	873	218	38
Haplosticanthus reticulata	HAPLBB	11	2286	1383	809	94	9.6
Leea congesta	LEEACG	12	2245	483	943	819	6.1
Dipterocarpus validus	DIPTVA	13	1081	697	317	67	56.2
Praravinia sablanensis	PRARSB	14	1624	553	616	455	21
Leptonychia bahanensis	LEPTBA	15	1194	424	405	365	49
Microcos stylocarpa	GREWST	16	885	354	377	154	39.5
Litsea fulva	LITSFU	17	1324	862	394	68	20.6
Aglaia edulis	AGLAED	18	1236	549	478	209	25.5
Shorea philippinensis	SHORPH	19	356	248	80	28	74.5
Aglaia elliptica	AGLAEL	20	885	550	220	115	58.6
Litsea garciae	LITSGA	21	836	441	272	123	62.4
Litsea albayana	LITSAL	22	1108	609	350	149	17.6
Shorea guiso	SHORGU	23	228	115	85	28	126
Xanthophyllum excelsum	XPHLFL	24	631	246	246	139	37.5
Ficus congesta	FICUCO	25	852	522	183	147	33.2
Lepisanthes tetraphylla	LEPITE	26	971	595	276	100	15.6
Calophyllum blancoi	CALOBL	27	666	480	134	52	64
Palaquium tenuipetiolatum	PALATP	28	422	300	67	55	124
Dacryodes rostrata	DACRRO	29	477	378	63	36	88
Cynometra inaequifolia	CYNOIN	30	423	270	57	96	68.5

Table 5.1. Top 30 dominant species in the PFDP, ranked according to I.V. with corresponding number of stems in each sapling (SA), juvenile (JU), and adult (AD) size class, and maximum stem diameter.

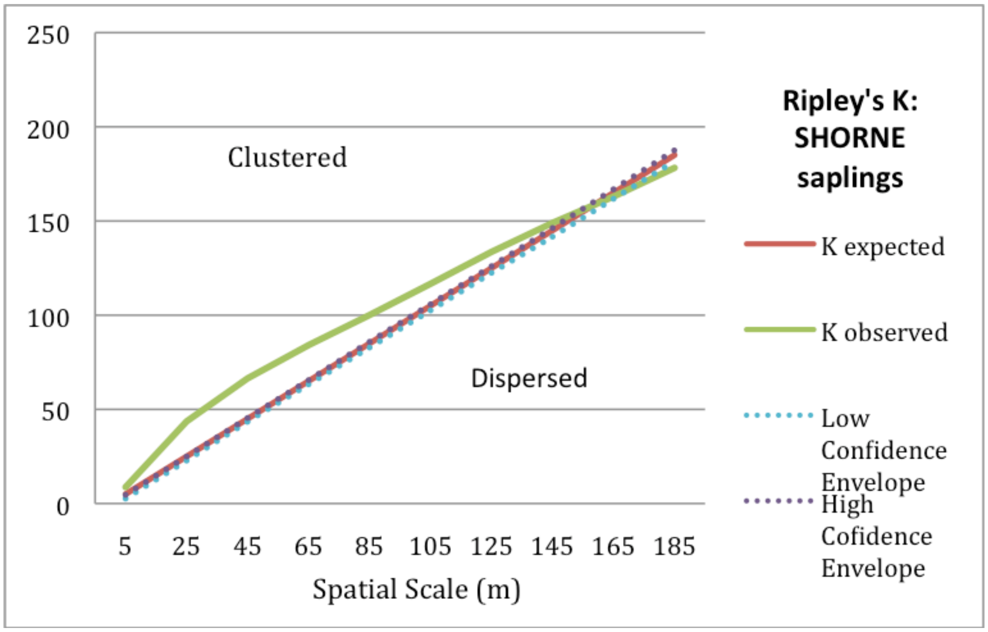

Figure 5.1.a. Ripley's K graph of *Shorea negrosensis* saplings. Clustering occurs from 5m to 145m, peaking at 45m. Confidence Envelopes are at 0.01 significance level.

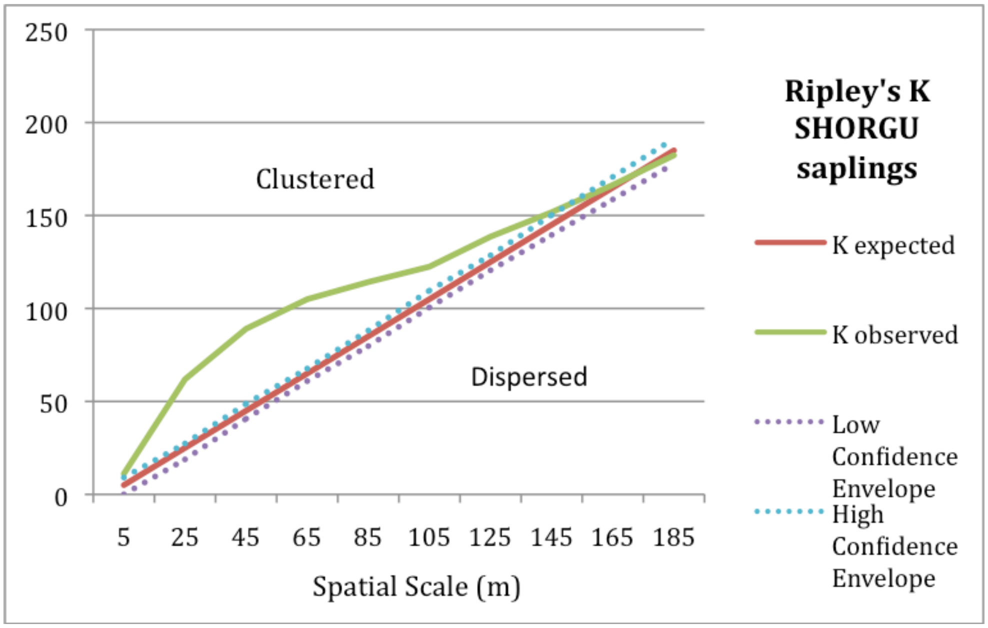

Figure 5.1.a. Ripley's K graph of *Shorea guiso* saplings. Clustering occurs from 5m to 145m, peaking at 45m. Confidence Envelopes are at 0.01 significance level.

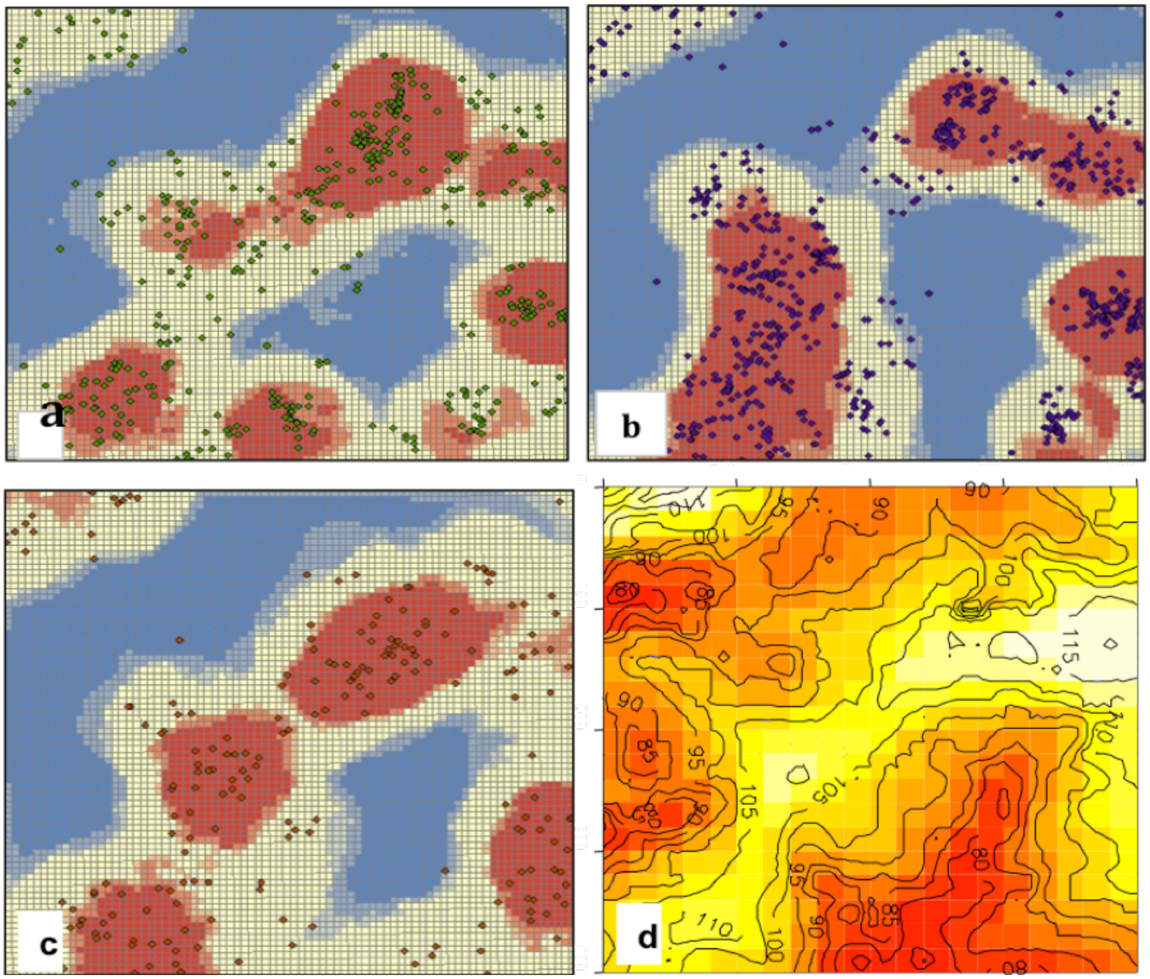

Figure 5.2. Hotspot maps showing areas with high densities of individuals (in red) and areas with fewer individuals than expected from random chance (in blue). a-c, *Shorea negrosensis* saplings (a), juveniles (b), and adults (c); d, elevation map showing gradient in elevation from red to pale yellow (low to high elevation).

			Ripley's K Distance (m)		
Family	**Species**	**IV**	**Saplings**	**Juveniles**	**Adults**
Dipterocarpaceae	*Shorea negrosensis*	1	45	45	45
Dipterocarpaceae	*Shorea palosapis*	2	45	45	25
Sapindaceae	*Nephelium ramboutan-ake*	3	45[a]	45	45
Dipterocarpaceae	*Shorea contorta*	4	85	105[a]	45
Putranjivaceae	*Drypetes megacarpa*	5	45	45	45
Malvaceae	*Diplodiscus paniculatus*	6	45	65	45
Dipterocarpaceae	*Shorea polysperma*	7	25	65	85
Olacaceae	*Strombosia philippinensis*	8	45	45[a]	45[a]
Meliaceae	*Dysoxylum oppositifolium*	9	45	45	65
Meliaceae	*Chisocheton pentandrus*	10	65	45	45
Annonaceae	*Haplosticanthus reticulata*	11	45	65	45
Leeaceae	*Leea congesta*	12	85[a]	45[a]	45
Dipterocarpaceae	*Dipterocarpus validus*	13	45	45	45
Rubiaceae	*Praravinia sablanensis*	14	25	45	45
Malvaceae	*Leptonychia bahanensis*	15	85	65	65
Malvaceae	*Microcos stylocarpa*	16	25	45	25
Lauraceae	*Litsea fulva*	17	65	85	25
Meliaceae	*Aglaia edulis*	18	65	45[a]	65
Dipterocarpaceae	*Shorea philippinensis*	19	25	45	65
Meliaceae	*Aglaia elliptica*	20	45	65	25[a]
Lauraceae	*Litsea garciae*	21	125	185	25
Lauraceae	*Litsea albayana*	22	45[a]	25	25
Dipterocarpaceae	*Shorea guiso*	23	45	85	25
Polygalaceae	*Xanthophyllum excelsum*	24	25	45	65
Moraceae	*Ficus congesta*	25	85	105	105
Sapindaceae	*Lepisanthes tetraphylla*	26	85	65	25
Clusiaceae	*Calophyllum blancoi*	27	45	25	25
Sapotaceae	*Palaquium tenuipetiolatum*	28	65	85	45
Burseraceae	*Dacryodes rostrata*	29	85	65	25
Fabaceae	*Cynometra inaequifolia*	30	45[a]	45	45

Table 5.2. Varying spatial scales where clustering is exhibited in saplings, juveniles, and adult life stages for each of the 30 dominant tree species in the PFDP.

[a] Second peak in clustering patterns at a larger scale than tested in the study (>185m).

			Correlation Coefficients			
Family	**CODE**	**IV**	**Sapling-Adult Clustering**	**Juvenile-Adult Clustering**	**Sapling-Distance to Adult**	**Juvenile-Distance to Adult**
Annonaceae	HAPLBB	11	0.467*	0.555	-0.318*	-0.363
Burseraceae	DACRRO	29	-0.007	0.025	-0.056	-0.040
Clusiaceae	CALOBL	27	-0.127*	0.085	0.220*	0.026
Dipterocarpaceae	DIPTVA	13	0.355*	0.306	-0.289*	-0.168
Dipterocarpaceae	SHORCO	4	0.262	0.274	-0.203	-0.185
Dipterocarpaceae	SHORGU	23	0.234	0.201	-0.357	-0.360
Dipterocarpaceae	SHORNE	1	0.745*	0.791	-0.600*	-0.630
Dipterocarpaceae	SHORPA	2	0.347	0.339	-0.288	-0.316
Dipterocarpaceae	SHORPH	19	0.295*	-0.112	-0.290*	0.122
Dipterocarpaceae	SHORPO	7	0.419*	0.712	-0.336*	-0.532
Fabaceae	CYNOIN	30	0.209	0.188	-0.188	-0.134
Lauraceae	LITSAL	22	0.240*	0.513	-0.289*	-0.382
Lauraceae	LITSFU	17	0.350*	0.431	-0.293*	-0.474
Lauraceae	LITSGA	21	0.197	0.207	-0.249*	-0.329
Leeaceae	LEEACG	12	0.557	0.366	-0.224	-0.262
Malvaceae	DPLDPA	6	0.707*	0.609	-0.505*	-0.443
Malvaceae	LEPTBA	15	0.750*	0.893	-0.385	-0.407
Malvaceae	GREWST	16	0.134	0.166	-0.095*	-0.152
Meliaceae	AGLAED	18	0.779	0.529	-0.263	-0.287
Meliaceae	AGLAEL	20	0.078*	0.216	0.033*	-0.007
Meliaceae	CHISPE	10	0.361*	0.232	-0.150	-0.115
Meliaceae	DYSOOP	9	0.652*	0.678	-0.373	-0.398
Moraceae	FICUCO	25	0.815	0.858	-0.374	-0.258
Olacaceae	STROPH	8	-0.029*	0.382	0.001*	-0.169
Polygalaceae	XPHLFL	24	0.385*	0.666	-0.329*	-0.406
Putranjivaceae	DRYPME	5	0.486	0.497	-0.294	-0.335
Rubiaceae	PRARSB	14	0.404*	0.558	-0.176*	-0.301
Sapindaceae	LEPITE	26	0.290	0.290	-0.402	-0.315
Sapindaceae	NEPHRA	3	0.410*	0.556	-0.243	-0.269
Sapotaceae	PALATP	28	0.356*	0.286	-0.195	-0.165

Table 5.3. Correlation coefficients of 30 dominant tree species in Palanan, Philippines. Correlations include: between clusters of saplings and adults; clusters of juveniles and adults; saplings with distance to the nearest adult; and juveniles with distance to the nearest adult.

* denotes significantly different values of sapling-adult clustering from juvenile-adult

			Ripley's K									
Species	**IV**		**5**	**25**	**45**	**65**	**85**	**105**	**125**	**145**	**165**	**185**
AGLAED	18	SA	-0.6	0.9	2.2	2.3	2.0	1.6	1.1	0.8	0.3	0.3
	18	JU	-0.5	0.3	1.0	0.8	0.5	-0.2	0.0	0.3	1.4	2.1
	18	AD	0.6	4.0	5.0	6.0	4.7	3.5	2.8	0.4	-3.2	-4.3
AGLAEL	20	SA	0.1	4.2	6.7	6.7	6.5	5.5	4.0	2.9	1.9	1.0
	20	JU	-0.1	3.9	5.7	6.2	4.6	2.9	1.4	-0.8	-3.4	-6.2
	20	AD	-5.0	0.4	-1.4	0.0	0.3	-0.5	-0.5	1.0	4.0	5.7
CALOBL	27	SA	-0.3	-0.2	0.9	0.5	-0.1	-0.8	-0.9	-0.7	-0.8	-1.9
	27	JU	-0.5	2.8	2.7	0.6	0.0	0.2	1.8	2.8	2.6	2.9
	27	AD	3.0	12.8	10.7	8.7	7.4	5.7	3.1	2.6	-1.0	-1.6
CHISPE	10	SA	-0.3	1.1	2.4	2.5	2.1	0.7	-0.6	-1.4	-1.7	-1.6
	10	JU	-0.3	0.5	1.1	0.7	0.2	-0.4	-0.8	-1.1	-1.2	-1.4
	10	AD	1.5	5.3	5.6	5.2	3.8	2.3	1.7	-0.8	-3.6	-6.0
CYNOIN	30	SA	-0.1	0.6	0.9	-0.2	-0.3	-0.3	0.2	0.9	2.1	3.2
	30	JU	-5.0	2.4	3.6	2.6	-1.0	-1.6	-3.4	0.7	-4.1	-2.8
	30	AD	-0.5	2.8	3.1	0.9	-0.9	-4.0	-5.7	-3.6	-2.3	-1.6
DACRRO	29	SA	0.3	2.8	4.5	5.7	6.0	5.4	4.3	3.3	2.4	1.5
	29	JU	-0.1	2.2	4.7	10.0	8.3	9.1	10.8	9.3	8.5	7.7
	29	AD	-5.0	-1.3	-7.2	-5.4	-8.7	-9.0	-9.9	-7.3	-9.1	-6.7
DPLDPA	6	SA	2.7	9.8	11.3	10.2	10.5	8.5	6.1	3.9	2.3	-0.4
	6	JU	0.6	9.7	13.9	14.2	12.9	10.4	7.8	4.3	1.3	-0.7
	6	AD	1.7	9.6	10.9	7.6	5.0	4.3	3.7	1.1	0.0	-1.2
DIPTVA	13	SA	0.9	9.8	11.1	8.1	4.3	0.4	-1.3	-1.0	-0.9	-1.1
	13	JU	-0.6	4.7	6.1	4.7	3.4	2.8	2.1	1.4	1.6	2.1
	13	AD	1.3	5.4	10.9	7.4	7.7	5.0	4.0	3.6	-0.7	-1.0
DRYPME	5	SA	0.3	1.1	2.4	2.1	1.2	1.1	0.8	-0.5	-1.8	-2.9
	5	JU	0.0	1.6	2.5	2.1	1.8	0.5	0.0	-0.7	-1.3	-1.6
	5	AD	-0.7	3.0	4.5	4.1	3.3	2.3	2.0	2.1	2.2	2.9
DYSOOP	9	SA	1.0	11.5	15.5	13.9	10.9	8.3	6.8	5.0	3.2	2.0
	9	JU	1.1	9.7	13.5	12.1	8.7	6.1	4.0	0.5	-2.8	-5.4
	9	AD	0.1	4.4	8.1	8.4	7.0	4.1	2.7	0.9	0.1	-0.8
FICUCO	25	SA	1.2	8.0	9.2	9.5	10.7	10.5	9.8	8.4	8.2	8.2
	25	JU	1.2	7.9	10.8	11.4	12.3	12.8	10.4	7.1	5.3	4.8
	25	AD	4.7	14.3	18.7	18.9	19.1	19.6	18.8	18.6	17.9	14.5
HAPLBB	11	SA	-0.8	1.2	2.3	2.3	2.1	1.5	0.5	-0.6	-2.0	-3.5
	11	JU	-0.8	0.5	1.5	2.1	1.4	0.8	-0.2	-1.7	-2.9	-4.4
	11	AD	-0.4	3.6	4.2	3.9	2.0	2.1	0.6	-2.9	-3.4	-6.3
LEEACG	12	SA	-0.2	4.2	6.3	6.9	7.4	7.0	6.9	6.7	6.3	7.0
	12	JU	-0.3	4.1	5.6	5.5	5.4	5.0	4.8	5.8	7.3	8.4
	12	AD	0.8	5.3	6.7	6.7	6.2	5.1	4.3	3.7	2.5	1.3

Appendix 5.1 Ripley's K values for all 30 species including sapling (SA), juvenile (JU), and adult (AD) size classes.

			Ripley's K									
Species	**IV**		**5**	**25**	**45**	**65**	**85**	**105**	**125**	**145**	**165**	**185**
LEPITE	26	SA	1.3	2.6	2.9	3.3	4.2	4.1	3.4	3.7	3.6	3.2
	26	JU	0.1	3.5	4.4	4.6	4.1	5.0	4.1	3.8	3.4	4.5
	26	AD	2.8	4.9	2.6	1.4	1.4	0.9	2.1	0.4	-0.6	-2.6
LEPTBA	15	SA	0.1	4.0	5.2	6.5	7.1	6.7	4.3	1.5	-0.9	-3.2
	15	JU	1.2	7.8	9.8	10.1	9.3	8.5	6.4	3.1	-0.9	-3.1
	15	AD	0.6	7.0	9.4	10.4	9.8	7.8	5.1	2.1	-0.7	-2.1
LITSAL	22	SA	-0.4	2.6	3.9	3.5	3.0	2.6	2.8	2.9	3.8	5.6
	22	JU	1.9	4.3	3.7	2.0	0.5	0.4	2.0	2.5	2.9	3.2
	22	AD	2.5	5.8	4.8	2.1	2.4	1.1	2.1	1.9	-0.7	-3.2
LITSFU	17	SA	-0.3	1.2	2.0	2.1	2.1	1.6	0.9	0.7	0.7	0.7
	17	JU	0.7	2.9	3.8	4.7	5.5	5.0	4.9	5.0	4.4	4.1
	17	AD	5.8	9.5	7.6	5.6	6.6	8.9	9.9	6.6	5.1	4.3
LITSGA	21	SA	-0.6	2.8	4.5	4.9	5.6	6.1	6.5	6.0	5.0	3.9
	21	JU	-0.1	2.6	3.0	3.1	3.6	4.4	5.6	5.9	6.6	7.2
	21	AD	0.6	5.4	4.6	2.8	4.2	4.1	2.2	0.9	3.1	3.6
GREWST	16	SA	0.6	2.9	2.3	2.0	0.6	0.0	-0.3	0.1	0.4	1.1
	16	JU	-0.9	0.5	1.2	0.8	0.5	-0.4	-0.3	-0.7	-1.1	-1.2
	16	AD	-0.6	4.3	3.3	1.4	0.2	0.1	0.0	0.0	0.0	-0.2
NEPHRA	3	SA	-0.1	2.1	2.3	2.0	1.8	2.1	2.2	2.2	2.5	2.8
	3	JU	-0.5	1.0	1.4	0.9	0.7	0.6	0.9	1.1	1.8	2.5
	3	AD	-0.5	2.0	2.4	1.2	0.2	0.2	0.8	1.6	1.8	1.4
PALATP	28	SA	-0.6	5.7	10.2	12.4	11.9	11.5	10.0	8.6	8.0	7.6
	28	JU	3.0	10.1	14.9	18.9	21.8	21.4	19.7	16.6	16.2	17.9
	28	AD	0.5	1.6	2.0	0.3	-0.4	-3.7	-6.7	-5.1	-5.8	-1.6
PRARSB	14	SA	-0.6	1.5	1.5	0.5	0.1	-0.3	-0.7	-0.5	-0.3	0.0
	14	JU	-0.6	-0.2	1.2	0.7	0.3	-0.1	-1.0	-1.8	-2.2	-2.8
	14	AD	-0.8	2.5	3.3	2.3	1.9	1.4	0.3	-1.6	-3.9	-5.8
SHORCO	4	SA	2.0	12.2	16.4	17.5	18.3	17.7	16.5	15.5	13.5	11.2
	4	JU	0.2	4.7	4.8	5.8	5.9	6.8	6.6	6.2	7.4	8.1
	4	AD	0.3	10.1	15.7	13.6	9.9	5.0	-1.2	-5.2	-7.6	-9.0
SHORGU	23	SA	6.1	36.9	44.1	40.0	29.2	17.5	13.6	6.7	1.4	-2.6
	23	JU	1.3	17.3	30.0	33.9	35.2	31.0	29.6	27.1	25.8	26.3
	23	AD	-5.0	11.7	11.7	6.8	7.4	-0.9	-8.3	-4.4	-3.9	-5.7
SHORNE	1	SA	3.7	18.6	21.5	19.1	15.1	11.7	8.6	4.0	-2.0	-6.8
	1	JU	2.7	13.9	15.3	13.2	9.5	7.2	4.8	2.3	-0.3	-1.3
	1	AD	1.4	12.4	18.0	17.1	14.8	9.9	2.9	-2.0	-5.0	-5.2
SHORPA	2	SA	1.6	9.7	11.5	10.9	10.9	10.7	10.8	11.1	10.3	8.9
	2	JU	0.1	3.1	4.6	4.3	3.4	2.8	2.5	2.4	3.2	3.8
	2	AD	-0.7	3.0	2.2	0.9	0.2	-0.1	-0.4	-1.6	-1.6	-1.5

Appendix 5.1 continued….

			Ripley's K									
Species	**IV**		**5**	**25**	**45**	**65**	**85**	**105**	**125**	**145**	**165**	**185**
SHORPH	19	SA	5.8	21.4	18.2	14.6	16.6	15.4	14.5	9.8	5.3	2.4
	19	JU	2.7	6.6	7.6	6.7	3.8	4.1	5.7	3.4	4.7	5.4
	19	AD	12.9	23.5	24.4	28.0	26.1	22.5	15.5	2.4	-4.8	-11.9
SHORPO	7	SA	4.4	33.1	29.4	24.2	20.1	14.3	10.1	3.3	-2.7	-11.6
	7	JU	3.2	14.0	16.5	17.6	15.8	10.8	4.9	4.4	0.8	-2.1
	7	AD	-0.2	7.9	11.0	11.1	12.4	9.7	7.7	5.1	4.9	3.7
STROPH	8	SA	-0.6	2.6	3.3	2.6	2.8	2.7	3.2	2.6	2.2	1.5
	8	JU	-0.1	2.0	2.1	1.0	0.5	-0.1	0.2	0.8	1.8	2.2
	8	AD	-0.4	2.1	2.7	2.1	1.4	1.4	2.2	3.4	4.7	5.2
XPHLFL	24	SA	-0.5	5.6	4.0	3.6	3.0	0.3	-1.3	-2.3	-4.1	-5.2
	24	JU	-1.5	4.2	7.4	6.4	4.8	2.1	-0.1	-0.5	-0.4	-0.8
	24	AD	0.5	8.6	9.5	9.8	8.1	5.3	3.5	2.8	1.7	0.0

Appendix 5.1 continued…..

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