Assessing the Role of Seed Dispersal in Peat Swamp Forest Regeneration

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ABSTRACT

Both biotic and abiotic factors, especially seed dispersal, influence the process of forest regeneration, but there has been relatively little research on these factors in peat swamp forest ecosystems. Large-scale forest fires are the biggest disturbance affecting peat swamp forests, especially in the heavily degraded peatlands of Central Kalimantan, Indonesia. It is important to examine the barriers to forest regeneration in this system because peat swamp forest provides important ecosystem services for people and habitat for Indonesia's unique biodiversity. Several studies have suggested that seed dispersal limitation will be one of the most significant barriers to peat swamp forest regeneration. This study examined the composition of regenerating seedlings and saplings in the former Mega-Rice project area to determine if there was evidence for seed dispersal limitation in general, and how species with different seed dispersal mechanisms (wind, bird or bat, and primate) were distributed across the landscape. The results indicate that (1) there are more primary forest species present in the regenerating flora than expected and (2) seedling and sapling abundance is highest near the forest edge, declining significantly as distance from the edge increases. As predicted, primate-dispersed species were the most dispersal limited, and wind dispersed species were found at the furthest distances from the forest edge. However, of the species with known dispersal mechanisms, bird and bat dispersed species were the most common, suggesting that these animals play a significant role in peat swamp forest regeneration.

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INTRODUCTION

Tropical forest regeneration is driven by a number of biotic and abiotic factors, and it can follow many trajectories depending on the type and intensity of disturbance. Seed dispersal is one such biotic factor. Many tree species in tropical forests depend on frugivorous animals for dispersal, thus their ability to colonize secondary forest depends on how those animals interact with the post-disturbance landscape (Wunderle Jr. 1997). This study assesses the role of animal seed dispersal in a peat swamp forest regenerating from fire in Central Kalimantan, Indonesia and more generally examines the hypothesis that seed dispersal is a limiting factor in tropical forest regeneration.

Forest regeneration, a process that occurs naturally following disturbance, is a major topic in ecology and conservation biology (Brown and Lugo 1990, de Jong et al. 2001, Chazdon 2003, Chazdon et al. 2009). Disturbances that cause forest degradation or destruction can be anthropogenic (*e.g.*, clearing for agriculture, logging) or natural (*e.g.*, hurricanes, fires), and there are often adverse interactions between anthropogenic and natural disturbances that lead to further forest degradation. For example, selective logging can open up the forest canopy, causing the soil to dry and become more susceptible to naturally occurring fires (Cochrane 2003). Regeneration of previously forested land is possible if the area is left alone after a disturbance (provided it has not entered an alternative stable state), and secondary regrowth has been observed across the tropics (Guariguata et al. 1997, Aide et al. 2000, Guariguata and Ostertag 2001, Carrière et al. 2002). There are currently an estimated 500 million hectares (Mha) of degraded primary and secondary tropical forest worldwide, which represents approximately 60% of the world's total tropical forest area (ITTO 2002). Secondary regrowth can restore ecosystem function and services (*e.g.*, timber provisioning, carbon sequestration; Chazdon 2003). By mitigating some of the habitat loss from deforestation, regenerating forests may also be integral to biodiversity conservation, especially in places like Indonesia where a wealth of unique species occur but disturbance rates are high (Lamb et al. 2005).

Early studies on tropical secondary forests generally focused on successional patterns (Brown and Lugo 1990). Regeneration after a natural disturbance such as a fire or hurricane generally follows a predictable pattern, with light adapted pioneer trees establishing early and gap-intolerant hardwood species appearing after the canopy has closed (Horn 1974, Finegan 1996). Regeneration after anthropogenic disturbance often follows different trajectories depending on the nature and severity of the disturbance (Chazdon 2003).

Recent work on secondary forests, in contrast to earlier work, focuses on the barriers to forest regeneration that could have a significant impact on the composition of the resulting vegetation. The exact trajectory of forest regeneration depends on a multitude of factors, including post-disturbance soil characteristics, the state of the soil seed bank, the proximity to nearby undisturbed forest, and other environmental factors that may affect recruitment of new vegetation (Aide and Cavelier 1994, Holl 1999, Cubina and Aide 2001). Given the same type and intensity of disturbance, a regenerating patch with an intact soil seed bank that is close to a patch of undisturbed forest will likely recover much more quickly and have greater species richness than a regenerating patch with no soil seed bank that is farther away from primary forest.

Understanding the processes that create secondary forest is especially important in Indonesia, a country with high biodiversity but also the highest rate of forest loss in the world. Between 2000 and 2005, Indonesia’s forest declined by 2.0% per year. This was partly due to agricultural expansion (Koh and Wilcove 2008, Sodhi et al. 2010), but fires have played a significant role in the loss of Indonesia's tropical forest, especially lowland peat swamp forests (hereafter PSF) [cite]. Undisturbed PSF is globally important for carbon storage (Page et al. 2011), and on the local scale it provides both regulating (e.g. hydrological maintenance) and provisioning services (van Eijk and Leenman 2004, Wösten et al. 2006). However, logging and conversion of PSF for agriculture cause drainage and degradation of the peat soil, making these areas highly vulnerable to fires. Fires in PSF are distinct from other forest fires in that they consume both the vegetation and the soil (Page et al. 2009). The outlook for post-disturbance PSF regeneration is unclear, especially in areas where remaining forests are already degraded. There are complex interactions between the soil, vegetation, and hydrology of PSF, however, and given the importance of Indonesia's PSF for global carbon storage and biodiversity conservation, assessments of natural regrowth are needed to examine the potential barriers to forest regeneration.

The major factors that will limit PSF regeneration are the lack of adequate hydrological function, lack of seed dispersal, and competition with the herbaceous communities, especially ferns, that establish quickly after fire. Management action to restore the hydrology of degraded PSF is currently underway (Aldhous 2004, Page et al. 2009), but less is known about the role of seed dispersal in PSF regeneration. Unlike fires in tropical forest systems with mineral soils, peat fires destroy both above- and below-ground plant biomass. This severely impairs the potential for regrowth from the soil seed bank as well as resprouting from belowground stems and roots, both of which are important propagule sources in other regenerating tropical forests (Paciorek et al. 2000, Dalling and Hubbell 2002, Chazdon 2003). This suggests that natural regeneration of burned PSF will occur mainly through seed dispersal from the nearby forest patches. In tropical forests, most seed dispersal occurs via frugivorous animals (Howe and Smallwood 1982). This mechanism may be diminished in degraded landscapes where extensive disturbance has led to forest fragmentation, thus shrinking habitats for animal seed dispersers (Wunderle Jr. 1997). Of the known seed dispersing animals in Bornean PSF, only birds and bats are likely to travel into deforested areas; previous research suggests that other animals are restricted to forested areas which provide them with food and protection (Wunderle Jr. 1997, Corlett 1998, Graham and Page 2011). This, combined with the observation that the trees most commonly found growing in the burned areas are wind dispersed, has led to the hypothesis that seed dispersal limitation is one of the most significant barriers to PSF regeneration (Page et al. 2009).

It is important to remember that seed dispersal alone does not guarantee successful establishment; once a seed is dispersed it will only establish and recruit if environmental conditions are favorable. Understanding the importance of dispersal in forest regeneration is well developed theoretically, but field studies that document tree species distributions in secondary regrowth are important, especially given the urgent needs of conservation practice and management (Corlett and Hau 2000). Studies that assess seed rain alone are useful for understanding the range of species that could colonize a secondary forest, but these should be coupled with vegetation surveys that determine what ecological factors regulate (promote or hinder) successful recruitment (*e.g.* the establishment of seedlings). This study addresses these issues by (1) assessing the composition of regenerating forest two years after a fire and (2) examining the role of seed dispersal by wind, birds and bats, and primates in PSF regeneration. Additionally, for comparative purposes, surveys of the nearby forest fragment were done to determine the effect of the fire on the structure and composition of the intact forest.

STUDY SITE

This research was carried out in the former Mega-Rice project (MRP) area (2°36’48”S, 114°13’10.3”E), which is located on the edge of the Sabangau River catchment in southern Central Kalimantan, Indonesia (Figure 1). The MRP site, which covers one million hectares of PSF, has a unique land use history that makes it a useful natural laboratory for studying PSF regeneration. From 1996 to 1998 the area underwent extensive deforestation to clear the land for rice agriculture and over 4,500 kilometers of canals were dug to facilitate transport of the logs out and provide irrigation for the future rice crop (Boehm and Siegert 2001, Aldhous 2004, Page et al. 2009). However, in 1999 the project was halted after it became clear that the soil was too acidic to grow rice (Aldhous 2004). The forest that remains today is fragmented and the peat soil heavily degraded, making the MRP area highly vulnerable to fire. The forest in the MRP was previously contiguous with a nearby protected forest (Sabangau National Park) where there is active forest monitoring and primate research. That forest used as a primary reference site for this study. For a more in-depth description of the Mega-Rice area, see Page (2009).

This study was carried out in Block C, one of five blocks and the westernmost part of the MRP. The area of the Block C is approximately 4,490 km^2. The combination of deforestation for the MRP and forest fires have reduced the extent of PSF in Block C from 42.7% of the total area in 1997 to just 13.1% in 2003 (Page et al., 2009). Most of this area has been burned at least once over the past 20 years, and analyses by Page et al. (2009) indicate that some sites have been burned [up to] four times. The last major fire at the study site occurred in 2009, and all data were collected in the dry season (June-August) of 2011 from areas known to be under forest cover before the 2009 fire.

METHODS

Field methods

PLOT STRUCTURE—A nested plot structure was utilized for data collection. Each plot consisted of a 10 m x 10 m plot for adult trees (DBH≥6.0 cm), with 3 m x 3 m subplots for saplings (DBH<6.0 cm, height≥1 m) and 1 m x 1 m subplots for seedlings (height≤1 m) nested inside of the adult tree plots (Figure 2). Each individual stem was identified to species and the stem diameter at 1.3 m (DBH) measured. Seedling height was measured in cm., but for saplings and trees height was estimated in 2- and 5-m increments, respectively. Canopy cover was measured with a spherical densiometer in both the seedling plots and the tree plots. The percent cover by ferns was also estimated and recorded for each subplot. The same field assistant estimated cover in each plot and subplot to control for observer bias.

FOREST SURVEYS—Four 500-m transects were used to survey undisturbed forest (Figure 1). Each transect extended from the forest edge toward the interior of the forest. This transect length was chosen to detect and account for any edge effects that may have resulted from the 2009 fire. Plots were established every 50 meters along each transect, for a total of 11 plots per transect. Eleven plots in the forest interior (600-1000 meters from any forest edge; not associated with any transect) were also surveyed to collect additional data and for use as reference plots in detecting edge effects. A total of 55 forest plots were surveyed.

BURNED AREA SURVEYS—Eight 250-m transects, extending perpendicularly from the forest edge out into a clearing, were used to survey the burned area. Four of these transects were continuations of the forest transects; these four transects were located spaced at least 300 meters apart to minimize spatial autocorrelation. Given that seedling and sapling numbers were expected to be highest close to the forest and quickly decline past 25 meters from the edge, plots were surveyed at 0, 10, and 25 meters, and then in 25-meter increments thereafter. In some areas canals and fallen logs from the fire made it impossible to survey the entire length of the transect. The shortest transect length was 150 meters. A total of 79 burned area plots were surveyed.

Statistical Methods

All data analyses were performed using RStudio (version 0.95.263); unless specified, the vegan package (Oksanen et al. 2011) was used. For all analyses, the subplots for seedlings and saplings were pooled since they were not independent of each other.

FOREST STRUCTURE—To detect edge effects in the forest plots, seedling, sapling, and tree abundance were tested against distance from the forest edge with a generalized linear model using the negative binomial to account for overdispersion in the data. The relationships between both canopy cover and sapling diversity (Shannon diversity index value; Shannon and Weaver 1949) and distance from the edge for the forest plots was tested with a linear model.

COMPARISON BETWEEN FOREST AND BURNED HABITAT—Mean stem densities were compared across burned and unburned plots using a two-tailed t-test. Rarefaction curves were built using the rarefy function (Oksanen et al. 2011). Because there were such small numbers of small stems, seedlings and saplings were pooled to compare species richness between the two habitats. The total observed and projected species pool (Chao estimator) was found using the estimateR function (Oksanen et al. 2011). The dissimilarity matrix was calculated with the vegdist function using the Chao estimator (see Chao et al. 2005). This estimator was selected because it is less sensitive to differences in sample size than other metrics and works with abundance data. It also accounts for unobserved shared species, which is important given that the total area sampled was relatively small. Principal components analysis was performed using the pca function in the labdsv package (Roberts 2010) to illustrate relationships among the plots from the forest and burned area, and to determine which species had the highest loadings on component axes.

SEED DISPERSAL MECHANISMS—Information on seed dispersal mechanisms was gathered from the primary literature, interviews with field assistants, and the Kew database (Royal Botanic Gardens Kew, 2008). Species-specific data were used whenever possible, but in some cases information from congenerics in Southeast Asia were used. Although inferring dispersal mechanisms from seed morphology can be a reliable method, there was not enough information available to do this with confidence for many species and so I used only known dispersal mechanisms. Species for which the seed dispersal mechanism is known are shown in Table 4. The distances from the forest edge at which each seedling or sapling of these species were recorded in the burned plots were tabulated and compared among dispersal mechanisms to determine if there were significant differences between primate, bird/bat, and wind dispersed species. Since sample sizes were unbalanced, these data were analyzed with a Kruskal-Wallis test to test for differences among the three mechanisms, and post-hoc analysis was done using paired Wilcoxon tests with a Bonferroni correction. Seedling and sapling abundances from the plots ≥ 25 meters from the forest were tested with a two-tailed t-test to determine if there was a relationship between the presence of an adult tree (representing a perching structure for frugivorous birds/bats) and the abundance of regrowth. Plots past this distance were chosen because to avoid biasing the analysis with the naturally high seedling and sapling abundances near the forest edge. Finally, to evaluate the effect of distance from the edge on the amount of regrowth in the burned area plots, seedling and sapling abundance were modeled against distance from the forest edge using a hurdle model to correct for zero inflation and overdispersion in the data (package pscl; Jackman 2011). The hurdle model splits the data into two parts (non-zero counts and zeros) and models each of these separately, using a zero-truncated Poisson distribution for the counts and a binomial distribution for the zeros. The model can be customized to use different predictor variables for the count and zero data. Both distance and presence of a remnant tree (binary variable) were used as predictor variables in the hurdle model, and all combinations were tested for both the zero and count predictor equations.

RESULTS

UNDISTURBED FOREST STRUCTURE—A total of 115 species across all of the forest plots were observed and identified. The dominant species and their relative densities in each of the three size classes surveyed are shown in Table 1; the relative densities of the 10 most common species represent 45% of the trees, 48% of the saplings, and 73% of the seedlings surveyed in the forest. There were no significant structural edge effects observed as a result of the fire, but in general there was more variation in abundance and diversity between transects than among the interior forest plots.

COMPARISON OF FOREST AND BURNED HABITATS—There was high disparity between the number of total individuals sampled in the forest (5,331 stems) and the burned plots (1,375 stems), even though more total area was sampled in the burned area than in the forest. Densities of seedlings, saplings, and adult trees were significantly lower in the regenerating area than in the intact forest (seedling $t_{89.4}= 4.96$, $p<0.0001$; sapling $t_{130.7}= 13.0$, $p<0.0001$; tree $t_{92.4}= 18.3$, $p<0.0001$; Figure 3). Species richness for both the regrowth and adult trees was lower in the regenerating area than in the intact forest, even after correcting for the number of individuals through rarefaction (Figure 4). Table 2 shows the observed and projected species richness (with standard error) for the total species pool of trees and seedlings + saplings; the projected species pool is significantly higher in the forest than in the burned area.

The ten most dominant species in each size class (Table 1) represent similar proportions of the total individuals between habitats (e.g., the ten most common seedling species in both the forest and burned area combined make up about 70% of the total seedlings, and so on), but the identities of the most dominant species vary between size classes and habitat types. *Syzygium lineatum* (Myrtaceae) was the most commonly observed species overall. The Chao dissimilarity index values indicate that most similar communities were the forest seedlings and saplings (0.042), with trees and saplings from the burned plots being the most dissimilar (0.43; Table 3). The average value across all combinations of size class (tree, sapling, seedling) and habitat type (forest, burned) is 0.20.

A principal components analysis of the forest and burned plots (Fig. 4) shows that there is more variation among the burned plots than among the forest plots, but there is substantial similarity between the two habitats. However, the first two component axes explain only 14.5% of the variation in the data, which is very low. Species loadings indicate that scores on PC1 most strongly reflect the abundance of *Tetractomia tetrandra* (Rutaceae), and PC2 reflects abundances of *Antidesma coriaceum* (Euphorbiceae), *Koompassia malaccensis* (Fabaceae), and hambitik (local name; scientific name unknown).

SEED DISPERSAL AND THE REGENERATING FOREST—Of the species observed in the burned plots with known dispersal mechanisms (Table 4), 67% were bird or bat dispersed, 19% wind dispersed, and 14% primate dispersed (Table 5). There was a significant difference in the average dispersal distance between primate, bird/bat, and wind dispersed seeds (H=21.4, d.f.=2, $p<0.0001$). Mean dispersal distances are shown in Table 5. Individuals dispersed by wind were observed significantly farther from the forest than bird/bat ($p=0.016$) and primate ($p<0.0001$) dispersed individuals, and bird/bat dispersed individuals were also, on average, dispersed significantly farther from the forest than primate dispersed species ($p=0.0021$; Figure 6).

Seedling and sapling abundances in the burned area were highest near the forest edge and declined as distance from the forest edge increased (Figure 7). Distance from the edge was a significant predictor of seedling abundance ($p<0.01$), and distance and the presence of a remnant tree were both significant predictors of sapling abundance ($p<0.05$). Plots that contained an adult tree (representing potential perching sites for birds and bats) also had significantly more seedlings ($t_{43.6}$= -3.04, $p<0.0001$) and saplings ($t_{53.1}$= -4.19, $p<0.0001$) than plots that did not contain an adult tree (Figure 8).

DISCUSSION

UNDISTURBED FOREST STRUCTURE—Given that the remaining forest fragments in the MRP are heavily degraded and have been selectively logged, the observed species richness of 112 species of trees, saplings, and seedlings all forest plots is higher than was expected. However, this is low compared to the Natural Laboratory of Peat Swamp Forest study site in the Sabangau forest, which also has a history of logging but is now a protected area. Approximately 220 species have been observed at Sabangau (OuTrop, unpublished data), which is much higher than any of the extrapolated estimates (Table 2). Prior to the initiation of the Mega-Rice project, the study site was continuous with the Sabangau forest and likely shared the same species pool. The study plots at Sabangau cover a greater total area than those surveyed in this study, but this comparison suggests that there has still been substantial species loss over the past 20 years. More vegetation surveys should be done in the MRP study site to better estimate the true species richness in the remaining forest fragments.

Analyses of the forest vegetation data indicate that there are no discernible structural edge effects. Previous studies of edge effects in tropical forest systems indicate that both sapling and tree abundance and sapling diversity are significantly different near the edges than in the interior of the forest. These studies have found that tree abundance can be either higher or lower near the edge (Williams-Linera 1990), whereas sapling abundance and diversity should be higher near the edge (Harper et al. 2005), where post-disturbance regeneration occurs. An increase in sapling abundance at the edge of the fragment was expected because it has been two years since the last major fire, which is enough time for new individuals to establish but not long enough that they would have reached adult tree size, but this analysis indicates that there was no significant difference between either seedling or sapling abundance near the forest edge and in the interior.

Slik et al. (2011) also observed that there were limited edge effects in a lowland dipterocarp forest seven years post-fire. Their results are consistent with the findings of this study, that there is a sharp delineation between the unburned and burned forest with little effect on the structure of the unburned forest near the boundary. In order to draw stronger conclusions about the effects of peat fires on the structure and composition of forest fragments, more vegetation data, as well as additional data on physical and chemical soil characteristics, should be collected. This would provide more insight into the ecological processes driving the observed vegetation patterns (Ries et al. 2004, Hooper et al. 2005). Understanding the effects of fire on forest edges is important because edges mediate the flow of species into and out of the forest (Murcia 1995). For example, changes species composition or abundance can alter fruit abundance at forest edges, attracting frugivorous birds and thus increasing the likelihood that seeds of forest species are dispersed into a regenerating area (Restrepo et al. 1999).

COMPARISON BETWEEN FOREST AND BURNED HABITATS—Stem densities for all size classes are significantly lower in the burned plots than in the forest plots (Figure 3). These differences are not surprising, considering it has only been two years since the fire. Cleary and Priadjati (2005) found similar results in their multi-year study in lowland dipterocarp forest in East Kalimantan. They observed significant differences in density two, three, and four years post-fire, with no significant increase in densities over time. This suggests that regrowth in the Mega Rice site will also be suppressed for multiple years. There was high spatial variation in abundances of regrowth, however, with most stems found within 25 meters of the forest edge (Figure 7). Stem densities in the burned plots past 25 meters were close to zero. With the current study design it is impossible to determine if this spatial variation is due to dispersal or recruitment limitation, but it indicates that forest recovery at this site will likely begin at the burned-unburned boundary and proceed outward.

Species richness is significantly higher in the forest than in the burned area for both trees and the pooled seedling+sapling communities (Fig. 4). This is not surprising given that the regenerating forest is only two years old, and the same trend has been seen after fire disturbance in other lowland forest types in the area (Cleary and Priadjati 2005, Slik et al. 2008). Recovery to forest-level species richness will most likely take decades, and even if this does happen the species composition of the secondary forest will be different than in the undisturbed forest (Aide et al. 2000). Seed dispersal limitation will further slow this process; late-successional species are most likely to be dispersal limited since they tend to be dispersed by large-bodied mammals (*e.g.*, orangutans, sun bears) and hornbills that prefer primary forest habitat (Wunderle Jr. 1997, Slik et al. 2008).

THE ROLE OF SEED DISPERSAL IN PSF REGENERATION—Dissimilarity metrics, where a 0 score means that two communities are compositionally identical and a score of 1 indicates that they have no shared species, can be used to draw conclusions about the ecological distance between various communities (Faith et al. 1987). The results indicate that, overall, the six communities measured in this study (seedlings, saplings, and trees from forest and burned habitat) are quite similar. Any two communities are, on average, 80% similar (dissimilarity metric = 0.20). Ingle (2003) puts forth the null hypothesis that, if seed dispersal is not a limiting factor to forest recovery, then species should be present in the regenerating forest proportionally to their representation in the source pool (here, the undisturbed forest), meaning that when size classes are compared across habitats the dissimilarity score would be close to zero. The regenerating seedlings and saplings at the MRP are very similar to their forest counterparts, with dissimilarity scores of 0.074 and 0.13 respectively. This result indicates that the factors that control community composition, including seed dispersal, in the regenerating area are similar to those that structure the forest community. However, the PCA (Figure 5) shows that the forest and burned area vegetation are still distinct from each other. This is likely due to the fact that only two years have passed since the fire; a long term study to determine the regeneration trajectory is needed.

Graham and Page (2011) have previously observed that most seed input at the MRP comes from "degraded zone" species (such as *Syzygium* sp.) and hypothesized that seed dispersal from surviving trees within the burned area was more important for regeneration than dispersal from the forest, but the dissimilarity metrics included here suggest that the opposite is true. The trees and seedlings in the burned area were found to be more different from each other than the forest trees and burned area seedlings (Table 3). This study indicates (1) that degraded zone species are common in the forest (Table 1), and therefore that it is not surprising that seeds of those species are part of the seed rain into the burned area, and (2) that seed dispersal from the forest may be a more significant contributor to the regeneration community than dispersal from within the burned area. The contrast between these results and those of Graham and Page (2011) warrants more investigation in the future.

The results of this study indicate that seed dispersal by animals, especially birds and bats, significantly contributes to PSF regeneration. In the absence of fine-scale surveys of seedling and sapling regrowth in burned PSF, it has been widely assumed that only wind-dispersed pioneer species will be able to colonize after fire, but this study suggests that the regenerating community is much more diverse than previously believed. The three most common wind-dispersed pioneer species at the study site are *Combretocarpus rotundatus, Shorea* sp. and

Cratoxylon arborescens. These species were also expected to be the most commonly observed species in the burned plots. This was not true; *C. rotundatus* was the third most dominant species of seedling (Table 1) but did not appear in the sapling community. *Shorea* sp. and *C. arborescens* were absent from the list of most dominant seedling and sapling species altogether.

The vast majority of the individuals and species (including those with unknown dispersal mechanisms) observed in the burned area were found within 25 meters of the forest edge (Figure 7). Of the 1,186 seedlings and saplings censused in the burned area plots, only 5% (60 individuals) were found further than 25 m from the forest. These 60 individuals come from 18 species, but *Syzygium lineatum* and *Combretocarpus rotundatus* clearly dominate, comprising 55% of the total stems. The other 16 species are each represented by four individuals or less. Many previous studies examining the role of seed dispersal on forest regeneration have also found that seedling and sapling density is highest near the edge and decreases as distance from the edge increases (Willson and Crome, 1989; Gorchov et al., 1993; Cubiña and Aide, 2001; Ingle, 2003; Hooper, 2005). This is likely due to two factors: the availability of suitable habitat and increased seed rain. Recruitment of forest species near the forest edge is likely higher than in areas far from the forest edge because the microclimate in this area is more hospitable to regenerating individuals (Holl 1999). The forest canopy cools the understory and maintains higher soil moisture levels, whereas areas without any cover are very hot and dry, creating environmental gradients that run perpendicular to the forest edge (Murcia 1995). Furthermore, undispersed seeds from forest trees generally land in close proximity to the parent plants on the forest edge (Seidler and Plotkin 2006), and the potential dispersal range of actively dispersed seeds are constrained by the movement patterns of their frugivorous dispersers, the majority of which are unlikely to travel into degraded areas (Howe and Smallwood 1982, Wunderle Jr.

1997). Thus, most seed rain occurs closest to the forest, decreasing as distance from the forest increases (Willson 1993).

In addition to the general decline in seed input with distance from the forest edge, the results indicate that dispersal mechanism significantly influences the distance a seed can travel. Wind dispersed species were, on average, dispersed farthest from the forest, followed by bird/bat and primate dispersed species (Figure 8; Table 5). Bird/bat and wind dispersed species had the largest dispersal range, with individuals of both categories observed up to 200 meters from the forest edge. Primate dispersed species had the most limited dispersal range, with most individuals found within 50 meters of the forest. One individual of *Diospyros bantamensis* was found 100 meters from the forest, which is an unexpected result that may be explained by the observation that there were also several orangutan nests in trees in the burned area (Malone, unpubl. data). If primates are still using vegetation in the degraded area there is an increased potential for dispersal of large-seeded tree species, but these observations may just be isolated incidents. Little is known about how primates use degraded PSF (Johnson et al. 2005), so much more research is necessary before drawing conclusions about the implications for seed dispersal.

Adult trees which presumably survived the fire could be another factor affecting seed dispersal into the burned area (Figure 8). Previous research indicates that remnant vegetation in disturbed areas promotes regrowth because it can serve as a perch or resting spot for various seed-dispersing birds and bats passing through the area (Galindo-González et al. 2000, Duncan and Chapman 2002, Herrera and Garcia 2009). However, others have suggested that perching structures lead to increased seed rain but not necessarily increased recruitment or diversity (Holl 1998, Graham and Page 2011). Graham and Page (2011) installed artificial bird perches 50 and 200 meters from the forest at the MRP research site and monitored both seed rain and recruitment underneath the perches. They found that perches significantly increased seed rain, but did not observe significantly more recruitment of animal-dispersed seedlings, and thus concluded that artificial perches have limited use in the restoration of this site. The data from this study, on the other hand, indicate that perches do lead to increased recruitment of animal-dispersed species, and therefore birds and bats will play a significant role in PSF regeneration. The remnant trees themselves may also produce seeds; *C. rotundatus* (wind-dispersed) is the most commonly observed species and these seedlings and saplings were found throughout the burned area (Table 1).

The key difference between the results from this study and those of Graham and Page (2011) is the presence of a living tree as opposed to an artificial structure. There are two mechanisms that may explain this. First, the fact that a given tree survived the fire may simply be due to the fact that the disturbance was less intense in that location. Fire behavior is complex, and due to environmental variables such as the amount of available fuel and moisture levels, fires can have varying effects on vegetation within the same landscape (Cochrane 2003). If the remnant trees are an artifact of fire "patchiness" and were exposed to less intense fire, then the seed bank in the peat beneath them may be intact and the regeneration occurring there is not a result of seed dispersal from the forest. Another explanation for this is that the presence of a large tree may facilitate recruitment by creating suitable habitat conditions. Shimamura and Momose (2005) demonstrated that organic matter dynamics play a significant role in species coexistence in peatswamp forests. Mounds of organic matter tend to form around trees in peat soil, and this alters the moisture conditions in the surrounding microhabitat. This in turn would allow for higher recruitment of individuals from seed rain. Further research should be done to demonstrate which of these mechanisms is driving the increased regrowth beneath remnant trees at the Mega-

Rice site, but either would explain the disparity between the observations in this study and those from the artificial perch study (Graham and Page 2011).

IMPLICATIONS FOR CONSERVATION

A number of early successional species have already been identified as potentially useful for PSF reforestation projects, and many of these were observed in this study. Shono et al. (2007) tested the performance of 45 early successional and primary species in reforestation plots in Singapore, and found that *Syzygium* species show consistently high survival and growth rates across a variety of disturbed landscapes. *Syzygium* was also the most common sapling and seedling species observed growing in the burned plots in this study. *Elaeocarpus mastersii, Campnosperma auriculatum,* and *Litsea* sp. also showed relatively high growth rates in the reforested plots, although *E. mastersii* and *C. auriculatum* tended to grow in bush form (Shono et al. 2007). Both *E. mastersii* and *Litsea sp.* were among the most common regenerating saplings in the MRP as well (Table 2), which supports the idea that they are good species to plant for reforestation. Additionally, both *E. mastersii* and *Litsea sp.* will likely attract avian frugivores to the regenerating forest (Graham and Page 2011; Corlett 1996) . Orangutans (and presumably other primates) are also known to feed on *E. mastersii*, and the seeds have been successfully germinated from orangutan fecal samples (Nielsen et al. 2011).

Assessing the role of seed dispersal in PSF regeneration is difficult because there have been virtually no studies on fruit-frugivore relationships in this forest type (Hatton 2012). Several authors have studied species-specific interactions, but these are restricted to large mammals (McConkey and Galetti 1999, McConkey and Chivers 2007, Nielsen et al. 2011). Corlett (1998) compiled an assessment of frugivory and seed dispersal for all of Southeast Asia, but this does not focus on PSF guilds, as this ecosystem has largely been ignored until recently. Birds and bats likely play a major role in dispersal for many PSF species and more research is needed to gather information on specific trees and their animal dispersers. Such research is integral to forest conservation because as forests become increasingly fragmented frugivorous species will likely go extinct (Corlett 1998, Moran et al. 2009) . Knowledge of the seed dispersal network will be integral in predicting the cascading effects of extinction on plant communities (Corlett 2011).

The MRP area is generally considered a “lost cause” for conservation. However, this study (and other unpublished data) indicate that, although the forest and burned areas are severely degraded, they still provide habitat for a variety of plants and animals. There has been extensive research on the carbon emissions and hydrology of the MRP site (Page et al. 2002; Boehm and Siegert 2001; Hirano et al. 2007) but ecological research has only recently become a priority. The first orangutan nest surveys in the MRP were done in 2009 (Cattau unpubl.) and repeated in 2011 (Cattau unpubl., Malone unpubl.). Biodiversity surveys to collect data on ants, birds, gibbons, and vegetation were also completed in 2011 (OuTrop unpublished, this study), but these were pilot studies to test sampling methods and should be repeated in the coming years. Preliminary results from these surveys are encouraging; primate population sizes and bird and tree species richness appear to be higher than expected. However, it is difficult to predict what may happen to these populations in the future with only one year of data, and much more research is needed to explore the relationships between faunal diversity and the vegetation sub-types found across the entire MRP area (Rieley and Page 2008).

There has also been discussion about protecting parts of the MRP, but it is unclear exactly how or when this will occur (Simon Husson, personal communication) . The area is globally important for carbon sequestration (Page et al. 2002), and several organizations, including Wetlands International, the Center for International Forestry Research, and Borneo Orangutan Survival are currently involved in REDD pilot projects in the MRP. In January 2012 the

President of Indonesia announced a new regulation that will protect 45% of Kalimantan by establishing a network of conservation areas, limiting the expansion of monoculture plantations (especially palm oil), and reforesting degraded areas. This study suggests that the MRP should be included as a conservation area, as it harbors a number of endemic animal and plant species, including a population of the tree *Shorea balangeran*, which is currently listed as critically endangered by the IUCN (Ashton 1998).

This study suggests that there are a number of management practices that should be strengthened, regardless of the protection status of the MRP. Efforts to restore the hydrology have already increased the water levels in the dry season (Aldhous 2004, Page et al. 2009) and should be continued. The fire-fighting infrastructure should also be expanded, with special focus placed on preventing fire spread near the forest edge where most regrowth occurs. Although this study indicates that relatively diverse regeneration after one fire event is possible, after multiple fires the likelihood of non-pioneer species establishing is low (Page et al. 2009) and regrowth is limited to *Combretocarpus rotundatus, Cratoxylon arborescens,* and *Ficus sp.* (Freund, pers. obs).

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TABLES

Table 1.

TREE (DBH>6 cm.)

Forest		**Burned**	
Species	Relative Density	Species	*Relative Density*
1. *Palaquium cochlearifolium*	6.86	1. *Lithocarpus rassa*	7.94
2. *Rapanea borneensis*	5.58	2. *Syzygium lineatum*	7.41
3. *Calophyllum hosei*	4.85	3. *Combretocarpus rotundatus*	6.88
4. *Mesua sp. 1*	4.76	4. *Palaquium cochlearifolium*	5.29
5. *Syzygium lineatum*	4.48	5. *Diospyros bantamensis*	4.76
6. *Tetractomia tetrandra*	4.03	6. *Neoscortechinia kingii*	4.76
7. *Xylopia fusca*	3.57	7. *Mesua sp. 1*	4.23
8. *Neoscortechinia kingii*	3.57	8. *Palaquium leiocarpum*	3.70
9. *Horsfieldia crassifolia*	3.48	9. *Shorea balangeran*	3.70
10. *Palaquium cf. xanthochymum*	3.29	10. *Eugenia spicata*	3.17
Total	**44.46**	**Total**	**51.85**

SAPLING (> 1 m. height, <6 cm. DBH)

Forest		**Burned**	
Species	Relative Density	Species	Relative Density
1. *Syzygium lineatum*	11.68	1. *Syzygium lineatum*	16.29
2. *Tetractomia tetrandra*	9.87	2. *Tetractomia tetrandra*	5.36
3. *Syzygium sp.*	3.72	3. *Ilex cymosa*	4.80
4. *Diospyros bantamensis*	3.59	4. *Antidesma coriaceum*	4.58
5. *Garcinia bancana*	3.55	5. *Lithocarpus rassa*	4.02
6. *Antidesma phanerophleum*	3.34	6. *Garcinia bancana*	3.24
7. *Tristaniopsis obovata*	3.30	7. *Litsea sp. 1*	2.90
8. *Ilex cymosa*	3.30	8. *Tristaniopsis obovata*	2.79
9. *Licania splendens*	2.89	9. *Antidesma phanerophleum*	2.57
10. *Calophyllum hosei*	2.64	10. *Elaeocarpus mastersii*	2.46
Total	**47.89**	**Total**	**49.00**

SEEDLING (< 1 m. height)

Forest		**Burned**	
Species	Relative Density	Species	Relative Density
1. *Syzygium lineatum*	21.41	1. *Syzygium lineatum*	37.24
2. *Mesua sp. 1*	10.14	2. *Antidesma coriaceum*	6.21
3. *Ficus sp.*	7.89	3. *Combretocarpus rotundatus*	5.17
4. *Ilex cymosa*	6.62	4. *Ficus sp.*	4.14
5. *Antidesma phanerophleum*	6.62	5. *Mesua sp. 1*	4.14
6. *Calophyllum hosei*	6.48	6. *Antidesma phanerophleum*	3.79
7. *Syzygium sp.*	5.77	7. *Campnosperma squamatum*	3.79
8. *Antidesma coriaceum*	3.66	8. *Xanthophyllum ellipticum*	3.45
9. *Tristaniopsis obovata*	2.82	9. *Tetramerista glabra*	2.76
10. *Ixora havilandii*	1.83	10. *Calophyllum hosei*	2.41
Total	**73.24**	**Total**	**73.10**

Table 2.

	No. species observed	Estimated richness (Chao)	Standard error (Chao)
Forest trees	88	98.2	7.1
Forest seedlings +saplings	95	101.4	6.9
Burned trees	46	52.0	6.0
Burned seedlings+saplings	74	75.4	2.5

Table 3.

	Tree (F)	Tree (B)	Sapling (F)	Sapling (B)	Seedling (F)	Seedling (B)
Tree (F)	—					
Tree(B)	0.1105	—				
Sapling (F)	0.0779	0.2060	—			
Sapling (B)	0.2258	0.2264	0.0743	—		
Seedling (F)	0.1581	0.3676	0.0418	0.1726	—	
Seedling (B)	0.3485	0.4271	0.2133	0.1535	0.1287	—

Table 4.

Family	Species	Dispersal Mechanism	Source
Anisophyllaceae	*Combretocarpus rotundatus*	W	Hudin, S.[1]
Aquifoliaceae	*Ilex cymosa*	B	Corlett (1996)
	Ilex hypoglauca	B	Corlett (1996)
Chrysobalanaceae	*Licania splendens*	B	Expert
Clusiaceae	*Garcinia sp. (multiple)*	P	Corlett (1996)
	Calophyllum hosei	B	Corlett (1996)
Dipterocarpaceae	*Shorea teysmannia*	W	CIFOR (1998)
	Shorea balangeran	W	CIFOR (1998)
Ebenaceae	*Diospyros bantamensis*	P	Hudin, S.
Elaeocarpaceae	*Elaeocarpus mastersii*	B	Hudin, S.
	Elaeocarpus acmocarpus	B	Hudin, S.
	Elaeocarpus sp.	B	Hudin, S.
Euphorbiaceae	*Antidesma phanerophleum*	B	Hudin, S.
	Antidesma coriaceum	B	Hudin, S.
	Neoscortechinia kingii	B	Ang et al. (2010)
Fabaceae	*Adenanthera pavonina*	B	Van der Pijl (1982)
Lauraceae	*Litsea sp.*	B	Corlett (1996)
	Litsea sp. cf. resinosa	B	Corlett (1996)
Moraceae	*Ficus sp.*	B	Hudin, S.
Myrtaceae	*Syzygium sp. (multiple)*	B	Hudin, S.
	Syzygium sp cf.campanulatum	B	Graham and Page (2011)
Rubiaceae	*Ixora havilandii*	B	Hudin, S.
Sapindaceae	*Nephellium lappaceum*	P	MacKinnon (1997)
	Nephellium maingayi	P	MacKinnon (1997)

Table 5.

Mechanism	**Number of species**	**Number of individuals**	**Average dispersal distance (m)**
Primate	4	45	10.9
Bird/bat	18	351	34.2
Wind	5	63	56.9

FIGURES

Figure 1.

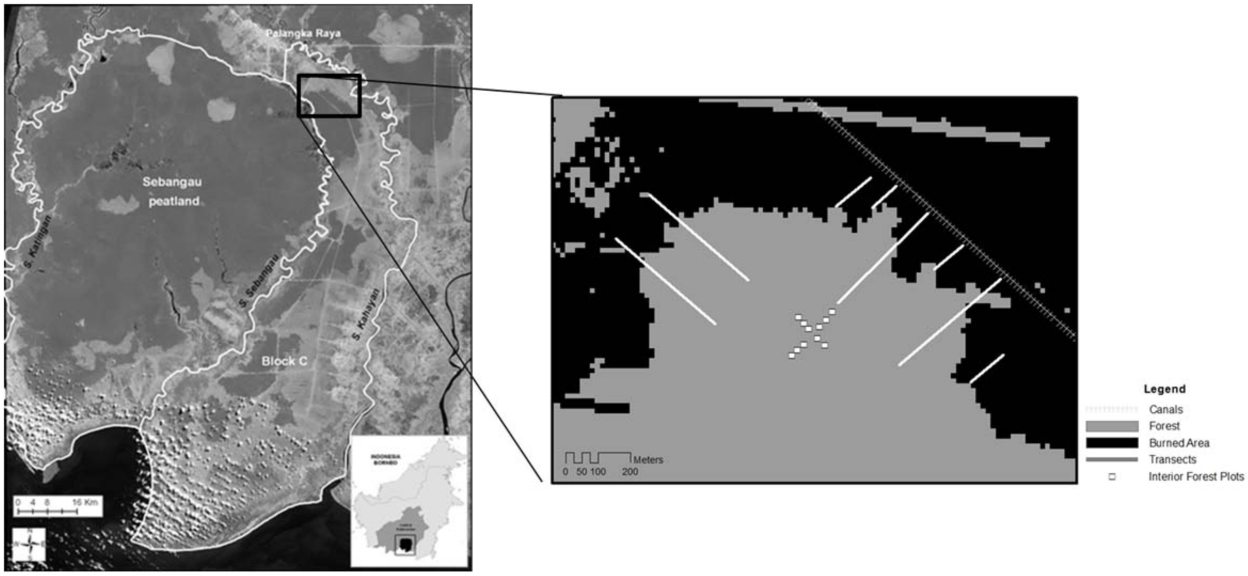


Figure 2.

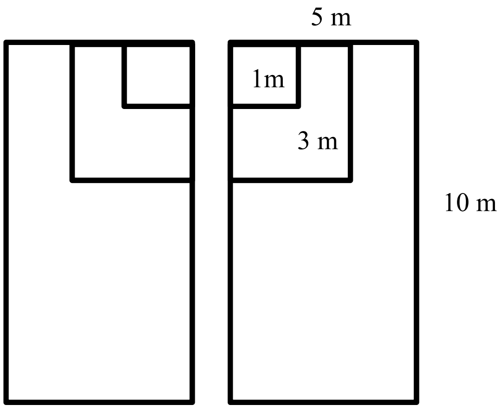
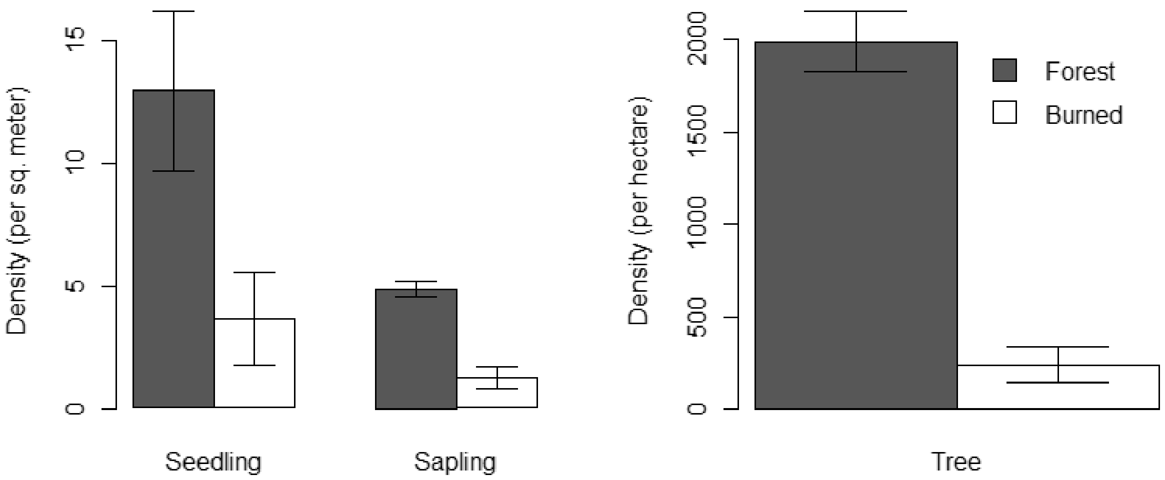


Figure 3.



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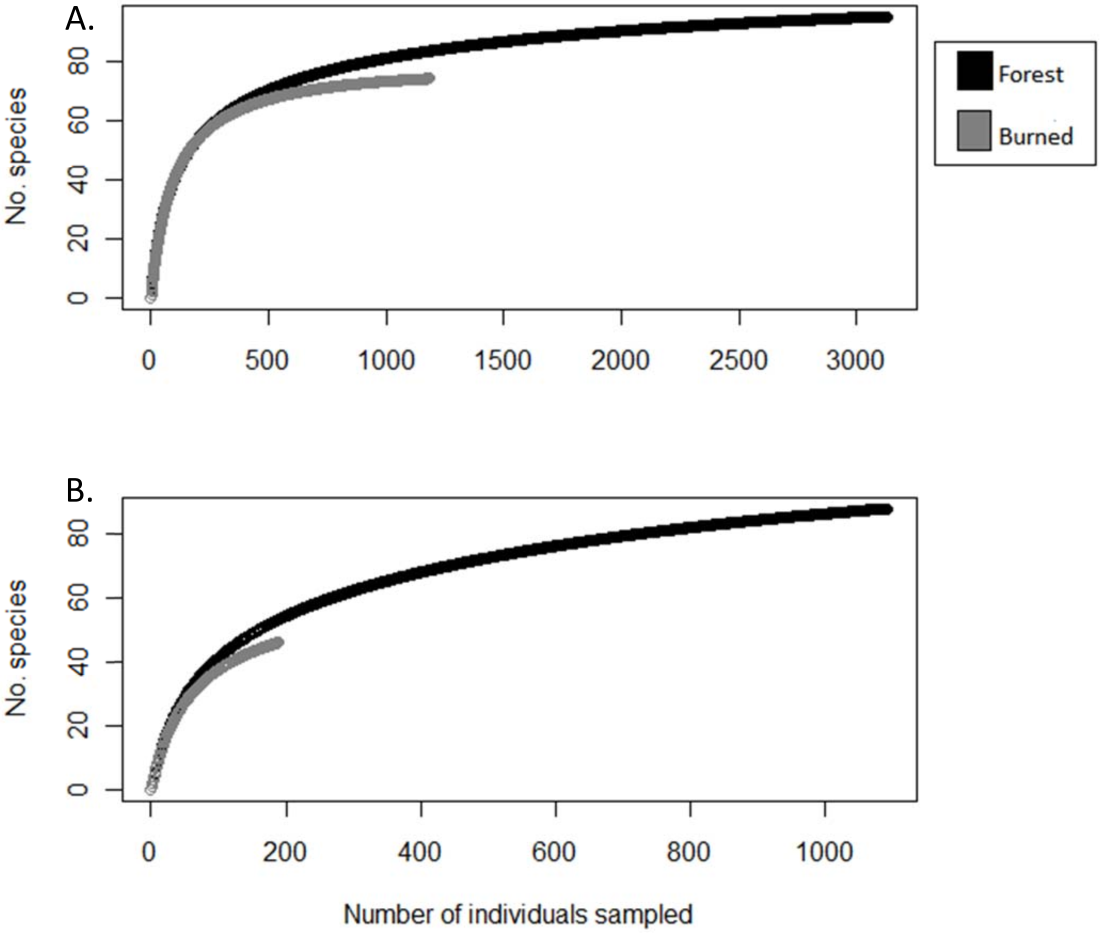


Figure 5.

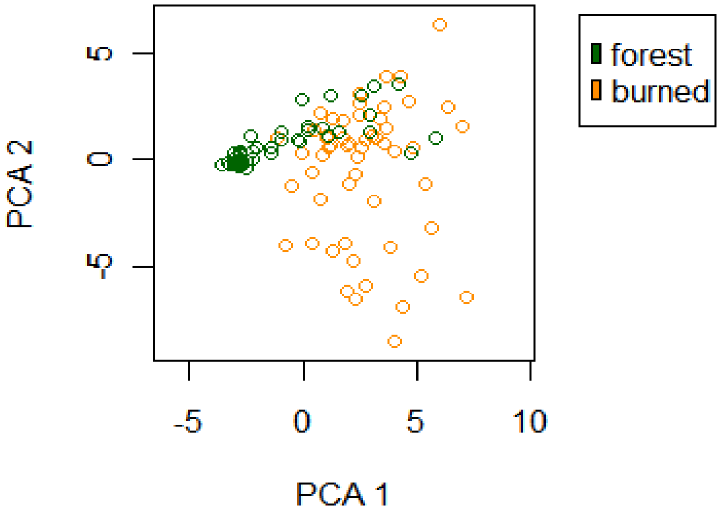


Figure 6.

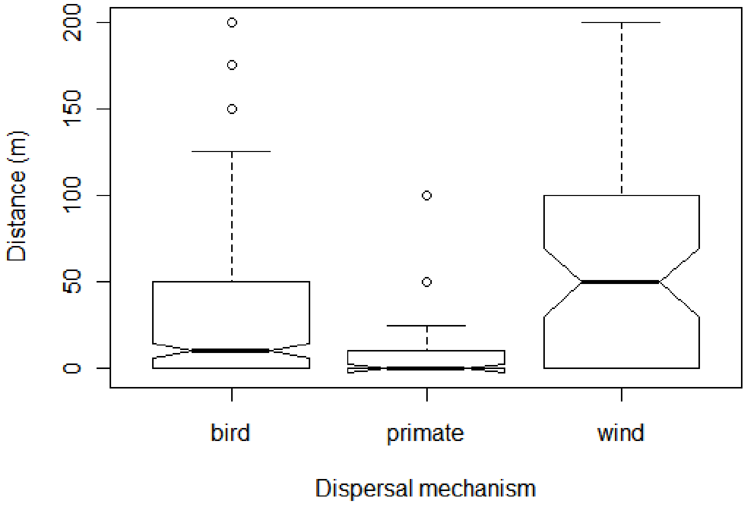


Figure 7.

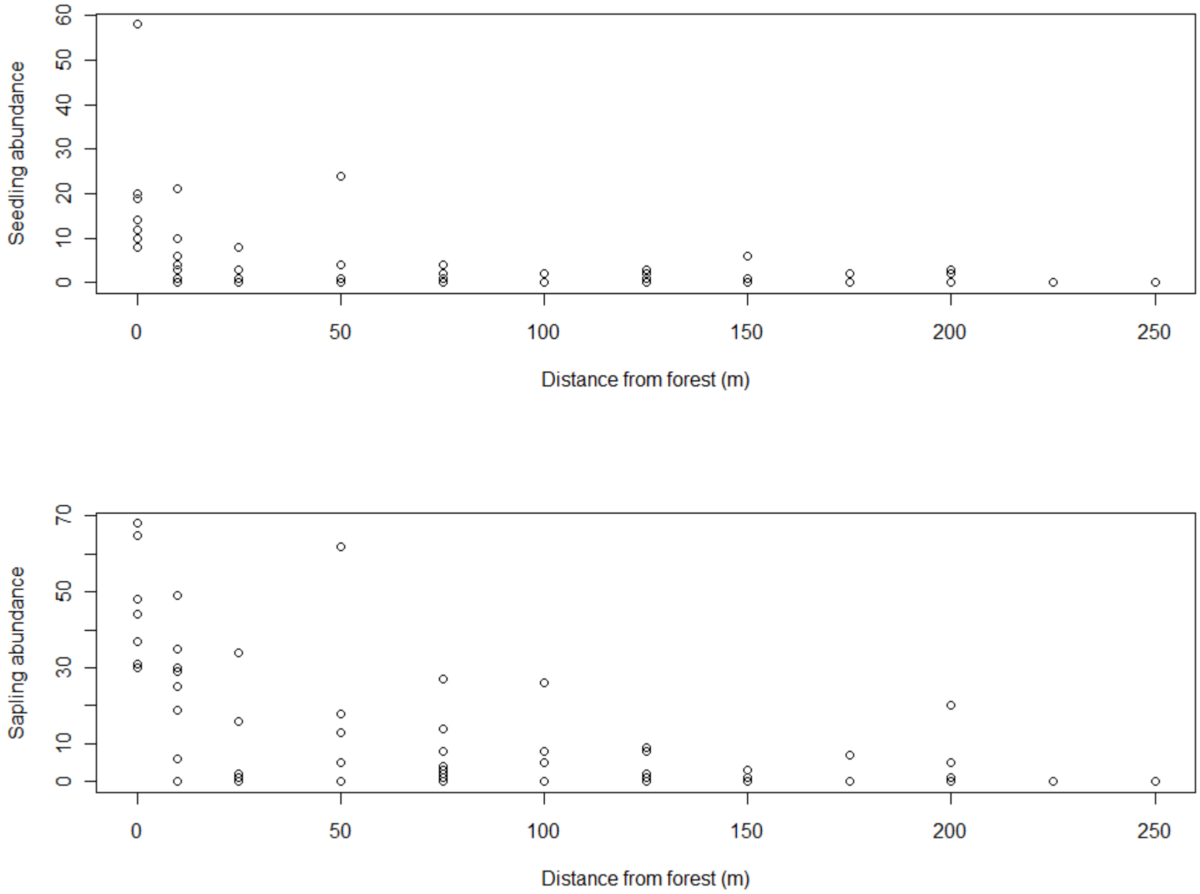
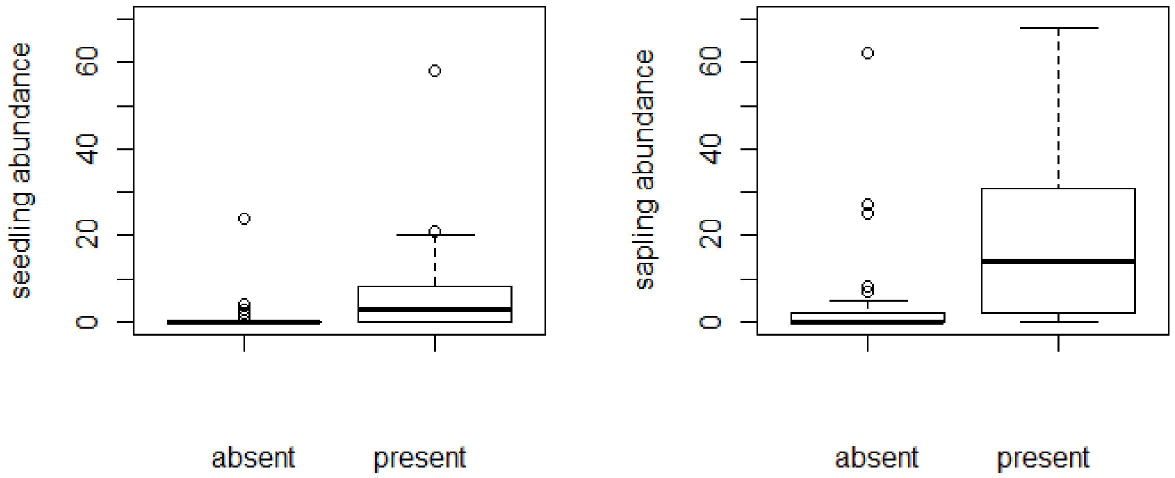

Seedling abundance
0
10
20
30
40
50
60
0
50
100
150
200
250
Distance from forest (m)
Sapling abundance
0
10
30
50
70
0
50
100
150
200
250
Distance from forest (m)

Figure 8.


seedling abundance
0
20
40
60
absent
present
sapling abundance
0
20
40
60
absent
present

Appendix

Scientific name, author, and local name for all tree species observed in this study, organized by family. Species were identified to local name in the field and then matched with a guide compiled by OuTrop.

Family	Latin name	Author	Local Name
Anacardiaceae	*Camnosperma auriculatum*	(Blume) Hook.f.	hantangan, tarantong putih
	Campnosperma coriaceum	(Jack) Hallier f.	tarontang
	Campnosperma squamatum	Ridl.	teres nyating
Anisophyllaceae	*Combretocarpus rotundatus*	(Miq.) Danser	tumih
Annonaceae	*Cyathocalyx biovulatus*	Boerl.	kerandau biasa
	Mezzettia parviflora	Becc.	pisang pisang besar, keripak
	Mezzettia umbellata	Becc.	pisang pisang kecil
	Polyalthia glauca	(Hassk.) Boerl.	kayu bulan
	Xylopia cf. malayana	Hook.f. and Thomson	tagula, jangkang hijau
	Xylopia coriifolia	Ridl.	nonang
	Xylopia fusca	Maingay ex Hook.f. & Thomson	jankang kuning, rahanhang
Apocynaceae	*Alstonia pneumatophora*	Baker ex Den Berger	pulai
	Dyera costulata	(Miq.) Hook.f.	jelutong
Aquifoliaceae	*Ilex cymosa*	Blume	kambasira
	Ilex hypoglauca	Loes.	sumpun
Burseraceae	*Canarium* sp., *Santiria* sp.		geronggang putih
	Santiria cf. laevigata	Blume	irat, kayu sepat
	Santiria griffithi	Engl.	teres bamban
Chrysobalanaceae	*Licania splendens*	(Korth.) Prance	bintan
Clusiaceae	*Calophyllum cf. lanigerum*	Miq.	mahadingan
	Calophyllum hosei	Ridl.	bintangor, jinjit
	Calophyllum sclerophyllum	Vesque	kapurnaga jangkar
	Calophyllum soulattri	Burm.f.	takal
	Garcinia bancana	Miq.	manggis, gantalan
	Garcinia sp.		aci
	Mesua sp.		tabaras, pasir pasir
Crypteroniaceae	*Dactylocladus stenostachys*	Oliv.	madang, mertibu II
Dipterocarpaceae	*Dipterocarpus borneensis*	Slooten	meranti keruing
	Shorea balangeran	Burck	balangeran, kahui

Dipterocarpaceae (cont.)	*Shorea* spp.		meranti, meranti kahui
	Shorea teysmanniana	Dyer ex. Brandis	meranti bitik/semut
	Shorea uliginosa	Foxw.	meranti batu
	Vatica mangachopai	Bianco	rasak napu
	Vatica rassak	Blume	rasak
Ebenaceae	*Diospyros bantamensis*	Koord. & Valeton ex Bakh.	malam malam
	Diospyros cf. evena	Bakh.	gulung haduk, lamijo
	Diospyros confertiflora	(Hiern) Bakh.	latuk manuk, arang
	Diospyros siamang	Bakh.	ehang, malam malam kuning
	Diospyros sp.		kayu arang
Elaeocarpaceae	*Elaeocarpus acmocarpus*	Stapf ex Weibel	patanak daun besar
	Elaeocarpus marginatus	Stapf ex Weibel	keijinjing
	Elaeocarpus mastersii	King	mangkinang
	Elaeocarpus sp.[a]		berang
	Elaeocarpus sp.		mankinang daun besar
Euphorbiaceae	*Antidesma coriaceum*	Tul.	buadawat
	Antidesma phanerophlebium	Merr.	matan undang, dawat
	Baccaurea bracteata	Müll. Arg.	rambai hutan
	Baccaurea stipulata	J.J. Sm.	kayu tulang, kopi kopi merah
	Blumeodendron elateriospermum	J.J. Sm.	kenari
	Cephalomappa sp.		kerandau
	Glochidion cf. glomerulatum	(Miq.) Boerl.	buah bintang
	Neoscortechinia kingii	(Hook.f.) Pax & K.Hoffm.	pupu palanduk
Fabaceae	*Koompassia malaccensis*	Benth.	kempas
Fagaceae	*Lithocarpus conocarpus*	(Oudem.) Rehder	pampaning bayang
	Lithocarpus rassa	(Miq.) Rehder	pampaning
	Lithocarpus sp. *cf. dasytachys*	(Miq.) Rehder	pampaning bitik
Hypericaceae	*Cratoxylum arborescens*	(Vahl) Blume	geronggang
Icacinaceae	*Stemonurus cf. scorpoides*	Becc.	tabaras akar tinggi
Lauraceae	*Alseodaphne coriacea*	Kosterm.	gemur
	Litsea sp. *cf. rufo-fusca,*	Kosterm.	tampang
	Litsea sp.		medang
Lauraceae (cont.)	*Litsea* sp. *cf. resinosa*	Blume	medang marakuwung

	Phoebe cf. grandis	(Nees) Merr.	tabitik
Lecythidaceae	*Barringtonia longisepala*	Payens	potot, katunay
Leguminoseae	*Adenanthera pavonina*	L.	tapanggang
Meliaceae	*Aglaia rubiginosa*	(Hiern) Pannell	kajalaki
	Sandoricum beccanarium	Baill.	papong
Moraceae	*Ficus spp.*		ficus
	Parartocarpus venenosus	(Zoll. And Mor.) Becc.	lilin lilin, tapakan
Myristicaceae	*Gymnacranthera farquhariania*	(Hook.f. & Thomson) Warb.	mendarahan daun kecil
	Horsfieldia crassifolia	(Hook.f. & Thomson) Warb.	mendarahan daun besar
	Knema intermedia	Warb.	kerandau merah
	Myristica lowiana	King	mendarahan hitam
Myrsinaceae	*Ardisia cf. sanguinolenta*	Blume	kalanduyung himba
	Ardisia sp.		kamba sulan
	Rapanea borneensis	(Scherr.) Mez	mertibu
Myrtaceae	*Eugenia spicata*	Lam.	kayu lalas
	Syzygium havilandii	(Merr.) Merr. & L.M. Perry	tatumbu
	Syzygium sp. *cf. spicata*	Lam.	galam ticus, kayu lalas daun kecil
	Syzygium sp. *cf. campanulatum*	Korth.	tampohot
	Syzygium sp. *cf. lineatum*	(DC.) Merr. & L.M. Perry	jambu jambu
	Syzygium spp.		jambu burung
	Syzygium spp.		jambu burung kecil
	Syzygium valevenosum	(Duthie) Merr. & L.M. Perry	kayu lalas daun besar
	Tristaniopsis obovata, whiteana	(Griff.) Peter G. Wilson & J.T. Waterh.	blawan
	Tristaniopsis sp. *cf. merguensis*	(Griff.) Peter G. Wilson & J.T. Waterh.	blawan putih
	Tristaniopsis sp.		blawan punai
Polygalaceae	*Xanthophyllum ellipticum*	Korth. ex Miq.	kemuning
Rhizophoreaceae	*Carallia brachiata*	(Lour.) Merr.	gandis
Rubiaceae	*Ixora havilandii*	Ridl.	keranji
Rutaceae	*Tetractomia tetrandra*	(Roxb.) Merr.	rambangun
Sapindaceae	*Nephelium lappaceum*	L.	rambutan, manamun
	Nephelium maingayi	Hiern	kelemun buhis
Sapotaceae	*Isonondra lanceolata*	Wight	nyatoh palanduk
	Madhuca cf. pierrei	(F.N. Williams) H.J. Lam	nytaoh undus

	Madhuca motleyana	(de Vriese) J.F. Macbr.	katiau
	Palaquium ridleyi	King & Gamble	nyatoh burung
	Palaquium cochlearifolium	P. Royen	nyatoh gagas
Sapotaceae (cont.)	*Palaquium leiocarpum*	Boerl.	hangkang
	Palaquium pseudorostratum	H.J. Lam	nyatoh babi
Sterculiae	*Sterculia rhoiidfolia*	Stapf ex Ridl.	loting
	Sterculia sp.		pendu
	Sterculia sp.		muara bungkang
Tetrameristaceae	*Tetramerista glabra*	Miq.	ponak
Theaceae	*Ploiarium alternifolium*	(Vahl) Melch.	asam asam
	Ternstroemia magnifica	Stapf ex Ridl.	tabunter
Thymeleaeaceae	*Gonystylus bancanus*	(Miq.) Kurz	ramin
Unknown	Unknown		kayu sutra, tagusari
	Unknown		lombok lombok
	Unknown		prupuk galaga
	Unknown		hambitik
	Unknown		kerandau putih

[a] This species is a "known unknown," in that has been analyzed by local botanical experts who identify it by the common name, but to their knowledge it has not yet been formally named.