# Scale- and trait dependent responses of bird communities to lowland rainforest restoration and frugivore bird-seed interaction networks in Sumatra, Indonesia

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# Chapter 1

# GENERAL INTRODUCTION

## IMPORTANCE OF TROPICAL LOWLAND SECONDARY FOREST

Tropical forests cover only 10% of the global land surface but support 50-60% of the world's species (Dirzo and Raven 2003). This high biodiversity habitat is vastly disappearing, particularly in Southeast Asia where it had been predicted to lose three quarters of its original forests by 2100 and up to 42% of its biodiversity due to deforestation (Sodhi et al. 2004). If continued unabatedly, Southeast Asia will lose not only most of the tropical forest but will also suffer from massive species declines and extinctions (Laurance 1999, Achard et al. 2002, Brook et al. 2003). Indonesia holds 2.3% of the global forest cover and 39% of Southeast Asia forests (Achard et al. 2002). It also houses two biodiversity hotspots, Sundaland and Wallacea (Myers et al. 2000). Unfortunately, this is also the region with the highest deforestation rate in the world (Margono et al. 2011, Hansen et al. 2013).

Looking at the landscape scale, tropical forest landscapes are currently dominated by modified and degraded forest. Deforestation is concentrated in the more accessible lowlands (Collins et al. 1991), hence Southeast Asian lowland faunas are under extreme threat (Brooks et al. 1999). For example in Sumatra Island, one of the biggest islands of Indonesia, a recent study revealed that between 1990 to 2010, 70% of the forest had been cleared and left 23.1 thousand km$^2$ of primary forest in degraded condition (Margono et al. 2012). This degraded forest is mostly located in the lowland areas, and the protected area network in Sumatra does not appropriately cover the tropical lowland forest (Gaveau et al. 2009). Since lowland tropical forest is misrepresented in the existing protected area network, and most of the lowland forests are in degraded condition, avoiding further degradation and/or conversion of degraded tropical secondary forest into other land-use should be avoided.

Degraded tropical forest can still support relatively good primary forest biodiversity, hence worth protecting. Tropical forest biota is vulnerable to forest disturbance (e.g. Peh et al. 2005, Barlow et al. 2007) but degraded forest can still support a proportion of the primary forest biota (e.g. Mitra and Sheldon 1993, Warkentin et al. 1995, Sodhi et al. 2005). Recent studies had strengthened the idea of protecting degraded forest for biodiversity conservation. Studies in Kalimantan shown that more than 75 % of bird and dung beetle species found in unlogged forest persisted within twice-logged forest, and globally threatened bird species did not decline further after second logging rotations (Edwards et al. 2011).

Due to the paucity of primary tropical forest and the contribution of degraded forest to maintaining primary forest biodiversity, protecting degraded forest from further degradation becomes increasingly important for conserving tropical biodiversity. For Indonesia, the opportunity to save degraded tropical forest arose in 2004, when the Indonesia Ministry of Forestry issued a new type of forestry license for production forests – namely a license for ecosystem restoration. This license has been granted for up to 95 years and requires the holder to protect and restore the forest ecosystem. As logging is forbidden, the holder is required to find income from alternative sources. This provides new hope for degraded forest, whereas most degraded forest tends to be converted into oil palm plantations (Fitzherbert et al. 2008). This opportunity for forest to “recover” rises new challenges for sustainable management (e.g. by extending the cutting cycle and reducing the logging effect on residual stands, Sianturi and Kanninen 2006).

Forest restoration is the re-establishment of the original ecosystem that has been degraded, damaged and or destroyed (Forest Restoration Research Unit 2008). This involves various forest restoration activities that are determined by three correlated components: existing biodiversity and ecosystem services, time and resources availability, and the state of degradation (Chazdon 2008). Better understanding of the state of degradation will have to come first before deciding which restoration activities can be implemented. For example, as depicted in Figure 1.1, secondary forest with low level of degradation and still high biodiversity is suitable for implementing natural forest regeneration. Unfortunately, most if not all degraded tropical forest will still require human assistance to recover (Chazdon 2003). In short, in addition to the protection from further degradation, active measures to assist the recovery of secondary forest are also required.

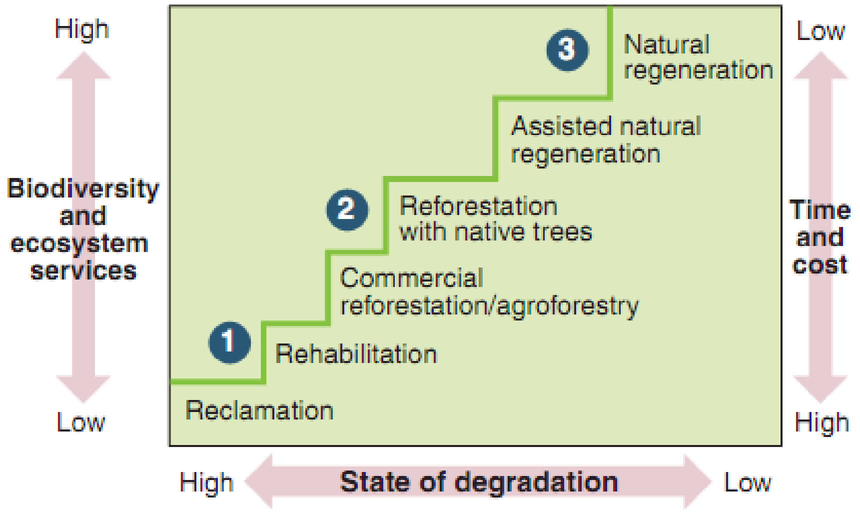


Figure 1.1. The restoration staircase (Chazdon 2008). The restoration activity implemented will depend on three correlated factors: existing biodiversity and ecosystem services, time and resources availability, and the state of degradation, with three possible outcomes: (1) restoring soil fertility, (2) production of timber and non-timber products, and (3) recovery of biodiversity and ecosystem services.

## BIRDS AND SELECTIVE LOGGING

As mentioned above, for forest restoration one needs to understand the current condition of the degraded forest before deciding on actions to be implemented. As the recovery process will take long time, wrong approaches can eventually lead to disastrous effects on biodiversity. However, despite the increasingly proportion of secondary forest in the tropical forest landscape, particularly in Indonesia, our understanding about this system is still limited.

Birds are perhaps the best studied organism group in relation to logging due to:

a. their well-established taxonomy and capacity to be identified in the field

b. the availability of biological and ecological information on most bird families and many species

c. their apparent sensitivity to specific changes in forest structure, microclimate and composition, and

d. their ecological role (e.g. pollination, seed dispersal, and seed predation; Fimbel et al 2001, Whelan et al. 2008).

We have good knowledge which species or species groups are negatively or positively affected by logging, through comparing the bird communities between logged and unlogged forest. The results from these studies can be summarized as follows:

1. Along with other biota, a meta-analysis by Sodhi et al. (2009) on the impacts of tropical deforestation and forest degradation in Southeast Asia on vascular plants, invertebrates, birds, and mammals revealed that species richness is 28.6% higher in pristine forest;
2. More specific for birds, a recent meta-analysis on bird responses to land-use intensity confirmed this pattern where the probability of bird species occurrence was 7.8% lower in low intensity (such as selective logging) than undisturbed habitat, and long-lived, large, non-migratory, primarily frugivorous or insectivorous forest specialists were both less likely to occur and less abundant in more intensively used habitats (Newbold et al. 2013);
3. Examining feeding guilds, abundance of granivores significantly increased

while insectivores and frugivores decreased (Gray et al. 2007);

4. Logging had the strongest negative effect on terrestrial insectivores and canopy bark-gleaning insectivores while moderately affecting canopy foliage-gleaning insectivores and frugivores, raptors, and large species in general (Cleary et al. 2007)
5. At least 25 Sundaic lowland forest birds had been identified as negatively affected by logging (Lambert and Collar 2002).

Considering that selectively logged forest tends to contain mosaic patches of secondary forest at different regenerating stages (Putz et al. 2001), habitat changes after logging were also measured but not correlated to changes in bird communities. This is why we cannot tell which habitat variables initiated negative or positive responses by birds (but *see* Cleary et al. 2005), so our understanding of how species or species groups are distributed in the forest regeneration mosaic is limited.

The information how species distribute in the secondary forest is useful for reliably predicting how they might respond to forest restoration activities. Although not directly aimed at the recovery of bird species, we can learn from limited studies that looked at the impact of forest management on biota (including birds). For example in Kalimantan, Ansell et al. (2011) found that liberation cutting in logged forest causes decline in all birds and frugivores. The Buff-rumped Woodpecker *Meiglyptes tristis* was less common in the logged forest of Peninsular Malaysia due to the logging scheme in Malaysia, where large non-commercial trees, lianas and snags were removed (Styring and Ickes 2001).

With the rapid disappearing of tropical lowland forest, we are also still lacking quantitative information on bird density estimates for many of Sundaic-lowland forest birds. This information is important as it can be used to evaluate the global population estimate for decisions on the global status of threatened birds (IUCN 2012).

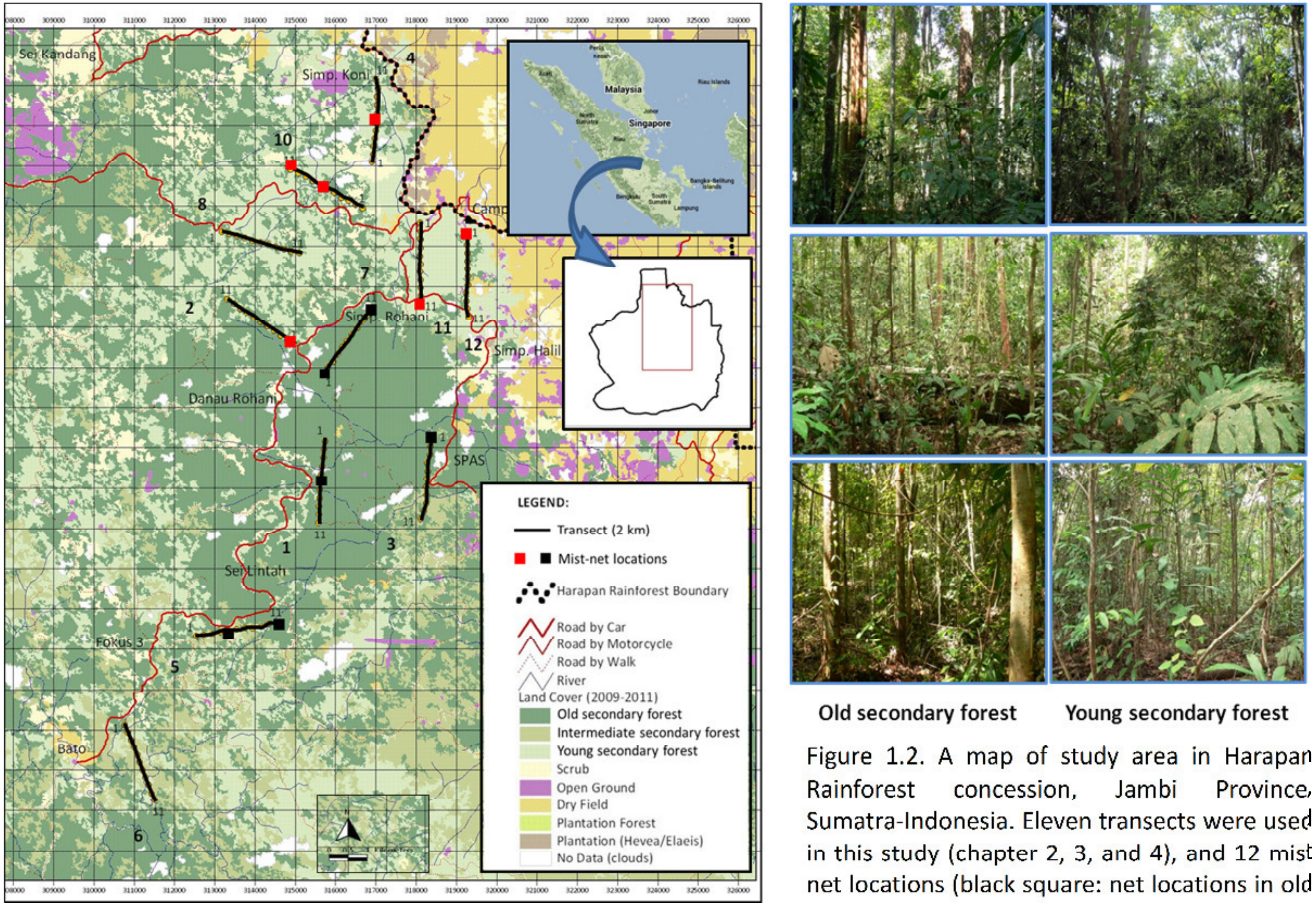
In addition, as bird seed dispersal plays an important role in forest regeneration (Wunderle Jr. 1997, Corlett and Hau 2000, Corlett 2002, Stiles 2000, Holl et al. 2000, Whelan et al. 2008) and maintenance of plant diversity in tropical forest (e.g. Terborgh et al. 2002), understanding this service in the secondary forest, e.g. by knowing what bird species dispersed which seed species, could certainly assist in the restoration activities (e.g. weed management, Chazdon 2008). Again, our understanding on this service is still limited, particularly in secondary lowland tropical forest of Southeast Asia.

## STUDY REGION AND SITES

The field works were conducted in the Harapan Rainforest (HRF, http://www.harapanrainforest.org). The HRF covers an area of 985.54 km$^2$, located in the Jambi and South Sumatra Provinces. It is the first ecosystem restoration project in a production forest in Indonesia. The whole area has been logged; hence the current habitat consists of mosaics of approximately 40% old secondary forest, 25% intermediate secondary forest, 25% young secondary forest (Figure 1.2). The remaining 10% comprises scrubs and open ground.

The Harapan Rainforest gained the concession right for the southern concession block (South Sumatra Province) in 28 August 2007, and the northern forest block (Jambi Province) in 25 May 2010. The Harapan Rainforest consists of two ex-logging concessions: PT. INHUTANI V in the southern part of the Harapan Rainforest (South Sumatra Province) and PT. Asialog in the northern part of the Harapan Rainforest (Jambi Province). The main target species logged during the logging concession time were tree species from Dipterocapaceae (most species within this family have wind dispersed seeds). The rapid vegetation survey conducted in Harapan Rainforest (Partomihardjo et al. 2004) showed that perhaps most of the forest area is dominated by pioneer species such as *Macaranga* spp. (Euphorbiaceae), except for some parts of the area that have been secured in the past (during the logging period) as source of genetic diversity. Similar results were found by Muslich (2010), with each secondary forest type having a different tree community. He also found that the young and intermediate secondary forest had lower commercial tree species composition (i.e. tree species from the Dipterocarpaceae).

The field study was conducted nine months spread over two years (2011-2012). We used the point transect method to collect bird and habitat variable data (Chapter 2, 3 and 4). Eleven transects were used, each was 2 km long and within each transect we had 11 points (each 200 meter apart). These transects were selected to cover mosaic habitat patches, particularly contrasting patches (i.e. old and young secondary forest). Bird and habitat data were collected at each of this point. Specifically for bird data, each transect was surveyed three times. A mist-net survey method was used to collect bird fecal samples in 12 locations: six locations in old and six in young secondary forest (Figure 1.2, Chapter 5). Each net location was at least 1 km apart.



**Old secondary forest** **Young secondary forest**

Figure 1.2. A map of study area in Harapan Rainforest concession, Jambi Province, Sumatra-Indonesia. Eleven transects were used in this study (chapter 2, 3, and 4), and 12 mist net locations (black square: net locations in old secondary forest, red square: net locations in young secondary forest, chapter 5)

## CHAPTER OUTLINE

The current work focused on bird communities and seed dispersal in the tropical secondary forest. The objectives were to provide understanding on how bird communities use secondary forest and how this use can be enhanced to assist the recovery of negatively affected species or species groups as well as the structure and composition of seed dispersal networks.

**Habitat-scale effects on birds.** The responses of bird species richness to forest structure on multiple spatial scales were analyzed, distinguishing between groups of species differing in habitat preference, body size and feeding guild. Specifically, we expected that different groups respond to different habitat scale-variables. Some groups should be affected by habitat availability at larger spatial scales, while others respond to habitat quality at a smaller scale (Chapter 2).

**Quantitative assessment of birds in lowland secondary forest.** We calculated density estimates for birds in our study area with the aim to (1) provide baseline estimates of bird densities in secondary forest and (2) to compare the derived bird density estimates to those from other studies conducted in Southeast Asia (Chapter 3). Subsequently, we also compared density estimates in our study area between two different habitat types (old vs young secondary forest). We expected that the preference for old versus young secondary forest (or vice versa) would reflect the aversion or affinity for logged forests (Chapter 4).

**Frugivore bird-seed interaction networks**. We focused on identifying plant-species interactions through examining bird fecal samples from frugivore birds capture using mist-nets, with a focus on identifying bird species that are responsible for dispersing different plant species (Figure 1.3, Chapter 5). We compared bird fecal samples between old and young secondary forests.

Figure 1.3. Collecting bird fecal samples and identifying seed species. Mist-net was used to capture birds (A), and kept in paper bag until they defecated (B) and ringed before released (C). Fecal samples collected (D) were examined for presence of seeds, and all seeds were identified up to the lowest taxonomy level. Interaction frequency (i.e. the number of fecal samples from each individual bird containing at least one intact seed of each plant species) between bird and seed species was then use to develop interaction network (E).

## RESULTS AND CONCLUSIONS

Chapter 2 addresses the responses of bird species richness, to forest structure on multiple spatial scales, distinguishing between groups of species differing in habitat preference, body size and feeding guild. From this study we established an understanding that different species richness groups responded to different sets of variable, which reflected their respective ecological traits. Moreover, most of the bird species groups were affected by understory related variables (particularly benefitting from rattan density in the understory). We highlighted the importance of reducing habitat structure variability between matrix and local forest patches to assist recovery of species from different functional groups. The information from this study can be used not only to predict how different groups respond to forest management but also for recommending potential restoration treatments assisting the recovery of species after logging.

Chapter 3 focuses on bird density estimates as an important basis for conservation management. There is limited information available on density estimates for most of the Southeast Asia lowland forest birds. In this chapter we presented density estimates for 102 lowland bird species (45% of Sumatran lowland forest birds) including 41 species with global conservation concern. Comparing densities from our study with densities from logged forest in Borneo revealed three species that had significant higher density and four had lower density in our study area. There appears to be variation in density estimates across different locations, which might reflect differences in habitat condition and anthropogenic pressure at each location. This variation highlights the importance of site specific density estimates as baseline for measuring success in forest restoration activities. Bird density estimates are important to establish population baselines, allowing comparisons between studies. Due to paucity of information, we urge more studies to be conducted to provide better understanding of variation of bird density over time and space, particularly in Southeast Asia.

In chapter 4 we present a comparison of bird density between two contrasting secondary forest types, old and young secondary forest. Up to now, such comparisons are still limited, particularly in global biodiversity hotspots such as the Indonesian Sundaic region. We expected that species that declined in logged forest would also have lower density in early secondary forest (and vice versa). This pattern was true for several species, but not for all species. We found that 10 species had significantly higher densities in old secondary forest, and nine species in young secondary forest, while 14 species showed no difference between the two habitat types. Mosaic patches of degraded and unlogged forest patches, a typical condition of selectively logged forest, might provide suitable habitat for species that have been found to respond negatively to logging. More studies are required to produce quantitative density estimates from different habitat types and disturbance levels as well as long term studies to establish understanding on species persistence in the secondary forest.

Chapter 5 focuses on understanding structure and composition of seed dispersal network by examining frugivore bird fecal samples in old and young secondary forests. In general, we found that frugivore bird-seed interaction networks in the study area were dominated by generalist dispersers with 16 bird species were found to having $\geq$ 2 seed species in their fecal samples. Frugivore bird-seed interaction networks were similar at network level between old and young secondary forest. However, there were differences in each species' importance in each secondary forest types. Bird density was positively related to the number of interactions and the number of seed species found in fecal samples. In conclusion, we provide here evidence for the important role of common birds (such as the bulbul species, Figure 1.4) as seed dispersers and vice versa, the importance of small fleshy multi-seed fruit species (and several weed species) for frugivore birds. However, we still need a better understanding of the relative role of bird and plant species and their spatio-temporal variation to reliably characterize bird-seed interaction networks and to improve management practices in rainforest restoration projects.

Grey-cheeked Bulbul *Alophoixus bres*

Yellow-bellied Bulbul *Alophoixus phaeocephalus*

Buff-vented Bulbul *Iole olivacea*

Streaked Bulbul *Ixos malaccensis*

Black-headed Bulbul *Pycnonotus atriceps*

Red-eyed Bulbul *Pycnonotus brunneus*

Grey-bellied Bulbul *Pycnonotus cyaniventris*

Spectacled Bulbul *Pycnonotus erythropthalmos*

Cream-vented Bulbul *Pycnonotus simplex*

Hairy-backed Bulbul *Tricholestes criniger*

Figure 1.4. Bulbul species captured during the mist-net surveys. These species contributed > 80% of frugivore-seed interactions in the study area.

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# Chapter 2

# Scale-and trait-dependent responses of bird communities to lowland rainforest structure in an Indonesian forest restoration project

Dark-necked Tailorbird *Orthotomus atrogularis* an abundant species in logged forest.

## ABSTRACT

Tropical secondary forests are increasingly viewed as valuable habitats that are worth to be protected and rehabilitated for biodiversity conservation. Logging has mostly negative effects on bird communities, but the role of the often heterogenous forest structure in already logged forest is little explored, despite its importance in informing forest restoration practices. We examined the responses of bird species richness, to forest structure on multiple spatial scales, comparing groups of species differing in habitat preference, body mass and diet. In the Harapan Rainforest Ecosystem Restoration concession in Jambi Province, Sumatra (Indonesia), we conducted point transects survey (11 transects, each 2 km long, 11 points per-transect, each 200 m apart, each transect was surveyed three times) between April and June 2011 to gather bird and habitat data. We analyzed multi-scale habitat effects on bird species richness grouped by body mass, habitat preference, and feeding guild. We found that each group of species exhibits an own response to forest disturbance depending on their habitat requirement, foraging behavior, diet preferences, or sensitivity to microclimate conditions. Most of the bird species groups were positively related to understory characteristics (particularly rattan density in the understory). Interestingly, large bird species responded to forest structure at smaller spatial scales, presumably because of their high dispersal ability allowing them to use the best local resources. In contrast, small birds were sensitive to large scale (transect-level) forest structure, presumably because they depend on complementary resources outside local patches. We underscored the importance of variable at transect scale which showed that management of secondary forest should be directed towards increasing similarity in habitat structure between relatively good patches with the degraded matrix. Lastly, the importance in understanding avian habitat preference not only to predict responses of birds to restoration treatments but also to indicate potential treatments in assisting the recovery of species after logging.

**Keywords:** habitat structure, secondary forest, foraging guild, selectively logged, avian preference, applied nucleation, strip planting

## INTRODUCTION

Tropical secondary forests, especially those resulting from selective logging, are worth to be protected from further degradation and conversion to other land use types. One important reason is because these forests can still support relatively good primary forest biodiversity (e.g. Sodhi et al. 2005, Sekercioglu et al. 2007, Edwards et al. 2009, Putz et al. 2012, Wilcove et al. 2013). In addition, the continuing deforestation of near-primary tropical forest, particularly in Southeast Asia lowland forest, (Sodhi and Brook 2006, Sodhi et al. 2010, Margono et al. 2012, Wilcove et al. 2013), increased the conservation value of even repeatedly logged forest (Edwards et al. 2010).

Despite increasing proportions of secondary forests in tropical forest landscapes, little is known on how animals use them and how its habitat suitability can be increased. Birds are perhaps the best studied organism group in terms of responses to logging (Lambert 1992, Johns 1996, Marsden 1998, Styring and Hussin, 2004, Peh et al. 2005, Cleary et al. 2007, Sodhi et al. 2008, Mead 2008). Results from these studies reveal which species or species groups are affected by logging. However, despite habitat structure after logging was quantified this has been rarely correlated with changes in bird communities (but see Cleary et al. 2005, Mead 2008). It is thus little known which habitat changes cause the positive or negative responses of species or species groups to logging.

Birds are generally sensitive to changes in vegetation structure (Cody 1985, Brawn et al. 2001, Guenette and Villard 2005**,** Lampila et al. 2005), such as plant heights and spatial arrangements, and to differences in plant species composition. Comprehensive knowledge of the habitat structures can explain increases or decreases of bird populations and is important in deciding appropriate forest restoration activities to assist the recovery of birds in secondary forest. For example, Reid et al. (2012) suggested that increasing canopy cover, as a result of tree planting, is related to an increase of bark-gleaning insectivore richness. However, impacts of forest restoration activities turn out only many years after their implementation (Chazdon 2008). For example, Ansell et al. (2011) assessed the impact of enrichment planting and liberation cutting on birds approximately 15 years after the treatment. They show that forest rehabilitation has no effect on species declined after logging. The knowledge of avian habitat preference is becoming more important for site specific management as selectively logged forests are often heterogeneous in structure and composition, e.g. due to differences in logging intensity and number of tree harvests (Putz et al. 2001, Cleary et al. 2005). Moreover, incorporating different spatial scales is important to understand effect of habitat disturbance on biodiversity (Hill and Hamer 2004). Particularly, as suggested by Prevedello and Vieira (2010), future studies should assess how different species respond to the same matrix type.

To tease out which components of habitat structure, measured at different spatial scales, are related to specific functional groups in the selectively logged forest, we cencused birds and measured vegetation structures in 11 transects spread over a mosaic of secondary forest in different regenerating stages. We grouped bird species based on their body mass, feeding type, and habitat preference. These traits are used as proxy for their ecological functioning (Tscharntke et al. 2008). Bird response to land-use intensity has been shown to depend on their traits (Newbold et al. 2013) and different species groups use habitats at different spatial scales (Tews et al. 2004). We expect that different groups respond to different habitat scale-variables and some groups are affected by habitat at larger spatial scales, while others respond to habitat quality at a smaller scale.

This study was conducted in the first ecosystem restoration project in Indonesia (http://www.harapanrainforest.org), the Harapan Rainforest Ecosystem Restoration Concession (HRF). Commercial logging was ceased in 2008. The concession covers 984.55 km$^2$ of tropical dry lowland Sundaic forest in Sumatra, Indonesia. Previous logging activities have left a mosaic of secondary forest habitats in different stages of regeneration (Lee and Lindsell 2011), which is typical for ex-logged forest (Putz et al. 2001). The HRF covers approximately 20% of the last Sundaic forest on Sumatra's dry lowlands. Dry lowland forest is the most important habitat for many lowland bird species in the Sundaic region (Lambert and Collar 2002).

## METHODS

*Study area and sampling.* Our study site is part of Harapan Rainforest concession in Jambi Province, Sumatra, Indonesia (camp coordinate: 103$^0$22.39'E, 2$^0$8.79'S)**.** Fieldwork was conducted from April to June 2011. Eleven transects (each transect was 2 km, and each was at least 1 km apart) were established across the mosaic secondary forest conditions. Within each transect, 11 data points were established (each point was 200 m apart). We collected bird and habitat structure data at each of these points.

*Avifauna.* Bird data were collected using a point-transect method. This method is a preferred method for surveying birds in dense forest habitats (Jones et al. 1995, Bibby et al. 2000, Lee and Marsden 2008). The 200 m distance between each point within a transect was selected as a compromise between travel time and independence of bird detections at consecutive points (Reynolds et al. 1980, Hutto et al. 1986). Surveys were conducted in the morning from 06:30 to 10:00 (10 minutes survey per-point), to coincide with the peak period of bird activity (Lee and Marsden 2008), performed by a single observer and one note taker. At each point, the survey was conducted immediately after the observer arrived (without settling down period). Any birds detected moving away from around the survey point on the observers' arrival were counted as being present during the count period. All birds observed/detected were recorded along with the estimated vertical height and horizontal distance from the survey point to the bird's initial position (estimated using a digital Rangefinder). Flying birds observed during the point count period were recorded but not used in the analysis. When present, crepuscular/nocturnal species (e.g. *Caprimulgus* spp.) and large raptors were recorded but not used in the analysis. Sound recordings were made at each point to aid species identification. Survey at each transect was conducted three times, usually during three consecutive days without rain or strong wind. When conditions were unsuitable the survey was delayed until the following day. We usually rotated the daily order in which points were visited. Repeating point transects in the opposite direction on different days helps to minimize the influence of changing bird activity and, hence, detection during a survey (Jones 1998). Sample size of scarce species can also be increased by repeating points (Buckland et al. 2001, Rosenstock et al. 2002).

*Habitat structure.* Habitat structure data were collected within a 25 m radius at each survey point for all 121 survey points, covering geographical and habitat structure variables. The circular sample-plot method (James and Shugart 1970) was used to collect vegetation data. At each point, the geographic variables collected were altitude and slope measured using Clinometer, and distance to water bodies. For the 10 nearest big trees (tree with diameter at breast height (DBH) > 20 cm and within 25 meter radius of the point) the following variables were measured: tree height, DBH, distance of each tree to the point center, and whether it is *Macaranga* spp. or not. *Macaranga* are common pioneer species in degraded forest, with higher proportions in young and medium secondary forest (Muslich 2010). Floristic data (e.g. plant species identity) were found to be important variables for the bird study (e.g. Lee and Marsden 2008). The number of dead standing trees (trees with DBH > 20 cm) within 25 radius was also counted. We divided each circular plot into four sections (i.e. quarters). Approximately in the middle of each quarter (within 10 m of the point center) four counts were taken for the following variables: canopy openness (using an array of 25 regularly spaced dots marked on a transparent Perspex sheet, 30cm x 30cm), understory openness (by counting the number of visible dots arranged evenly in an 8 x 8 configuration on a 1m x 1m plastic sheet (held by one observer at plot quarter) by an observer at the center of the point), estimate of ground layer cover (% cover by leaf). Understory vegetation density was estimated in each plot quarter using a 1 m radius circular plot (positioned 10 m from the plot point centre) where at each plot one observer stood holding a 1 meter stick perpendicularly at 1 m above the ground and turned 360° slowly on the spot while counting the number of stems < 5 cm DBH the stick touched. Each stem touched was then classified as a sapling, liana, palm, ginger, rattan or bamboo. All the geographical and structural variables were fully described in Appendix 2.1.

*Statistical analysis*. We used linear mixed-effects models (Pinheiro and Bates 2000, Venables and Ripley 2002) to determine what habitat variables correlate with richness of each bird functional group at which scale. In this analysis, only birds recorded within 50 meters of the point observation were used, and the three survey repetitions were pooled. We classified birds based on three criteria: body mass (derived from Dunning 2008), feeding guild (based on Lambert 1992, Lambert and Collar 2002, Styring et al. 2011) and preferred forest habitat (Styring et al. 2011). Based on body mass, bird species were classified into four classes: small species (weight < 20 g); medium species (20-69 g); medium-large (70-150 g); large (>150 g). Species were classified by habitat preference following Styring et al. (2011): forest specialists; edge tolerant forest specialists; edge specialists; open countryside species; generalists. Feeding guilds used in the analysis were: terrestrial insectivore; arboreal foliage gleaning insectivore; arboreal foliage gleaning insectivore understory specialist; bark gleaning insectivore; sallying substrate-gleaning insectivore; sallying insectivore; arboreal foliage-gleaning insectivore/frugivore; arboreal frugivore/predator; arboreal frugivore; miscellaneous insectivore/piscivore; nectarivore /insectivore/ frugivore; nectarivore/insectivore; terrestrial omnivore. In total we had 22 functional groups, and we used richness of each group as our response variables. Richness is defined as the total number of species per point observation for a particular functional group (e.g. sallying insectivore species richness, small size species richness, forest specialist species richness).

For the explanatory variables, we used 15 habitat variables (*see* Appendix 2.1 for detail) per spatial scale. The three different habitat scales were from small to large: point, sub-transect and transect scale. At the point scale all vegetation variables are measured at the point count level (within 25 meter radius). The sub-transect habitat scale is the average of the values of a particular variable at the neighboring points (points located 200 m from the particular point). For example, the tree height value for point 1 at sub-transect scale was derived from the value of tree height at point 2, while the tree height for point 2 at sub-transect scale was derived from the average tree height values from point 1 and 3, etc.  The transect habitat scale is the average value of the variables from 10 points. For example, tree height value for point 1 at transect scale would be the average value from 10 points except the value from point 1.

We standardized the explanatory variables, so that their effect sizes could be compared between response variables within specific richness group (i.e. richness of bird species group by body size, habitat preference, and feeding guild). The standardization method consisted in centering and dividing by two times the standard deviation (Gelman 2007).

The analysis was conducted in two steps to avoid overfitting and reducing the number of predictors (in total 45 explanatory variables). The first step was to select the best explanatory variable at each scale using the subset regression method. For each response variables, we first fit the habitat scale parameters separately. For each scale, we checked the effect of each habitat variables on the response variables by fitting one model per explanatory variable and keeping all models with delta AIC<2. In the second step, all the selected explanatory variables were put into one single lme model, fitted all model subsets and conducted model averaging for those models with delta AIC<2. We presented only significant habitat-scale variables ($p < 0.05$). The final results were reported graphically using bipartite package (Dormann et al. 2008) to highlight similarities and dissimilarities in drivers between the different functional groups.

The analyses were conducted in R version 2.8.1 (R Development Core Team 2008) with additional functions provided by the R packages “nlme” (Pinheiro and Bates 2000) and “MuMIn” (R functions for model selection and model averaging, Bartoń 2009), and “bipartite” (Dormann et al. 2008).

## RESULTS

A total of 149 bird species were recorded during the point-transect survey (Appendix 2.2), of which 145 species were recorded within 50 meter of the point center hence used in the analysis. In the final model for each functional group larger coefficients are indicative of larger ecological effect sizes of a particular predicting variable, and can be compared with the coefficients of other variables in the same models. For example, richness of forest specialists was significantly correlated with tree height at the point scale (coefficient of 0.011389, p=0.00176), rattan density in the understory (coefficient of 0.01175, p=0.00272) and tree density (coefficient of 0.012006, p=0.02653) at the transect scale. From these three significant explanatory variables, the strongest predictor was tree density at transect scale (i.e. highest coefficient). Based on the coefficient values (coefficients, standard errors, z- and P-values from final model averaging of lme model are presented in Appendix 2.3), Figure 2.1 shows graphically all the significant predictors for each richness group while Table 2.1 summarized only the significant predictors with strong effect sizes.

Different sets of variables affected different species richness groups. For instance, canopy openness (sub-transect), leaf litter cover (sub-transect), and tree height (point) were significant predictors only for medium size birds and not for other size groups (Figure 2.1a). Moreover, the best explanatory models always included more than one scale. For instance, in Figure 2.1b, edge tolerant and generalist were correlated with variables at sub-transect scale and point scale, edge specialist was correlated with variables at transect and point scales, and forest specialist was correlated with variables at transect and point scales. Overall, 14 habitat variables were found to be correlated with the bird richness groups (Figure 2.1). These variables can be grouped into three main categories: tree related variables (canopy openness, number of dead tree, tree density, tree height, maximum tree diameter, number of *Macaranga* trees), understory related variables (rattan density in the understory, liana density in the understory, leaf litter cover, ginger density in the understory, and understory openness), and geographic variables (slope, altitude).

Four tree related variables (canopy openness, tree height, maximum tree diameter, and number of dead tree) and three understory related variables (leaf litter cover, liana density, rattan density) were the significant predictors for richness of bird species grouped by body size (Figure 2.1a). Looking only at the strong predictor, liana density at transect scale was a strong predictor for richness of small size birds, while medium-large and large size groups were strongly affected at point scale by ground leaf cover and the number of dead trees respectively (Table 2.1). Leaf litter cover at sub-transect scale was the strong predictor for richness of medium size birds (Table 2.1).

Examining the habitat scale effects on species richness grouped by habitat preference revealed that four tree related variables (tree height, tree density, canopy openness, number of *Macaranga*), two understory related variables (rattan and liana density in the understory) and one geographic variable (slope) were the significant predictors (Figure 2.1b). Moreover, habitat at transect scale was the strong predictor for all groups, with different habitat variable affecting different groups: rattan density for edge specialists and edge tolerant groups, tree density for forest specialists, and slope for generalists (Table 2.1).

Figure 2.1c depicts significant predictors on 12 feeding guild groups, consisted of five tree related variables (canopy openness, tree height, tree density, maximum tree diameter, and number of dead tree), five understory related variables (liana density, ginger density, rattan density, understory openness, and ground leaf cover), and three topo-geographic variables (distance to water body, slope, and altitude). There were variations in the habitat scale at which effects on richness of species grouped by feeding guild were observed. Habitat variables at transect scale were the strong predictor for four feeding guild groups: rattan density for arboreal frugivore, arboreal foliage-gleaning insectivores/frugivore and arboreal foliage gleaning insectivores; tree density for the sallying/gleaning insectivore group; distance to water body for terrestrial insectivore of forest interior.  Habitat variables at sub-transect scale were the strong predictor for three groups: rattan density for arboreal frugivore/predator, and leaf litter cover for arboreal foliage-gleaning understory specialists and nectarivore/insectivore. Variables at point scale were the strong predictor for bark-gleaning insectivore (canopy openness), terrestrial omnivore (canopy openness), and sallying insectivore (tree height). Lastly, the analysis revealed that no habitat variables at any scale were important predictor for the miscellaneous insectivore/piscivore group (e.g. Banded Kingfisher *Lacedo pulchella* and Blue-eared Kingfisher *Alcedo meninting*).

Table 2.1. Particularly strong predictors after final model averaging for each species richness group. The bold-italic groups indicated negative correlation with that particular habitat-scale variable.

| Variable group | Habitat variable | Species groups at different spatial scales | | |
|---|---|---|---|---|
| | | Point | Sub-transect | Transect |
| Understory related variables | Rattan density in the understory | | Arboreal frugivore/predator | Edge tolerant; Edge specialist; Arboreal frugivore; Arboreal foliage-gleaning insectivore/frugivore; Arboreal foliage-gleaning insectivore |
| | Leaf litter cover | Medium-large | Medium species; Arboreal foliage-gleaning insectivore understory specialist; Nectarivore/insectivore | Nectarivore/insectivore/frugivore |
| | Liana density in the understory | | | ***Small species*** |
| Tree related variables | Canopy openness | ***Bark-gleaning insectivore***; Terrestrial omnivore | | |
| | Number of dead tree | Large species | | |
| | Tree density | | | Sallying substrate-gleaning insectivore; Forest specialist |
| | Tree height | Sallying insectivore | | |
| Geographic | Slope | | | ***Generalist*** |
| | Distance to water body | | | ***Terrestrial insectivore of forest interior*** |

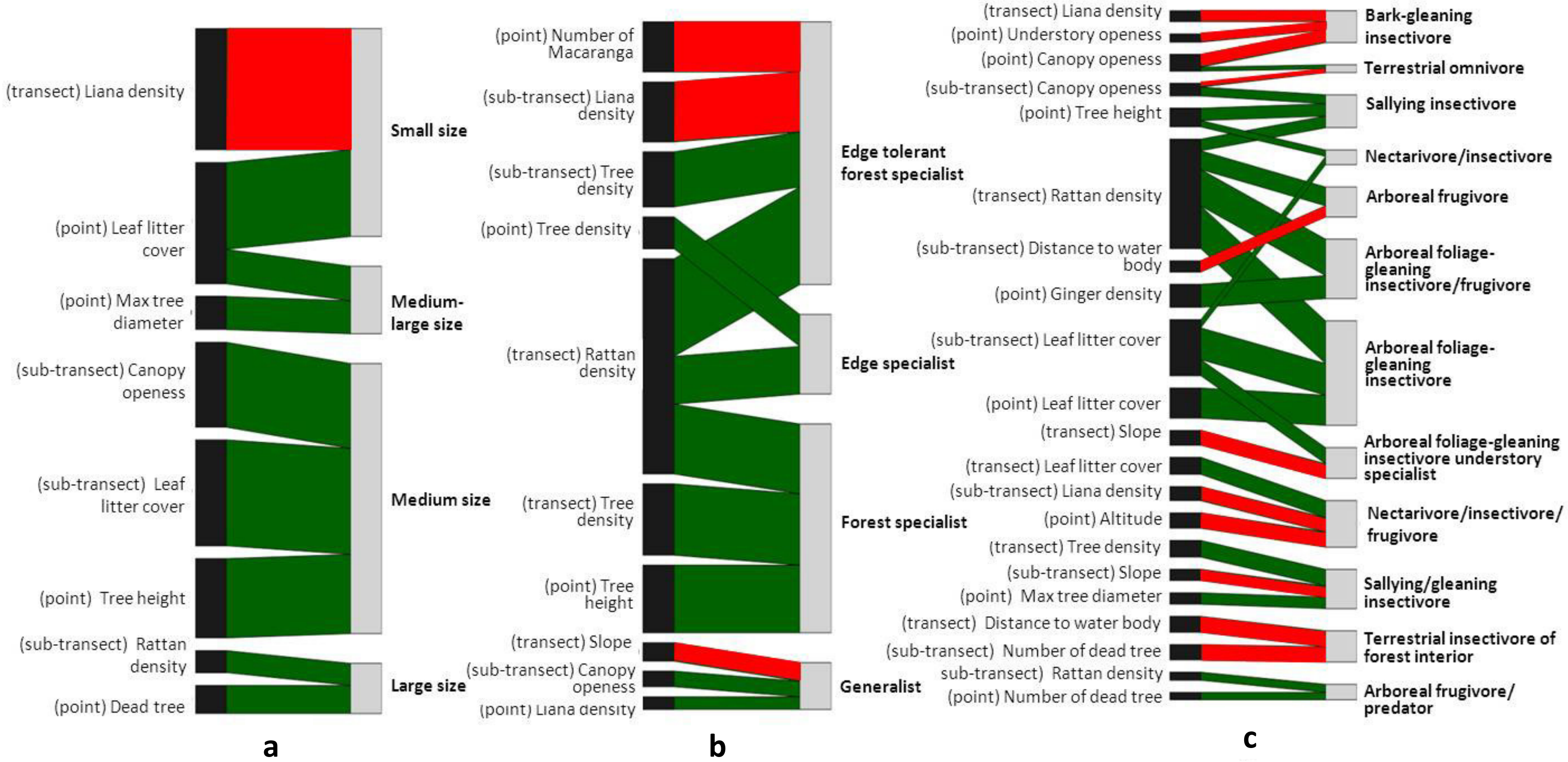

Figure 2.1. Significant effects of habitat variables on richness of birds grouped by (**a**) body size, (**b**) habitat preference, (**c**) feeding type. The black block represents the explanatory variables, their width the effect size and the grey block the response variables. The positive and negative effect was indicated by the color of the connector: green for positive and red for negative effects. Texts in brackets indicate the scales (small to large): point, sub-transect, and transect. For example in Figure 2.1b, edge specialist richness was significantly and positively correlated with rattan density in the understory at transect scale and tree density at point scale, but with rattan density as the stronger predictor (wider connector). For simplicity, label of explanatory variables were shortened.

## DISCUSSION

In this study we looked at the respond of habitat at different spatial scale effect on bird species richness of different functional groups in the selectively-logged primary forest in Sumatra. This is one of few studies in Sundaic region that examined the correlation between vegetation structure in logged forest and bird functional groups. We found that richness of each bird functional group responded to different set of habitat-scale variables. The best predictors were understory related variables, particularly at the transect scale. The importance of variables at transect scale indicated that increasing structural similarity between local patches (point scale) and their surrounding (transect or sub-transect scale) facilitated higher richness of most of the functional groups tested in this study. Incorporating different spatial scales in trying to understand species responses to habitat disturbance is important as different species has different operational scales (Tews et al. 2004, Hill and Hamer 2004). Moreover, bird response to land-use intensity has been shown to depend on their traits (Newbold et al. 2013). By examining different functional groups, species traits associated with habitat changes can be revealed (Tscharntke et al. 2008), which might not be revealed if only looking at general feeding guild (i.e. frugivore, insectivore etc., Edwards et al. 2013).

The impact of logging on birds is well documented. Most of these studies are conducted by comparing species or group of species between logged and unlogged forest. Bird species richness is similar to that of unlogged forest in the short term after logging, (e.g. Marsden 1998, Dunn 2004, Cleary et al. 2005, Sodhi et al. 2008), but lower in the longer term (in naturally regenerating logged forest, Edwards et al. 2009). Moreover, there seems to be general agreement that insectivores are more vulnerable to logging than frugivores (Johns 1986, Lambert 1990, Hussin 1994, Gray et al. 2007). This is also means that terrestrial insectivores, arboreal foliage-gleaning insectivores, terrestrial insectivores-frugivores, bark-gleaning insectivores, sallying-substrate-gleaning insectivores, and sallying insectivores may all be affected. Johns (1996) shows that the first three groups is indeed decreased in number, while arboreal foliage-gleaning insectivores-frugivores, nectarivores-frugivores, and nectarivores/insectivores/ frugivores increased in numbers. In general term, insectivore species that are vulnerable to logging are terrestrial (Thiollay 1992); foliage-gleaning (Thiollay 1992, Mason 1996, Owiunji 1998); bark-gleaning (Thiollay 1992, Mason 1996); sallying (Thiollay 1992, Mason 1996, Owiunji 1998, Marsden 1998). These negatively affected species or group can be used as target for habitat improvement of secondary forest. This would also mean that respond on birds to changes in habitat structure variables should be understood if we want to assist the recovery of these negatively affected species.

Vegetation changes after logging has been well documented in the tropics, where in general logged forest tends to be dominated by pioneer species (Abdulhadi et al. 1981), has higher canopy openness (Slik et al. 2002), higher liana density (Marsden et al. 2002, Scnitzers and Bongers 2002), lower density of big trees (Slik et al. 2002), and a higher density in climbing bamboos (Ansell et al.

2011). These habitat changes are the possible reasons for the different responses of species groups to logging.

In our analysis, stronger predictors were habitat-scale variables that had higher coefficient value in final linear-mixed effect models. Understory-related variables were strong predictors for 11 species richness groups, particularly rattan density in the understory as the best predictor for six richness groups and leaf litter cover for four richness groups (Table 2.1). Higher rattan density indicates areas where light can penetrate down to the forest floor, and as it is a woody vine, it needs trees for further development (Weinstock 1983). Rattan has been found to grow well in logged forest or secondary forest, particularly in area with canopy permitting 50% to 60% light penetration to the ground (Feaw 1992). High richness of these six groups (arboreal frugivore/predator, edge tolerant forest specialist, edge specialist, arboreal frugivore, arboreal foliage-gleaning insectivore/frugivore, and arboreal foliage-gleaning insectivore) in area with high rattan density indicated their relative tolerance to disturbance. Moradi et al. (2009) shows a similar result for arboreal-foliage gleaning insectivore where it is found to positively correlate with ground cover, light intensity, shrub cover, and percent of shrub cover between 0.5 and 2 m high. In addition, some of these groups have been found not susceptible to logging.

We found that the best explanatory models always included more than one scale but with differences in importance. Several studies show contrasting importance of local and landscape-scale variables (MacFaden and Capen 2002, Seoane et al. 2002, Tews et al. 2004, Cleary et al. 2005). For example, in Borneo, Cleary et al. (2005) found that the best explanatory models for bird community similarity and species richness contained variables at local and landscape scales. In North America, MacFaden and Capen (2002) found a contrasting result with local microhabitat characteristics more strongly associated to bird communities than coarser scale characteristics. We found that transect scale was a strong predictor for 11 species richness groups, while the other groups were strongly influenced at the sub-transect (4 groups) or point scale (4 groups, Table 2.1). These differences might be due to differences in the methods used to measure environmental variables and to analyze the data, rather than to differences in the ecological characteristics of the bird species assemblage studied (Cleary et al. 2005). Also, the heterogeneity in results should not mask the general importance of incorporating different spatial scales in trying to understand species responses to habitat disturbance (Hill and Hamer 2004).

In addition, though it might first seem surprising, we found that richness of large birds was best predicted by variables at smaller spatial scales, and richness of small birds by variable averaged over larger scales. Large bird species such as hornbills (Holbrook et al. 2008) and fruit-pigeons (Corlett 2009) have strong flight ability and are able to utilize resources in fragmented landscapes. Johns (1989) also found that most hornbill species were still able to persist 5-6 years after selective logging in the lowland tropical forest in Malaysia. They were also adapted to exploit rare fruit resources that were widely dispersed in the tropical rainforest, hence no barrier for movement.

On the other hand, understanding why richness of small birds was more affected by habitat variables at larger scales, specific species examples are again useful. The importance of larger scale variables indicates that matrix surrounding the local patches influence species ability to use the matrix. For instance, Castellon and Sieving (2006) shows through translocation experiment of Chucao Tapaculo (*Scelorchilus rubecula*) that the species spent longer time in patches surrounded by open habitat than in patches surrounded by dense shrubs or wooded corridors. This indicates that high structural contrast between matrix and local patch hinder movement of this bird. A review by Prevedello and Vieira (2010) on the importance of matrix shows that the type of matrix surrounding habitat patches influence the abundance/richness in the patch.

In forest restoration, the decision on whether to implement active or passive restoration should be based on three components: the intrinsic ecosystem resilience, the level of human degradation, and the characteristics of the landscape around the focal area (Holl and Aide 2011). Passive restoration is considered less costly (Morrison et al. 2011), and combine with applied nucleation (i.e. planting small patches of trees as focal areas for recovery, Corbin and Holl 2012) has been proposed as restoration approach in regenerating pastures (e.g. Reid et al. 2012). For selectively logged forest, passive and active restoration approaches might be combined to assist the recovery of negatively impacted species. Several studies show that several species or species groups do not recover even years after abandonment. Johns (1992) found that even after 12 years there was no sign that the avifaunal community re-converges to that of unlogged forest. Also, Thiollay (1997) found that the understory bird community was worse 10-12 years after abandonment compared to 1-2 years after logging, and with still no appreciable change 3-5 years later. Understory insectivores are negatively affected by logging, and, in terms of species richness, this group did not recover even 25 years after logging (Wong 1985). Based on this, active restoration seems unavoidable.

Moreover, we also wanted to underscore the importance of spatial scale in evaluating bird respond to disturbance, particularly the larger scale. By looking at local and large spatial scales one can indicate whether, for example, richness of specific functional group is high due to habitat at the patch or at larger spatial scale. In this study, the importance of matrix condition was shown by the strong effect of transect scale variables on most of bird functional groups. Managing matrix by increase its structural similarity with the forest patch is important in facilitating habitat use by birds (Sieving et al. 1996, Castellon and Sieving 2006, Preverdello and Vieira 2010). For example, as shows previously, rattan density at transect scale was a strong positive predictor for five richness groups. Creating habitat that is suitable for rattan growth (i.e. areas with relative open canopy) through planting of pioneer species in scrub dominated areas could create canopy covers which shade-out grasses and weeds (Lamb et al. 2005). This approach might increase the richness of several bird functional groups (e.g. arboreal foliage-gleaning insectivores). Increasing matrix structural similarity with the forest patch could averse this condition.

Table 2.2. Potential effects of tree planting on bird species richness. (*) bold indicates group that are negatively affected by logging.

| Method and characteristic of secondary forest | Effect(s) of intervention | Scale of intervention | (*)Species group affected | Example of potential specific restoration method |
|---|---|---|---|---|
| Tree planting in low canopy cover (< 40%) area | Increase canopy cover, tree density, and reduced variability | Transect | Implemented at this scale may increase the number of edge tolerant, edge specialist, **arboreal frugivore, arboreal foliage-gleaning insectivore/frugivore**, and **arboreal foliage-gleaning insectivore species** using the area. Next description should be read as described here, otherwise will be explained. | Strip planting and applied-nucleation are two possible approaches that could be implemented. For instance strip planting with 3 x 1000 m strips and each 50 m apart in relatively large open area could speed up canopy closure. However, this might require significant amount of resources depending on the number of species planted. Reducing the number of species planted in applying applied nucleation approach, i.e. planting small patches of trees at certain distance (e.g. every 200 meters) could also produce similar result with lower cost (Corbin and Holl 2012). Nevertheless, the basic idea is to reduce variability in the matrix. |
| | | Transect | Sallying-substrate gleaning insectivore, and **forest specialist**. | |
| | | Sub-transect | Arboreal frugivore/predator | |
| | | Point | **Bark-gleaning insectivore**, and Terrestrial omnivore. | |
| | | Point | Sallying insectivore. | |
| Tree planting in shrubs dominated or open areas | Increase vertical structure, canopy cover, and reduce variability | Transect | Nectarivore/insectivore/frugivore. | |
| | | Sub-transect | Medium species, **Arboreal foliage-gleaning insectivore understory specialist**, Nectarivore/insectivore. | |
| | Provide perching | Point | Scattered planting in relatively open areas may increase the number of large bird species use the area by providing staging point for movement between suitable habitats. | |

The present study provided the basis to decide what vegetation structure and what scale need to be improved to facilitate the recovery of negatively impacted bird species. By knowing what habitat scale variables correlate with changes in bird communities, targeted restoration treatments can enhance favorable habitat structure for species that have declined after logging. Results from restoration activities will only prove their effectiveness many years after their implementation, hence predicting potential impacts of restoration treatments in advance could enhance efficient use of limited restoration resources (Reid et al. 2012). With a better understanding of the reliability of predictor variables, undesirable outcomes could be prevented. For instance, Ansell et al. (2011) shows that 15 years after enrichment planting and liberation cutting species that declined after logging are not positively affected. Though the decision for these treatments was not aimed for birds, but if it were, a better treatment could be selected. Incorporating brakes in liberation cutting to maintain dense vine tangle and microhabitats is suggested to overcome this effect (Ansell et al. 2011). By understanding avian habitat preference, prediction on the possible effect of restoration treatments could be made. A recent study by Reid et al. (2012) shows that increasing canopy cover, as a result of tree planting, was correlated with an increase of bark-gleaning insectivore richness. Our result also found a similar trend.

Tree planting is a dominant method used in active forest restoration (e.g Grandwohl and Greenberg 1988, Guariguata et al. 1995, Lamb et al. 2005, Benayas et al. 2009, Reid et al. 2012, Corbin and Holl 2012). Depending on which area this planting is implemented, the effect might be different for each bird groups. Based on our results we have several insights on the potential effect of tree planting on bird richness (Table 2.2). For example, in large open area strip planting could be implemented to increase canopy cover. Unfortunately, resources available for forest restoration activities have always been limited in which a wait and see approach might be ideal than immediate action (Holl and Aide 2011). However, as we showed previously, this passive approach might not work at least for some of the bird groups. It is also important to clearly state the goal before restoring habitat for birds (Reid et al. 2012). Our results demonstrate that each group responds to a different set of habitat variables and at different scale. If increasing richness of bark-gleaning insectivore is desired, the approach implemented might be the same (i.e. tree planting) but at different scale than if we want to increase richness of sallying insectivore (Table 2.2).

The tropical forest landscape is currently dominated by secondary forest (i.e. logged forest). These forests also still support relatively good primary forest biodiversity hence they should be managed and protected from further disturbance (e.g. Edwards et al. 2010). Our results indicated the potential benefit of understanding habitat scale effects on bird community in logged forest for species conservation and also restoration of logged forest. There was substantial heterogeneity in the scales at which habitat affected species groups, as some groups were more affected by large scale variables while the other groups were affected by small scale variables. Understanding how bird communities are distributed in the secondary forest and how that use can be increased is a pivotal question in bird conservation and forest restoration, given the ecological function importance of birds such as seed dispersers, pollinators, insect predators (e.g. Stiles 2000, Sekercioglu et al. 2004, Moran et al. 2010). The decision on forest management activities should incorporate understanding on the biodiversity in the degraded forest and the barriers to natural regeneration (Hobbs 2007), in order to provide beneficial effect for those species negatively affected by logging.

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Appendix 2.1. Description of the geographic and vegetation structure variables based on direct measurement or calculated after based on the direct measurement.

| **Variable type** | **Habitat variable** | **Code** | **Sampling radius** | **Description** |
|---|---|---|---|---|
| Geographical | Altitude | alt | n/a | Taken from GPS fix |
| Geographical | Slope | slope | n/a | Taken using Clinometer |
| Geographical | Distance to water bodies | rivdist | 25 m | The nearest rivers/streams |
| Structural | *Macaranga* | maca | 25 m | The number *Macaranga* spp. trees among the 10 measured trees (nearest 10 trees with DBH >20 cm) |
| Structural | Tree diameter max | dmtmax | 25 m | The biggest tree diameter within the 10 measured trees (nearest 10 trees with DBH >20 cm). Tree diameter was measured using phi-band. |
| Structural | Tree density | treeden | 25 m | Using the farther distance of the 'tree' as the radius and converted into number of trees per hectare |
| Structural | Average tree height | treeht | 25 m | Tree height measured using Clinometer, and then averaged for all the 10 trees measured (nearest 10 trees with DBH >20 cm) |
| Structural | Canopy openness | can | 10 m | A canopy-scope (Brown et al. 2000), an array of 25 regularly spaced dots marked on a transparent Perspex sheet (30cm x 30cm), was used to assess canopy openness. Using a 20cm length of string attached to the corner of the canopy-scope, it was held a set distance from the observer's face and facing up towards the largest opening in the canopy. The surveyor counted the number of dots with clear sky behind them. Four counts were made, one in each plot quarter 10m from the central point. If any of these points were within 1m of a tree trunk, then the observation point was moved slightly so that it was at least 1m from the nearest tree trunk. The counts were then summed and averaged to represent the average canopy openness for that point transect. |
| Structural | Dead standing tree | dtree | 25 m | Number of standing dead tree (with DBH >20 cm). |

| | | | | |
|---|---|---|---|---|
| Structural | Understory openness | und | 25 m | Understory vegetation cover was measured by counting the number of visible dots arranged evenly in an 8 x 8 configuration on a 1m x 1 plastic sheet. One observer held the sheet between 0.5 and 1.5m above the ground and 10m from the central point in each plot quarter. A second surveyor stood at the plot's central point and counted the number of dots not obscured by vegetation cover. The counts were then summed and averaged to represent the average canopy openness for that point transect. |
| Structural | Understory density (sapling, liana, ginger, rattan) | sap<br>lian<br>ging<br>rat | 2 m | Understory vegetation density was estimated in each plot quarter positioned 10m from the plot's central point. An observer stood holding a 1m long stick perpendicular 1m above the ground and turned slowly on the spot counting the number of stems <5cm DBH the stick touched. Each stem touched was classified as a sapling, liana, palm, ginger, rattan. |
| Structural | Ground layer cover | leaf | 10 m | The percentage of the ground layer covered by leaf litter was estimated in each plot quarter and 10m from the central point. |

## Appendix 2.2. Bird recorded in secondary forest of Harapan Rainforest concession

| No | Family | Common name | Scientific name | [a]IUCN | [b]size | [c]hb | [d]guild |
|---|---|---|---|---|---|---|---|
| 1 | Accipitridae | Crested Serpent-eagle | *Spilornis cheela* | | large | gene | dp |
| 2 | Aegithinidae | Green Iora | *Aegithina viridissima* | NT | small | edgetol | afgin |
| 3 | Alcedinidae | Blue-eared Kingfisher | *Alcedo meninting* | | small | edgetol | afginus |
| 4 | Alcedinidae | Rufous-collared Kingfisher | *Actenoides concretus* | NT | medlarge | forspe | mip |
| 5 | Alcedinidae | Black-backed Kingfisher | *Ceyx erithaca* | | small | forspe | afginus |
| 6 | Alcedinidae | Rufous-backed Kingfisher | *Ceyx rufidorsa* | | small | forspe | afginus |
| 7 | Alcedinidae | Banded Kingfisher | *Lacedo pulchella* | | medium | forspe | mip |
| 8 | Bucerotidae | White-crowned Hornbill | *Aceros comatus* | NT | large | forspe | afp |
| 9 | Bucerotidae | Wrinkled Hornbill | *Aceros corrugatus* | NT | large | edgetol | afp |
| 10 | Bucerotidae | Wreathed Hornbill | *Aceros undulatus* | | large | edgetol | afp |
| 11 | Bucerotidae | Black Hornbill | *Anthracoceros malayanus* | NT | large | edgetol | afp |
| 12 | Bucerotidae | Rhinoceros Hornbill | *Buceros rhinoceros* | NT | large | edgetol | afp |
| 13 | Bucerotidae | Helmeted Hornbill | *Rhinoplax vigil* | NT | large | edgetol | afp |
| 14 | Bucerotidae | Bushy-crested Hornbill | *Anorrhinus galeritus* | | large | forspe | afp |
| 15 | Campephagidae | Lesser Cuckooshrike | *Coracina fimbriata* | | medium | edgetol | afgin |
| 16 | Campephagidae | Black-winged Flycatcher-shrike | *Hemipus hirundinaceus* | | small | edgetol | afgin |
| 17 | Campephagidae | Scarlet Minivet | *Pericrocotus flammeus* | | medium | edgetol | afgin |
| 18 | Caprimulgidae | Large-tailed Nightjar | *Caprimulgus macrurus* | | medium | openco | npi |
| 19 | Chloropseidae | Blue-winged Leafbird | *Chloropsis cochinchinensis* | | medium | edgetol | nif |
| 20 | Chloropseidae | Lesser Green Leafbird | *Chloropsis cyanopogon* | NT | medium | edgetol | nif |
| 21 | Chloropseidae | Greater Green Leafbird | *Chloropsis sonneratii* | | medium | edgetol | nif |
| 22 | Columbidae | Mountain Imperial-pigeon | *Ducula badia* | | large | edgetol | af |
| 23 | Columbidae | Thick-billed Green-pigeon | *Treron curvirostra* | | medlarge | edgetol | af |
| 24 | Columbidae | Emerald Dove | *Chalcophaps indica* | | medlarge | edgetol | af |
| 25 | Columbidae | Green Imperial-pigeon | *Ducula aenea* | | large | forspe | tom |
| 26 | Coraciidae | Asian Dollarbird | *Eurystomus orientalis* | | medlarge | openco | si |
| 27 | Corvidae | Crested Jay | *Platylophus galericulatus* | NT | medlarge | forspe | afgin |
| 28 | Corvidae | Black Magpie | *Platysmurus leucopterus* | NT | large | forspe | dp |
| 29 | Corvidae | Slender-billed Crow | *Corvus enca* | | large | openco | afgif |
| 30 | Cuculidae | Rusty-breasted Cuckoo | *Cacomantis sepulcralis* | | medium | edgetol | afgin |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 31 | Cuculidae | Banded Bay Cuckoo | *Cacomanthis sonneratii* | | medium | edgetol | afgin |
| 32 | Cuculidae | Violet Cuckoo | *Chrysococcyx xanthorhynchus* | | small | edgetol | afgin |
| 33 | Cuculidae | Hodgson's Hawk-cuckoo | *Cuculus fugax* | | medlarge | edgetol | afgin |
| 34 | Cuculidae | Drongo Cuckoo | *Surniculus lugubris* | | medium | edgetol | afgin |
| 35 | Cuculidae | Raffles's Malkoha | *Phaenicophaeus chlorophaeus* | | medium | edgetol | afgin |
| 36 | Cuculidae | Chestnut-breasted Malkoha | *Phaenicophaeus curvirostris* | | large | edgetol | afgin |
| 37 | Cuculidae | Black-bellied Malkoha | *Phaenicophaeus diardi* | NT | medium | edgetol | afgin |
| 38 | Cuculidae | Green-billed Malkoha | *Phaenicophaeus tristis* | | medlarge | edgetol | afgin |
| 39 | Cuculidae | Short-toed Coucal | *Centropus rectunguis* | VU | large | forspe | afgin |
| 40 | Cuculidae | Plaintive Cuckoo | *Cacomantis merulinus* | | medium | gene | afgin |
| 41 | Cuculidae | Himalayan Cuckoo | *Cuculus saturatus* | | medlarge | gene | afgin |
| 42 | Cuculidae | Indian Cuckoo | *Cuculus micropterus* | | medlarge | openco | afgin |
| 43 | Cuculidae | Greater Coucal | *Centropus sinensis* | | large | openco | afgin |
| 44 | Dicaeidae | Yellow-vented Flowerpecker | *Dicaeum chryssorheum* | | small | edgetol | nif |
| 45 | Dicaeidae | Plain Flowerpecker | *Dicaeum concolor* | | small | edgetol | nif |
| 46 | Dicaeidae | Scarlet-backed Flowerpecker | *Dicaeum cruentatum* | | small | edgetol | nif |
| 47 | Dicaeidae | Orange-bellied Flowerpecker | *Dicaeum trigonostigma* | | small | edgetol | nif |
| 48 | Dicaeidae | Yellow-breasted Flowerpecker | *Prionochilus maculatus* | | small | edgetol | afgif |
| 49 | Dicaeidae | Crimson-breasted Flowerpecker | *Prionochilus percussus* | | small | edgetol | afgif |
| 50 | Dicaeidae | Scarlet-breasted Flowerpecker | *Prionochilus thoracicus* | NT | small | edgetol | afgif |
| 51 | Dicruridae | Greater Racket-tailed Drongo | *Dicrurus paradiseus* | | medlarge | edgetol | sgi |
| 52 | Eupetidae | Rail-babbler | *Eupetes macrocerus* | | medium | forspe | tifi |
| 53 | Eurylaimidae | Dusky Broadbill | *Corydon sumatranus* | | medlarge | edgetol | af |
| 54 | Eurylaimidae | Banded Broadbill | *Eurylaimus javanicus* | | medlarge | edgetol | sgi |
| 55 | Eurylaimidae | Black-and-yellow Broadbill | *Eurylaimus ochromalus* | NT | medium | edgetol | sgi |
| 56 | Eurylaimidae | Asian Green Broadbill | *Calyptomena viridis* | NT | medium | forspe | sgi |
| 57 | Falcondiae | Black-thighed Falconet | *Microhierax fringillarius* | | medium | edgespe | ain |
| 58 | Hemiprocnidae | Whiskered Treeswift | *Hemiprocne comata* | | small | openco | si |
| 59 | Irenidae | Asian Fairy-bluebird | *Irena puella* | | medium | edgespe | af |
| 60 | Meropidae | Red-bearded Bee-eater | *Nyctyornis amictus* | | medlarge | forspe | si |
| 61 | Monarchidae | Black-naped Monarch | *Hypothymis azurea* | | small | edgetol | si |
| 62 | Muscicapidae | Malaysian Blue-flycatcher | *Cyornis turcosus* | NT | medium | edgetol | si |
| 63 | Muscicapidae | Pale Blue-flycatcher | *Cyornis unicolor* | | medium | edgetol | si |
| 64 | Muscicapidae | White-rumped Shama | *Copsychus malabaricus* | | medium | edgetol | si |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 65 | Muscicapidae | Grey-headed Canary-flycatcher | *Culicicapa ceylonensis* | | small | forspe | si |
| 66 | Muscicapidae | Large-billed Blue-flycatcher | *Cyornis caerulatus* | VU | small | forspe | si |
| 67 | Muscicapidae | Rufous-winged Philentoma | *Philentoma phyrrhopterum* | | small | forspe | sgi |
| 68 | Muscicapidae | Grey-chested Jungle-flycatcher | *Rhinomyias umbratilis* | NT | small | forspe | afgin |
| 69 | Muscicapidae | Rufous-tailed Shama | *Trichixos pyrrhopygus* | NT | medium | forspe | afgin |
| 70 | Muscicapidae | White-crowned Forktail | *Enicurus leschenaultii* | | medium | forspe | afgin |
| 71 | Muscicapidae | Oriental Magpie-robin | *Copsychus saularis* | | medium | openco | tifi |
| 72 | Nectariniidae | Ruby-cheeked Sunbird | *Anthreptes singalensis* | | small | edgespe | nin |
| 73 | Nectariniidae | Plain Sunbird | *Anthreptes simplex* | | small | edgetol | nif |
| 74 | Nectariniidae | Grey-breasted Spiderhunter | *Arachnothera affinis* | | medium | edgetol | nif |
| 75 | Nectariniidae | Spectacled Spiderhunter | *Arachnothera flavigaster* | | medium | edgetol | nif |
| 76 | Nectariniidae | Long-billed Spiderhunter | *Arachnothera robusta* | | medium | edgetol | nif |
| 77 | Nectariniidae | Purple-naped Sunbird | *Hypogramma hypogrammicum* | | small | edgetol | nin |
| 78 | Nectariniidae | Crimson Sunbird | *Aethopyga siparaja* | | small | gene | nin |
| 79 | Nectariniidae | Little Spiderhunter | *Arachnothera longirostra* | | small | gene | nin |
| 80 | Nectariniidae | Plain-throated Sunbird | *Anthreptes malacensis* | | small | openco | nif |
| 81 | Nectariniidae | Olive-backed Sunbird | *Nectarinia jugularis* | | small | openco | nif |
| 82 | Oriolidae | Black-hooded Oriole | *Oriolus xanthonotus* | | medium | edgetol | afgif |
| 83 | Phasianidae | Great Argus | *Argusianus argus* | NT | large | forspe | tom |
| 84 | Picidae | Maroon Woodpecker | *Blythipicus rubiginosus* | | medlarge | edgetol | bgi |
| 85 | Picidae | Rufous Woodpecker | *Celeus brachyurus* | | medlarge | edgetol | bgi |
| 86 | Picidae | White-bellied Woodpecker | *Dryocopus javensis* | | large | edgetol | bgi |
| 87 | Picidae | Grey-and-buff Woodpecker | *Hemicircus concretus* | | medium | edgetol | bgi |
| 88 | Picidae | Buff-rumped Woodpecker | *Meiglyptes tristis* | | medium | edgetol | afgin |
| 89 | Picidae | Buff-necked Woodpecker | *Meiglyptes tukki* | NT | medium | edgetol | bgi |
| 90 | Picidae | Checker-throated Woodpecker | *Picus mentalis* | | medlarge | edgetol | bgi |
| 91 | Picidae | Crimson-winged Woodpecker | *Picus puniceus* | | medlarge | edgetol | bgi |
| 92 | Picidae | Rufous Piculet | *Sassia abnormis* | | small | edgetol | bgi |
| 93 | Picidae | Olive-backed Woodpecker | *Dinopium rafflesii* | NT | medlarge | forspe | bgi |
| 94 | Picidae | Orange-backed Woodpecker | *Reinwardtipicus validus* | | medlarge | forspe | afginus |
| 95 | Pittidae | Garnet Pitta | *Pitta granatina* | NT | medium | edgetol | tifi |
| 96 | Pittidae | Javan Banded Pitta | *Pitta guajana* | | medlarge | edgetol | tifi |
| 97 | Pittidae | Hooded Pitta | *Pitta sordida* | | medium | edgetol | tifi |
| 98 | Psittacidae | Blue-crowned Hanging-parrot | *Loriculus galgulus* | | medium | edgetol | af |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 99 | Psittacidae | Blue-rumped Parrot | *Psittinus cyanurus* | NT | medium | forspe | af |
| 100 | Pycnonotidae | Buff-vented Bulbul | *Iole olivacea* | NT | medium | edgespe | afgif |
| 101 | Pycnonotidae | Red-eyed Bulbul | *Pycnonotus brunneus* | | medium | edgespe | afgif |
| 102 | Pycnonotidae | Olive-winged Bulbul | *Pycnonotus plumosus* | | medium | edgespe | afgif |
| 103 | Pycnonotidae | Cream-vented Bulbul | *Pycnonotus simplex* | | medium | edgespe | afgif |
| 104 | Pycnonotidae | Streaked Bulbul | *Ixos malaccensis* | NT | medium | edgetol | afgif |
| 105 | Pycnonotidae | Spectacled Bulbul | *Pycnonotus erythropthalmos* | | small | edgetol | afgif |
| 106 | Pycnonotidae | Black-crested Bulbul | *Pycnonotus melanicterus* | | medium | edgetol | afgif |
| 107 | Pycnonotidae | Yellow-bellied Bulbul | *Alophoixus phaeocephalus* | | medium | forspe | afgif |
| 108 | Pycnonotidae | Black-headed Bulbul | *Pycnonotus atriceps* | | medium | forspe | afgif |
| 109 | Pycnonotidae | Puff-backed Bulbul | *Pycnonotus eutilotus* | NT | medium | forspe | afgif |
| 110 | Pycnonotidae | Hairy-backed Bulbul | *Tricholestes criniger* | | small | forspe | afgif |
| 111 | Pycnonotidae | Grey-cheeked Bulbul | *Alophoixus bres* | | medium | forspe | afgif |
| 112 | Pycnonotidae | Yellow-vented Bulbul | *Pycnonotus goavier* | | medium | gene | afgif |
| 113 | Ramphastidae | Gold-whiskered Barbet | *Megalaima chrysopogon* | | large | edgetol | af |
| 114 | Ramphastidae | Yellow-crowned Barbet | *Megalaima henricii* | NT | medlarge | edgetol | afp |
| 115 | Ramphastidae | Red-crowned Barbet | *Megalaima rafflesii* | NT | medlarge | edgetol | af |
| 116 | Ramphastidae | Brown Barbet | *Calorhamphus fuliginosus* | | medium | edgetol | af |
| 117 | Ramphastidae | Blue-eared Barbet | *Megalaima australis* | | medium | gene | afgif |
| 118 | Rhipiduridae | Pied Fantail | *Rhipidura javanica* | | small | forspe | sgi |
| 119 | Rhipiduridae | Spotted Fantail | *Rhipidura perlata* | | small | forspe | sgi |
| 120 | Sittidae | Velvet-fronted Nuthatch | *Sitta frontalis* | | small | forspe | bgi |
| 121 | Sturnidae | Hill Myna | *Gracula religiosa* | | large | gene | af |
| 122 | Sylviidae | Dark-necked Tailorbird | *Orthotomus atrogularis* | | small | edgespe | afgin |
| 123 | Sylviidae | Ashy Tailorbird | *Orthotomus ruficeps* | | small | edgespe | afgin |
| 124 | Sylviidae | Rufous-tailed Tailorbird | *Orthotomus sericeus* | | small | edgespe | afgin |
| 125 | Sylviidae | Yellow-bellied Warbler | *Abroscopus superciliaris* | | small | edgetol | afgin |
| 126 | Timaliidae | White-chested Babbler | *Trichastoma rostratum* | NT | medium | edgespe | tifi |
| 127 | Timaliidae | Short-tailed Babbler | *Malacocincla malaccensis* | NT | medium | edgetol | tifi |
| 128 | Timaliidae | Black-capped Babbler | *Pellorneum capistratum* | | medium | edgetol | tifi |
| 129 | Timaliidae | Sooty-capped Babbler | *Malacopteron affine* | | small | edgetol | tifi |
| 130 | Timaliidae | Moustached Babbler | *Malacopteron magnirostre* | | small | edgetol | tifi |
| 131 | Timaliidae | Chestnut-winged Babbler | *Stachyris erythroptera* | | small | edgetol | afginus |
| 132 | Timaliidae | Chestnut-rumped Babbler | *Stachyris maculata* | NT | medium | edgetol | afgin |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 133 | Timaliidae | Black-throated Babbler | *Stachyris nigricollis* | NT | medium | edgetol | afgin |
| 134 | Timaliidae | Rufous-fronted Babbler | *Stachyris rufifrons* | | small | edgetol | afgin |
| 135 | Timaliidae | Pin-striped Tit-babbler | *Macronous gularis* | | small | edgetol | afgin |
| 136 | Timaliidae | Fluffy-backed Tit-babbler | *Macronous ptilosus* | NT | small | edgetol | afgin |
| 137 | Timaliidae | Striped Wren-babbler | *Kenopia striata* | NT | small | forspe | afgif |
| 138 | Timaliidae | Large Wren-babbler | *Turdinus macrodactylus* | NT | medium | forspe | afgin |
| 139 | Timaliidae | Abbott's Babbler | *Malacopteron abboti* | | medium | forspe | afginus |
| 140 | Timaliidae | Scaly-crowned Babbler | *Malacopteron cinereum* | | small | forspe | afgin |
| 141 | Timaliidae | Rufous-crowned Babbler | *Malacopteron magnum* | NT | medium | forspe | afginus |
| 142 | Timaliidae | Chestnut-backed Scimitar-babbler | *Pomatorhinus montanus* | | medium | forspe | afginus |
| 143 | Timaliidae | Brown Fulvetta | *Alcippe brunneicauda* | NT | small | forspe | afginus |
| 144 | Timaliidae | White-necked Babbler | *Stachyris leucotis* | NT | medium | forspe | afginus |
| 145 | Timaliidae | Grey-headed Babbler | *Stachyris poliocephala* | | medium | forspe | afginus |
| 146 | Timaliidae | Ferruginous Babbler | *Trichastoma bicolor* | | medium | forspe | afginus |
| 147 | Trogonidae | Diard's Trogon | *Harpactes diardi* | NT | medlarge | forspe | sgi |
| 148 | Trogonidae | Scarlet-rumped Trogon | *Harpactes duvaucelii* | NT | medium | forspe | sgi |
| 149 | Trogonidae | Red-naped Trogon | *Harpactes kasumba* | | medlarge | forspe | sgi |

[a] IUCN status (IUCN 2012): VU= vulnerable, NT=near threatened

[b] small – small species (weight < 20 g); medium – medium-sized (20-69 g); medlarge – medium-large (70-150 g); large – large (>150 g)

[c] Species were assigned to habitats used by Styring et al. (2011): forspec=forest specialist,edgetol=Edge tolerant forest specialist, edgespe=Edge specialist, openco=Open country species, gene=Generalist

[d] Feeding guilds are based on Lambert (1992): dp=diurnal predator; npi= nocturnal predator; tifi= terrestrial insectivore; afgin= arboreal foliage gleaning insectivore; afginus=arboreal foliage gleaning insectivores understory specialist; ain=aerial insectivores; bgi=bark gleaning insectivore; sgi=sallying substrate gleaning insectivore; si= sallying insectivore; afgif= arboreal foliage gleaning insectivore–frugivore; afp= arboreal frugivore–predator; af=arboreal frugivores; mip=miscellaneous insectivores/piscivores; nif=nectarivores/insectifores/frugivores; nin=nectarivores/insectivores; tom=terrestrial omnivores.

Appendix 2.3. Results from model averaging of linear mixed-effects model (fit by Maximum Likelihood) the effect of habitat scales on richness groups. Top model set after model averaging only, and shows only for significant predictors.

| Richness group | Response variables | $^{d}$Scale | $^{e}$Explanatory variables | Estimate | s.e. | adj.se | z.value | p.value |
|---|---|---|---|---|---|---|---|---|
| $^{a}$Body mass | small | point | leaf | 0.00849 | 0.004 | 0.004 | 2.321 | 0.020 |
| | small | transect | lian | -0.011854 | 0.006 | 0.006 | 2.019 | 0.044 |
| | med | point | treeht | 0.007756 | 0.004 | 0.004 | 2.038 | 0.042 |
| | med | sub-transect | can | 0.008302 | 0.004 | 0.004 | 2.338 | 0.019 |
| | med | sub-transect | leaf | 0.010363 | 0.004 | 0.004 | 2.691 | 0.007 |
| | medlarge | point | leaf | 0.003371 | 0.002 | 0.002 | 2.201 | 0.028 |
| | medlarge | point | maxdmt | 0.003229 | 0.001 | 0.001 | 2.217 | 0.027 |
| | large | sub-transect | rat | 0.002156 | 0.001 | 0.001 | 2.392 | 0.017 |
| | large | point | dtree | 0.002749 | 0.001 | 0.001 | 3.080 | 0.002 |
| $^{b}$Habitat preference | edgetol | point | maca | -0.008451 | 0.004 | 0.004 | 2.199 | 0.028 |
| | edgetol | sub-transect | lian | -0.010009 | 0.004 | 0.004 | 2.707 | 0.007 |
| | edgetol | sub-transect | treeden | 0.009258 | 0.004 | 0.004 | 2.377 | 0.018 |
| | edgetol | transect | rat | 0.01644 | 0.004 | 0.004 | 4.128 | 0.000 |
| | generalist | point | lian | 0.002135 | 0.001 | 0.001 | 2.313 | 0.021 |
| | generalist | sub-transect | can | 0.002627 | 0.001 | 0.001 | 2.864 | 0.004 |
| | generalist | transect | slope | -0.00311 | 0.001 | 0.001 | 3.326 | 0.001 |
| | edgespe | point | treeden | -0.005375 | 0.002 | 0.002 | 3.146 | 0.002 |
| | edgespe | transect | rat | 0.008028 | 0.003 | 0.003 | 3.054 | 0.002 |
| | forspec | point | treeht | 0.011389 | 0.004 | 0.004 | 3.128 | 0.002 |
| | forspec | transect | rat | 0.01175 | 0.004 | 0.004 | 2.998 | 0.003 |
| | forspec | transect | treeden | 0.012006 | 0.005 | 0.005 | 2.218 | 0.027 |
| $^{c}$Feeding guild | af | sub-transect | rivdist | -0.002552 | 0.001 | 0.001 | 1.977 | 0.048 |
| | af | transect | rat | 0.004263 | 0.002 | 0.002 | 2.030 | 0.042 |
| | afgif | point | ging | 0.005248 | 0.002 | 0.002 | 2.195 | 0.028 |
| | afgif | transect | rat | 0.008282 | 0.003 | 0.003 | 2.736 | 0.006 |
| | afgin | sub-transect | leaf | 0.007202 | 0.003 | 0.003 | 2.383 | 0.017 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | afgin | point | leaf | 0.00688 | 0.003 | 0.003 | 2.357 | 0.018 |
| | afgin | transect | rat | 0.009719 | 0.003 | 0.003 | 3.127 | 0.002 |
| | afginus | sub-transect | leaf | 0.0036765 | 0.001 | 0.001 | 2.611 | 0.009 |
| | afginus | transect | slope | -0.003338 | 0.002 | 0.002 | 2.066 | 0.039 |
| | afp | sub-transect | rat | 0.0018459 | 0.000 | 0.001 | 3.662 | 0.000 |
| | afp | point | dtree | 0.0016843 | 0.001 | 0.001 | 3.284 | 0.001 |
| | bgi | point | can | -0.0028819 | 0.001 | 0.001 | 3.093 | 0.002 |
| | bgi | point | und | -0.0018766 | 0.001 | 0.001 | 2.057 | 0.040 |
| | bgi | transect | lian | -0.0024686 | 0.001 | 0.001 | 2.492 | 0.013 |
| | nif | sub-transect | lian | -0.002063 | 0.002 | 0.002 | 2.088 | 0.037 |
| | nif | point | alt | -0.0034873 | 0.002 | 0.002 | 2.192 | 0.028 |
| | nif | transect | leaf | 0.0038893 | 0.002 | 0.002 | 2.334 | 0.020 |
| | nin | sub-transect | leaf | 0.0019217 | 0.001 | 0.001 | 2.664 | 0.008 |
| | nin | point | treeht | 0.0014533 | 0.001 | 0.001 | 2.114 | 0.034 |
| | sgi | sub-transect | slope | -0.0025665 | 0.001 | 0.001 | 2.137 | 0.033 |
| | sgi | point | maxdmt | 0.0025895 | 0.001 | 0.001 | 2.132 | 0.033 |
| | sgi | transect | treeden | 0.0037868 | 0.001 | 0.001 | 2.629 | 0.009 |
| | si | sub-transect | can | 0.0020411 | 0.001 | 0.001 | 2.063 | 0.039 |
| | si | point | treeht | 0.0027972 | 0.001 | 0.001 | 2.836 | 0.005 |
| | si | transect | rat | 0.0026577 | 0.001 | 0.001 | 2.636 | 0.008 |
| | tifi | sub-transect | dtree | -0.003489 | 0.001 | 0.001 | 3.035 | 0.002 |
| | tifi | transect | rivdist | -0.0036352 | 0.001 | 0.001 | 2.748 | 0.006 |
| | tom | sub-transect | can | -0.0008326 | 0.000 | 0.000 | 2.052 | 0.040 |
| | tom | point | can | 0.0009331 | 0.000 | 0.000 | 2.288 | 0.022 |

[a] small – small species (weight < 20 g); medium – medium-sized (20-69 g); medlarge – medium-large (70-150 g); large – large (>150 g)

[b] Species were assigned to habitats used by Styring et al. (2011): forspec=forest specialist, edgetol=Edge tolerant forest specialist, edgespe=Edge specialist, openco=Open country species, gene=Generalist

[c] Feeding guilds are based on Lambert (1992): tifi= terrestrial insectivore of forest interior; afgin= arboreal foliage gleaning insectivore; afginus=arboreal foliage gleaning insectivores understory specialist; bgi=bark gleaning insectivore; sgi=sallying substrate

gleaning insectivore; si= sallying insectivore; afgif= arboreal foliage gleaning insectivore–frugivore; afp= arboreal frugivore–predator; af=arboreal frugivores; mip=miscellaneous insectivores/piscivores; nif=nectarivores/insectifores/frugivores; nin=nectarivores/insectivores; tom=terrestrial omnivores.

[e] Scale factors (small to large): point,sub-transect, transect

[d] Habitat variables (*see* Appendix 1 for explanation of the explanatory variables): alt (altitude), slope (slope), rivdist (distance to water body), can (canopy openness), dtree (number of dead standing tree), ging (understory ginger density), lian (understory liana density), rat (understory rattan density), und (understory openness), treeht (tree height), treeden (tree density), maxdmt (highest tree diameter among the tree measured), maca (number of *Macaranga* tree among the tree measured).

# Chapter 3

## Densities of forest birds in a secondary tropical lowland forest restoration concession in Sumatra, Indonesia

Bushy-crested Hornbill *Anorrhinus galeritus* shows density variations between different habitat types.

## ABSTRACT

Bird density estimates (hereafter density) are an important basis for conservation management, but data are lacking for many Southeast Asia birds. In this study the point-transect method was used to collect bird data in the secondary lowland forest in Harapan Rainforest Ecosystem Restoration concession (HRF), Sumatra, Indonesia. Between April and June 2011, bird surveys were conducted in 2 km long transects (11 transects @ 11 points, each point 200 m apart, each transect was surveyed three times). We also compared our results to published bird densities from Southeast Asia. A total of 149 bird species were recorded, including two globally threatened species (Short-toed Coucal *Centropus rectunguis* and Sunda Blue-flycatcher *Cyornis caerulatus*) and 39 globally near-threatened species. We present densities for 102 species (45% of lowland bird specialist (i.e. species occur below 200 meter boundary in Sumatra). The Wilcoxon rank test revealed that the density of threatened/near-threatened species was significantly lower than that of the non-threatened species. Compared to densities from secondary forest in Borneo, three species in our study area had significant higher density while four species had lower density. The mosaic of secondary forest habitats in different stages of regeneration in the HRF appears to support some groups better (mostly woodpeckers such as the Buff-rumped Woodpecker *Meiglyptes tristis* of 11.6 birds/km$^2$ in HRF, but 2.2 birds/km$^2$ in Borneo), and others less well (e.g. understory insectivores such as Brown Fulvetta *Alcippe brunneicauda*: 9.4 birds/km$^2$ in HRF, but 57.8 birds/km$^2$ in Borneo). Bird densities are important to establish population baselines, allowing comparisons between studies. Due to paucity of information, we urge more studies to be conducted to provide better understanding on variation of bird density over time and space, particularly in Southeast Asia.

**Keywords:** Avifauna, secondary forest, abundance, threatened species, Sumatra, Sundaic

## INTRODUCTION

Tropical forests cover only 10% of the land surface, but support high species density (Dirzo and Raven 2003). However, tropical forest is disappearing fast, especially in Southeast Asia (Laurence 1999, Sodhi et al. 2010). With about 138 million ha or 10% of the world's remaining tropical forests, Indonesia holds one of the largest areas of tropical forest of any country, but also the highest deforestation rate in the world. On Sumatra, the sixth largest island in the world, secondary forest has replaced much of its primary tropical rainforest, particularly in the lowland area (Wilcove et al. 2013). A recent study reveals that 70% of the island's forested areas have been intensively cleared from 1990 through to 2010 and have left just 23.1 thousand km$^2$ of primary forest in degraded condition, with logging as the main driver (Margono et al. 2012).

The importance of secondary forest (i.e. selectively logged primary forest) for tropical biodiversity conservation has been increasingly acknowledged (Johns 1989, Sodhi et al. 2005, Sekercioglu et al. 2007, Edwards et al.2010, Edwards et al. 2011, Wilcove et al. 2013). In Southeast Asia, logged forests are now perhaps the main forest habitat remaining for forest-dependent birds. Unfortunately, the value of logged forest is still largely unevaluated (Waltert et al. 2004). It is necessary to accurately determine the actual conservation value of logged forest, which may influence decisions in forest management (Barlow et al. 2006). Densities of animals are the basis for monitoring populations and assessing the success or failure of conservation management (Gale and Thongaree 2006). Accurate assessments of habitat suitability through measurement of density estimate (hereafter density) that incorporates information about detectability can provide a more valuable insight to the forest managers as they can be compared over time or space without the risk of bias (Karanth and Nichols 1998, Fancy and Sauer 2000, Norvell et al. 2003).

There are few published quantitative studies of bird species density in Indonesia (e.g. Marsden et al. 1997, Marsden 1999), and only two Sumatran studies provide densities, four hornbill species (Anggraini et al. 2000) and the Argus pheasant *Argusianus argus* (Winarni et al. 2009). The aim of this study was to: (1) provide baseline bird densities in secondary forest and (2) to compare the derived bird densities to those from other studies conducted in Southeast Asia.

## METHODS

*Study area*. Harapan Rainforest Ecosystem Restoration Concession (HRF, 984.5km$^2$) is the first ecosystem restoration concession in Indonesia (http://www.harapanrainforest.org), covering two large selectively logged primary forest that are located in Jambi (491.8 km$^2$) and South Sumatra Provinces (492.7 km$^2$), Indonesia. The overall aim is to conserve and restore the forest to its original primary condition for the benefit of biodiversity, local communities and ecosystem services. Previous logging activities have left a mosaic of secondary forest habitats in different stages of regeneration (Lee and Lindsell 2011). The HRF is a lowland site ranging in elevation from 30-120 m above sea level. The study was conducted in Jambi Province, where logging was ceased in 2006 and the license was granted in 2010 (Yusup Cahyadin *pers.comm*, Lee and Lindsell 2011).

*Survey methodology*. We conducted bird point-transect surveys between April-June 2011, during the breeding season of most birds in Sumatra (Marle and Voous 1988, Thiollay 1995). The point transect method is a preferred method for surveying multi-species surveys in tropical forests (Bibby et al. 2000, Lee and Marsden 2008). Eleven transects (each transect was 2 km long and at least 1 km apart from the next transect) were placed randomly to cover various secondary forest conditions in the study area. Within each transect, we had 11 point observations, each point was spaced 200 m apart to maintain independent bird detection at consecutive points (Reynolds et al. 1980, Hutto et al. 1986). Although recording the same birds at consecutive points is a mild violation of the method's assumption that detections are independent and does not introduce bias (Buckland 2006). Surveys were conducted in the morning from 06:30 to 10:00 (10 minutes survey per point) to coincide with the peak period of bird activity (Lee and Marsden 2008), and were conducted by a single observer (the first author who has experienced on bird survey in Sumatra) and one note taker for the whole survey to reduce observer bias. At each point, survey was conducted immediately after the observer arrived (without settling down period) and any birds detected moving away from around the survey point on the observer's arrival was counted as being present during the count period (Lee and Marsden 2008). All birds observed/detected were recorded along with the estimated vertical height and horizontal distance from the survey point to the bird's initial position or to center of single species group (estimated using digital Rangefinder). We recorded flying birds observed during the point count period but omitted them from the analysis as they violate an assumption of the method (Buckland et al. 2001). We also recorded crepuscular/nocturnal species (e.g. *Caprimulgus* spp.) and large raptors, but these were also omitted from the analysis this survey method cannot be used to survey this group effectively (Marsden 1998). Sound recordings were also made per point to aid species identification by discussing with other bird experts and comparing with known bird recordings (e.g. from http://www.xeno.cantho.org). Each transect was surveyed three times, if possible on three consecutive days (during the non-rainy day and no strong winds), but if not the survey was conducted on the next possible day. Whenever possible we rotated the daily order in which transects was visited. Repeating point transects in the opposite direction on different days helps minimize the influence of changes in bird activity, hence detection during a survey (Jones 1998). Sample size of scarce species is increased by repeating points (Buckland et al. 2001, Rosenstock et al. 2002).

*Statistical analysis.* In the analysis, transect was taken as the sampling unit, and bird records from the three survey repetitions per transect were pooled per transect, thus the total survey effort for each transect was 33 (11 points/transect times three survey repetitions per point-transect). Both aural and visual observations were combined. We used Distance v.6.0 (Thomas et al. 2010) to calculate bird densities. Densities were calculated for species that were recorded $\geq$ 10 times. For each species, we right-truncated the data, trying several different truncation distances (and if necessary a posteriori grouping of data into several distance bands) and selecting the one that provided the lowest coefficient of variation of the density. We followed up by testing with different key functions (uniform, half normal, and hazard rate functions with adjustment) and selected the model with the lowest Akaike's Information Criterion (AIC; Akaike 1974) as the best model that fit the data (Buckland et al. 2001). In addition, to assess the model fit, we also used Chi-square test for grouped distance data or Kolmogorov-Smirnov goodness-of-fit and Cramér-von Mises goodness-of-fit statistic for distance data that were not grouped (Buckland et al. 2001).

To produce densities for rare species (i.e. species with low sample size) we applied multiple-species modeling framework as proposed by Alldredge et al. (2007). This framework was applied by “borrowing” the information about detection processes from more common similar species. However, the decision of which species should be grouped together is crucial as wrong grouping will produce unreliable densities (Mead 2008). To avoid this we proceeded as follows: for near-threatened species detected < 10 times (rare species), we found common species from the same genus or family with the rare species. We then considered their similarity in body size and call characteristics. For example, the Large-billed Blue-flycatcher *Cyornis caerulatus* is a rare near-threatened species in our study area. An intensive mist-net study in the same study area by Hua et al. (2011) only captured two individuals out of 454 total bird captures (Hua et al. 2011). To calculate density for this species using the multiple-species modeling framework, we borrowed the detection process from the Pale-blue

Flycatcher *Cyornis unicolor*. These species come from the same family (Muscicapidae) and genus (*Cyornis*), have similar body size (< 20 gram), and call characteristic (high pitch).

In this multiple-species analysis, species identity was entered as an observation-level variable which produces density per-species within a group through post stratification by species (Marques et al. 2001, Rosenstock et al. 2002). The model selection process was as explained previously in the single species approach, with an additional procedure where we conducted post stratification by species with a pooled detection function to produce density for each species.

A Wilcoxon Rank test was conducted to see if there were statistically significant differences between the densities of threatened/near-threatened species and non-threatened species. We searched literature for studies that provide bird density data for species in the Sundaic region (Sumatra, Java, Kalimantan, Peninsular Malaysia, and the Phillipine) and also recorded during the present study, and provided a summary and statistically compared these densities with results from our study. The comparison of densities was only conducted with studies that produced densities (and included coefficient of variations in their publications). The comparisons were conducted using the Z-tests (Plumptre 2000). The bird taxonomy in this study follows BirdLife International (2013a).

## RESULTS

A total of 149 bird species (5,317 individual birds) were recorded during the point-transect surveys. These included two vulnerable species (Large-billed Blue-flycatcher *Cyornis caerulatus* and Short-toed Coucal *Centropus rectunguis*) and 39 near-threatened species. Eight species were recorded 100 times or more, 83 species between 10 and 99 times, and 53 species less than 10 times. Based on habitat preference (Styring et al. 2011), 77 species were classified as edge tolerant forest specialist, 44 bird species as forest specialist, 11 species as edge specialist, 9 as open country species, and 8 species as generalist.

Overall, we were able to produce densities for 102 bird species, with reasonably precise estimates (as demonstrated by the coefficient of variation being < 50%). Full densities are provided in Appendix 3.1. We did not produce density for large raptors, and bird species with < 10 detections unless they were threatened or near-threatened species (BirdLife International 2013b). Densities of eleven species that were recorded < 10 times, consisting of one vulnerable species and 10 near-threatened species, were produced using the multiple-species modeling framework. Table 3.1 shows their densities, and also lists the bird species from which the detection function was borrowed. There are two exceptions in our species selection. To produce density for Short-toed Coucal (family Cuculidae), we combined it with data from Emerald Dove *Chalcophaps indica* (family Columbidae). We considered this as the best available species considering that the Emerald Dove shares similar characteristics with the Short-toed Coucal: deeper voice, and mostly active near the ground. The density for

Garnett Pitta *Pitta granatina* (family Pittidae) was produced by borrowing detection process from Rail Babbler *Eupetes macrocerus* (family Eupetidae). These two species mostly active near the ground and have similar call characteristics: similar rhythm but slightly different in pitch.

Table 3.1. Species groupings and densities for infrequently recorded (< 10 times) birds using multiple-species approach

| Species | Species | $^1$IUCN status | $^2$n | Density (birds/km$^2$) | %CV | 95% CI | |
|---|---|---|---|---|---|---|---|
| | | | | | | lower | upper |
| Cuculidae, > 100 gram understory bird | Short-toed Coucal *Centropus rectunguis* | VU | 8 | 0.6 | 26.7 | 0.4 | 1.1 |
| Columbidae, > 200 gram understory bird | Emerald Dove *Chalcophaps indica* | | 37 | | | | |
| Muscicapidae, < 22 gram understory flycatcher | Large-billed Blue-flycatcher *Cyornis caerulatus* | VU | 2 | 0.8 | 28.7 | 0.5 | 1.6 |
| | Malaysian Blue-flycatcher *Cyornis turcosus* | NT | 2 | 1.1 | 21.9 | 0.6 | 1.7 |
| | Pale Blue-flycatcher *Cyornis unicolor* | | 10 | | | | |
| Alcedinidae, 40-70 gram, foraging in understory | Rufous-collared Kingfisher *Actenoides* | NT | 7 | 0.9 | 0.5 | 0.9 | 1.0 |
| | Banded Kingfisher *Lacedo pulchella* | | 21 | | | | |
| Pycnonotidae, 25-36 gram | Puff-backed Bulbul *Pycnonotus eutilotus* | NT | 6 | 4.6 | 16.5 | 3.1 | 6.9 |
| | Cream-vented Bulbul *Pycnonotus simplex* | | 87 | | | | |
| Cuculidae, <62 gram arboreal foliage-gleaning insectivore malkoha | Black-bellied Malkoha *Phaenicophaeus diardi* | NT | 4 | 1.8 | 8.2 | 1.5 | 2.1 |
| | Raffles's Malkoha *Phaenicophaeus chlorophaeus* | | 39 | | | | |
| Picidae, medium-large (70-150 gram) woodpecker | Oliva-backed Woodpecker *Dinopium rafflesi* | NT | 2 | 0.5 | 16.7 | 0.4 | 0.7 |
| | Buff-rumped Woodpecker *Meiglyptes tristis* | | 25 | | | | |
| Timaliidae, < 24 gram arboreal foliage-gleaning insectivore/ understory, forest specialist babbler | White-necked Babbler *Stachyris leucotis* | NT | 2 | 0.7 | 29.2 | 0.4 | 1.3 |
| | Grey-headedBabbler *Stachyris poliocephala* | | 13 | | | | |
| Pittidae, 53 gram terrestrial insectivore of | Garnet Pitta *Pitta granatina* | NT | 6 | 1.9 | 23.8 | 1.2 | 3.1 |
| Eupetidae, 50 gram terrestrial insectivore of | Rail Babbler *Eupetes macrocerus* | | 21 | | | | |
| Timaliidae, 19-50 gram terrestrial insectivore of forest interior | Large Wren-babbler *Turdinus macrodactylus* | NT | 3 | 0.6 | 17.1 | 0.5 | 1.0 |
| | Striped Wren-babbler *Kenopia striata* | NT | 6 | 1.4 | 16.4 | 1.0 | 1.9 |
| | Black-capped Babbler *Pellorneum capistratum* | | 40 | | | | |
| Dicaeidae, < 20 gram flowerpecker | Scarlet-breasted Flowerpecker *Prionochilus thoracicus* | NT | 2 | 2.2 | 5.3 | 2.0 | 2.5 |
| | Orange-bellied Flowerpecker *Dicaeum trigonostigma* | | 76 | | | | |

Densities were only generated for species under Vulnerable and Near-threatened status. CI indicates the 95% confidence interval around the density and % CV the coefficient of variation of the density.

[1] VU, Vulnerable; NT, Near Threatened (BirdLife International 2013b)

[2] Observed count

The density of globally threatened and near-threatened species was significantly lower than that of non-threatened species (W=615, $p<0.001$). Figure 3.1 shows densities for globally conservation concerned species (40 species). The density for Large-billed Blue-flycatcher (a threatened species) was 0.8 birds/km$^2$. From a total of 39 near-threatened species, 30 species had densities less than 10 birds/km$^2$ with the lowest density for Olive-backed Woodpecker *Dinopium rafflesii* (0.3 birds/km$^2$), White-necked Babbler *Stachyris leucotis* (0.3 birds/km$^2$), and Helmeted Hornbill *Rhinoplax vigil* (0.4 birds/km$^2$), and only 10 species had densities $\geq$ 10 birds/km$^2$ particularly for Green Iora *Aegithina viridissima* and Buff-vented Bulbul *Iole olivacea* with density of more than 40 birds/km$^2$ (Figure 3.1). The density for the non-threatened species ranged from 1.0 birds/km$^2$ for Indian-cuckoo *Cuculus micropterus* to 164.7 birds/km$^2$ for Little Spiderhunter *Arachnothera longirostra*.

We compared our densities with densities from study using sampling method that incorporate detection probabilities. Unfortunately, only two studies in Southeast Asia that can be used, from logged forest in Borneo for understory birds (Mead 2008) and tropical lowland evergreen forest in Thailand for hornbills (Gale and Thongaree 2006). We compared our densities with densities from these studies (Table 3.2). Comparing with density from logged forest in Borneo, our densities showed significant difference for seven species: four species in our study area had lower density and three had higher density compared to logged forest in Borneo. Bird species in our study area that had higher densities than in Borneo for example were Buff-rumped Woodpecker *Meiglyptes tristis* and

Greater racket-tailed Drongo *Dicrurus paradiseus*. As for those with lower density than in Borneo were, for example, Hairy-backed Bulbul *Tricholestes criniger* and Little Spiderhunter *Arachnothera longirostra.* Comparing densities of hornbills between our results with results from a study in Thailand (Table 2) showed that one species had significant higher density (Wrinkled Hornbill *Aceros corrugatus*) and two had significantly lower density (e.g. Rhinoceros Hornbill *Buceros rhinoceros*) in our study area.

Tabel 3.2. Densities ($km^2$ with % Coefficient of variation) for birds found in Harapan Rainforest compared with densities from tropical lowland evergreen forest in Thailand ([a]Gale and Thongaree 2006) and logged forest in Borneo ([b]Mead 2008). Asterisks indicate significance at $p < 0.05$. The negative sign shows higher density in our study area while positive sign shows higher density in other studies.

| Species | Density from other study | Density from the current study | Z test |
|---|---|---|---|
| Wrinkled Hornbill *Aceros corrugatus* | 0.08(26)[a] | 0.7(37.3) | -2.37* |
| Bushy-crested Hornbill *Anorrhinus galeritus* | 0.64(36)[a] | 4.6(48.7) | -1.76 |
| Rhinoceros Hornbill *Buceros rhinoceros* | 2.69(14)[a] | 1.2(28) | 2.95* |
| Helmeted Hornbill *Rhinoplax vigil* | 1.21(19)[a] | 0.4(24.6) | 3.24* |
| Buff-rumped Woodpecker *Meiglyptes tristis* | 2.2(47.8)[b] | 11.6(16.2) | -4.37* |
| Buff-necked Woodpecker *Meiglyptes tukki* | 6.8(54.8)[b] | 8(18) | -0.3 |
| Rufous winged flycatcher *Philentoma pyrhopterum* | 12.2(41.1)[b] | 17.3(18.3) | -0.86 |
| Grey-chested Jungle-flycatcher *Rhinomyias umbratilis* | 6.1(26.3)[b] | 6.7(5.5) | -0.36 |
| Yellow-bellied Bulbul *Alophoixus phaeocephalus* | 28.6(22)[b] | 25.6(13.5) | 0.42 |
| Grey-cheeked Bulbul *Alophoixus bres* | 14.5(23)[b] | 9.7(6.4) | 1.41 |
| Hairy-backed Bulbul *Tricholestes criniger* | 238.5(22.5)[b] | 73.8(9.8) | 3.04* |
| Scarlet-rumped Trogon *Harpactes duvaucelii* | 1.1(53)[b] | 4.5(3.8) | -5.6* |
| Greater racket-tailed Drongo *Dicrurus paradiseus* | 10.6(27.5)[b] | 21.5(14.9) | -2.52* |
| Garnet Pitta *Pitta granatina* | 11.2(17.6)[b] | 1.9(23.8) | 4.60* |
| Asian Green Broadbill *Calyptomena viridis* | 3(37.1)[b] | 4(26.8) | -0.65 |
| Banded Broadbill *Eurylaimus javanicus* | 3.4(45.8)[b] | 3(10.4) | 0.25 |
| Maroon Woodpecker *Blythipicus rubiginosus* | 3(56.5)[b] | 5.2(34.6) | -0.89 |
| Purple-naped Sunbird *Hypogramma hypogrammicum* | 49.8(47.9)[b] | 25.2(12.1) | 1.02 |
| Brown fulvetta *Alcippe brunneicauda* | 57.8(15.9)[b] | 9.4(5.9) | 5.26* |
| Little spiderhunter *Arachnothera longirostra* | 413.7(18.1)[b] | 164.7(8.9) | 3.26* |

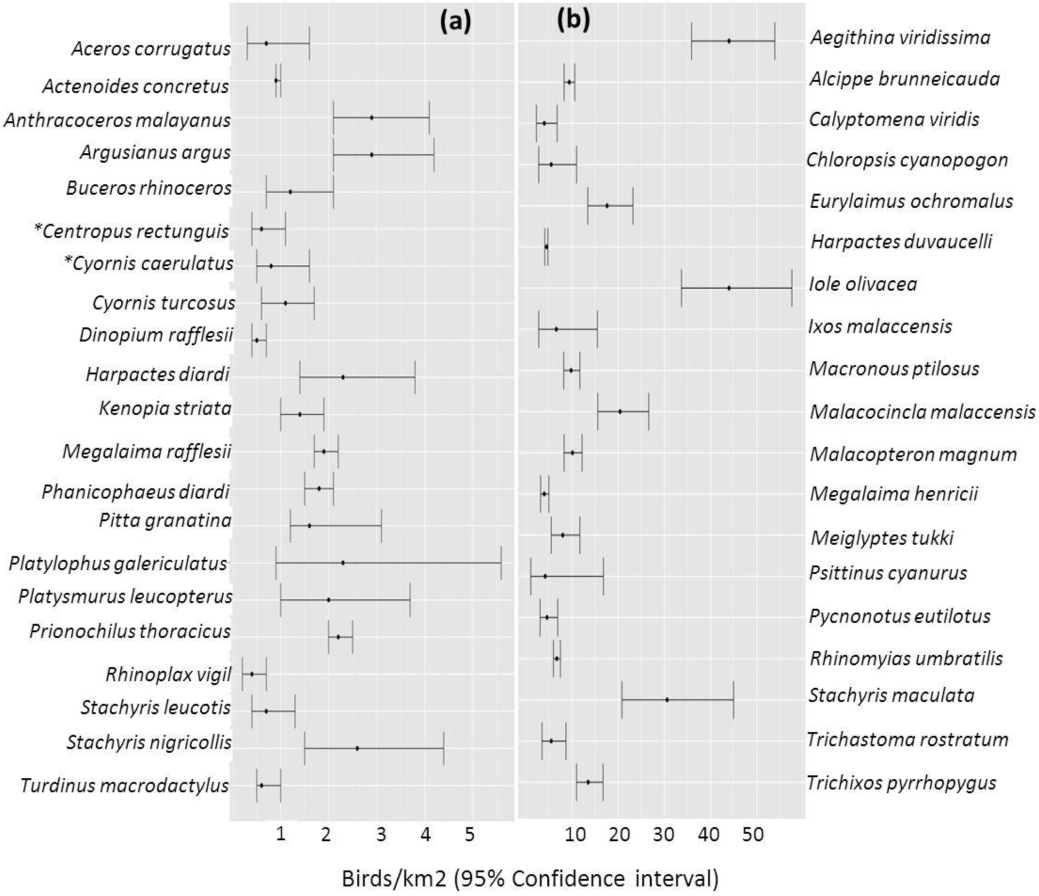

Figure 3.1. Densities (birds/km$^2$ with 95% Confidence interval) of threatened (*) and near-threatened species. (a) density < 5 birds/km$^2$, (b) density > 5 birds/km$^2$.

## DISCUSSION

We present densities for 102 lowland bird species in Sumatra (approximately 45% of the 228 lowland bird specialists (Wells 1985) in Sumatra), thereby improving the information status for density for avifauna in Sundaic region (Java, Sumatra, Kalimantan, Peninsular Malaysia, the Philippine). This is specifically important for Sumatra where densities were previously only available for four species (Anggraini et al. 2000, Winarni et al. 2009). Our results include densities for two threatened species, Large-billed Blue-flycatcher *Cyornis caerulatus* and Short-toed Coucal *Centropus rectunguis*, and 39 near-threatened species. Density information is still limited for many of these species, thus one reason why their global population sizes have not been quantified to date (BirdLife International 2013b). In addition, the densities presented here were resulted from collecting data using sampling method that utilize detection probabilities. This approach will assure that our results can be compared statistically with densities from other studies.

Multi-species modeling framework can be used to produce densities for rare species by borrowing information from more abundant congeners selected on the basis of similarity in phylogeny, body size, and qualitative assessment on bird call characteristics (Alldredge et al. 2007). While this can be dangerous when extrapolation is not carefully done, a transparent and well-justified species selection procedure makes it possible to produce reasonable estimates of density for rare species, which could otherwise not be produced. Nevertheless, for species that are recorded on fewer occasions, two or more species could be combined to create detection template, hence density can be estimated for the rare species (Marsden et al. 1997). For example Marsden et al. (1997) combine records of Tawny-backed Fantail *Rhipidura superflua* with similar but more often recorded species Northern Fantail *Rhipidura rufiventris* to model the detection function and calculate the density of the former. Also, records of the two *Monarcha* species and Dark-grey Flycatcher *Myiagra galeata* were combined to create a "monarch detection function" and this is used to calculate a density estimate for each species (Marsden et al. 1997). Using this approach, we managed to calculate densities for 12 species with global conservation concern. This information is an important component for establishing species global population size, particularly for 10 out of these 12 species where global population size have not been quantified. Particularly important are for species of global conservation concerned where their population size are unknown, i.e. Grey-chested Jungle-flycatcher *Rhinomyias umbratilis*, Malaysian Blue-flycatcher *Cyornis turcosus,* and Lesser Green Leafbird *Chloropsis cyanopogon* (BirdLife International 2013b). In our study area, the density for the two flycatchers were 0.8 birds/km$^2$ for Large-billed Blue-flycatcher and 1.1 birds/km$^2$ for Malaysian Blue-flycatcher, while for the leafbird it was 5.5 birds/km$^2$.

The global population sizes of two species with global conservation concern (Short-toed Coucal and Large-billed Blue-flycatcher) detected in our study area was available, and thus proportion from this global population within our study area could be defined. The global population size for Short-toed Coucal is 15,000 – 30,000 individuals, and 6000-15000 individuals for Large-billed Blue-flycatcher (BirdLife International 2013b). Extrapolating our results to cover part of HRF where the study was conducted (i.e. 491.8 km$^2$ concession area in Jambi Province) revealed that this area had approximately 1-2 % of the global population for Short-toed Coucal and 2-5 % for Large-billed Blue-flycatcher.

Extrapolation to cover a larger area or island based on survey in small part of the species distribution might yield unrealistic figures and should be avoided (Mallari et al. 2011). Differences in densities from different islands might reflect island or site level effects such as hunting pressure and specific habitat preference (McConckey and Chivers 2004) as well as scarcity of lowland habitat, habitat isolation, variations in forest fruit (Wich et al. 2011), and interspecific competition (Gale and Thongaree 2006). In other words, it is unrealistic to expect that densities from secondary forest in our study could reflect abundance in secondary forest elsewhere.

However, the variation of densities across different habitat types or areas could be statistically compared. This comparison can be made for studies that incorporate detection probabilities hence would allow comparison between sites, habitats and levels of disturbance more robust and easier to be done (Gale and Thongaree 2006). For studies that only produce encounter rate, it is difficult to compare over time and areas (Jones et al. 1995). Unfortunately, there are few studies in Southeast Asia tropical to date that incorporate distance estimation hence producing quantitative and comparable densities (Jones et al. 1995, Marsden et al. 1997, Gale and Thongaree 2006, Mallari et al. 2011), and only two for Sumatra birds (Anggraini et al. 2000, Winarni et al. 2009). Moreover, it should be noted that to compare densities between, for example, two areas statistically one also needs to know the standard error (or coefficient of variation) for the densities. Not all studies present this information. For example, Anggraini et al. (2000) provides one of the first densities for hornbills from Sumatra. Unfortunately we could not statistically compare the results with our study as the previous study does not provide information on the standard error.

Nevertheless, based on available densities from two studies (*see* Table 3.2) we found that compared to logged forest, several of our densities were significantly higher. For example, Scarlet-rumped Trogon *Harpactes duvaucelii* had significantly higher density in our study than in logged forest in Borneo (4.5 birds/km$^2$ and 1.1 birds/km$^2$, respectively). This species is found in lowland primary and logged forests, and intolerant of disturbance to canopy cover (BirdLife International 2013b). This difference in density might possibly due to different disturbance regimes between Borneo and our study area. Putz et al. (2001) concludes that different logging intensities in the tropics are creating great challenges for evaluating the effect of logging.

Moreover, comparing the hornbill densities with study from Bala forest (i.e. tropical lowland evergreen forest) in Thailand (Gale and Thonggaree 2006) also revealed interesting results. We found that one species had higher density in our study area, Wrinkled Hornbill *Aceros corrugatus*. Though it is first surprising, but we think that this is actually indicating the possible difference in natural abundance of hornbills between different forest types and areas. In their study, Gale and Thonggaree (2006) shows that hornbill densities in their study areas are generally lower (but not statistically tested) compared to areas in South and Southeast Asia. As pointed out earlier that scarcity of lowland habitat, habitat isolation, variations in forest fruit might cause different in density across areas from different region.  As such, density comparison perhaps should be conducted for studies within the same region (i.e. comparing our results from study in other part of Sumatra Island). This unfortunately was not statistically possible as the only available densities do not accompanied by information on standard error.

Although could not be compared statistically, we presented in Table 3.3 available densities from studies in Southeast Asia. This aims to provide general overview of density variation across different habitat and areas (islands). Our hornbill densities tend to be lower than densities from lowland tropical forest in the Bukit Barisan Selatan National Park in South-western Sumatra (BBS), particularly for Helmeted Hornbill *Rhinoplax vigil* (4 times lower) but not for Bushy-crested Hornbill *Anorrhinus galeritus*. For Helmeted Hornbill this is not surprising, as this species is classified as a forest dependent species (BirdLife International 2013), indicating that secondary forest is likely less suitable for this species.

On the other hand, Bushy-crested Hornbill prefers closed canopy forest and has been shown to strongly avoid disturbed areas (Anggraini et al. 2000).

Despite this, our density for Bushy-crested Hornbill is slightly higher than density from South-western Sumatra (BBS) and North Sumatra, and much higher if compared with density from Thailand (4.6 birds/km$^2$ in the study site vs 0.6 birds/km$^2$ in Thailand). We think that this reflects the mosaic secondary forest patches in the study site that still provides good habitat for this species. However, a long-term monitoring is needed to examine the possibility of temporal variations in density.

Woodpeckers in the Sundaic region have been well studied in Peninsular Malaysia (Styring and Hussin 2004(a)(b), Styring and Ickes 2001 (a)(b), Short 1978) and Kalimantan (Lammertink 2004). Our densities are mostly higher compared to densities from logged forest in Kalimantan and even compared to primary lowland forest in Peninsular Malaysia (Table 4.3). This might be due to the mosaic of habitat conditions such as high, medium and low secondary forest in our study, which provided suitable and heterogeneous habitat conditions for a wide range of woodpecker species. Based on perch diameters and microhabitats used, Styring and Hussin (2004b) divide the woodpeckers into two big groups: conventional foragers, which excavate frequently, use relatively larger perches and forage on snags and patches of dead wood, contrasting with novel foragers, which use smaller patches and microhabitats that are always available year round in the tropical forest such as arboreal ant/termite nests. The habitat mosaic in our study area might possess these suitable characteristics hence provides complementary resources supporting high abundance of woodpecker species.

Table 3.3. Densities (birds/km$^2$) for birds found in Harapan Rainforest compared with studies elsewhere in Southeast Asia

| Species | Present study | [(a)] Logged lowland forest, Gunung Palung, Kalimantan | [(b)] Logged forest outside Danum Valley, Sabah | [(c)] Lowland forest, Way Canguk, Sumatra | [(d)] Lowland dipterocarp, Barito Ulu, Cental Kalimantan | [(e)] Tropical lowland evergreen, Bala Wildlife Sanctuary, Thailand | [(f)] Lowland forest, Pasoh, Negeri Sembilan | [(g)] Primary forest, Danum Valley, Sabah | [(h)] Mature forest, Khao Yai National Park, Thailand | [(i)] Old growth, Puerto Princesa Subterranean River National Park, the Philippine |
|---|---|---|---|---|---|---|---|---|---|---|
| Wrinkled Hornbill *Aceros corrugatus* | 0.7 | | | | 0.3 | 0.1 | | | | |
| Bushy-crested Hornbill *Anorrhinus galeritus* | 4.6 | | | 3.05 | 5.5 | 0.6 | | | | |
| Black Hornbill *Anthracoceros malayanus* | 2.9 | | | | 3.4 | 0.1 | | | | |
| Rhinoceros Hornbill *Buceros rhinoceros* | 1.2 | | | 2.6 | 3.7 | 2.7 | | | | |
| Helmeted Hornbill *Rhinoplax vigil* | 0.4 | | | 1.9 | 0.7 | 1.2 | | | | |
| Maroon Woodpecker *Blythipicus rubiginosus* | 5.2 | 1.7 | 3 | | | | 3.9 | 22 | | |
| White-bellied Woodpecker *Dryocopus javensis* | 2.4 | 0.5 | | | | | 1.5 | | | |
| Buff-rumped Woodpecker *Meiglyptes tristis* | 11.6 | 0.9 | 2 | | | | 1.5 | 9 | | |
| Buff-necked Woodpecker *Meiglyptes tukki* | 8.0 | 5.3 | 7 | | | | 5.4 | 27 | | |
| Checker-throated Woodpecker *Picus mentalis* | 2.0 | 1.2 | | | | | 2.3 | | | |
| Crimson-winged Woodpecker *Picus puniceus* | 3.6 | 1.2 | | | | | 2.3 | | | |
| Orange-backed Woodpecker *Reinwardtipicus validus* | 5.8 | 4.3 | | | | | 1.5 | | | |
| Rufous Piculet *Sassia abnormis* | 12.4 | 4.9 | | | | | 3.9 | | | |
| Black-naped Monarch *Hypothymis azurea* | 25.6 | | | | | | | | 64 | 12.2 |
| Garnet Pitta *Pitta granatina* | 2.2 | | 11 | | | | | 10 | | |
| Chestnut-winged Babbler *Stachyris erythroptera* | 31.5 | | 50 | | | | | 164 | | |
| Fluffy-backed Tit-babbler *Macronous ptilosus* | 9.8 | | 41 | | | | | 63 | | |
| Short-tailed Babbler *Malacocincla malaccensis* | 20.4 | | 73 | | | | | 115 | | |
| Brown fulvetta *Alcippe brunneicauda* | 9.4 | | 58 | | | | | 224 | | |
| Grey-headed Babbler *Stachyris poliocephala* | 5.4 | | 49 | | | | | 21 | | |
| Little spiderhunter *Arachnothera longirostra* | 164.7 | | 414 | | | | | 255 | | |
| Grey-cheeked Bulbul *Alophoixus bres* | 9.7 | | 15 | | | | | 23 | | |
| Hairy-backed Bulbul *Tricholestes criniger* | 73.8 | | 239 | | | | | 212 | | |
| Purple naped Sunbird *Hypogramma hypogrammicum* | 25.27 | | 90 | | | | | 22 | | |
| Scarlet-rumped Trogon *Harpactes duvaucelii* | 4.5 | | 1 | | | | | 4 | | |
| Banded Broadbill *Eurylaimus javanicus* | 3.0 | | 3 | | | | | 11 | | |
| Grey-chested Jungle-flycatcher *Rhinomyias umbratilis* | 6.7 | | 6 | | | | | 22 | | |
| Rufous winged flycatcher *Philentoma pyrhopterum* | 17.3 | | 12 | | | | | 73 | | |
| Black-capped Babbler *Pellorneum capistratum* | 13.5 | | 8 | | | | | 72 | | |
| Greater racket-tailed Drongo *Dicrurus paradiseus* | 21.5 | | 11 | | | | | 14 | | |

[(c)] Anggraini et al. (2000), [(d)] McConkey and Chivers (2004), [(e)] Gale and Thongaree (2006), [(a)] Lammertink (2004), [(f)] Short (1978), [(g) (b)] Mead (2008), [(i)] Mallari et al. (2011), [(h)] Gale et al. (2009)

Styring and Ickes (2001a) suggest that the low abundance of Buff-rumped Woodpecker *Meiglyptes tristis* in logged forest in Peninsular Malaysia is due to the logging scheme in Malaysia. In this scheme, large non-commercial trees, lianas and snags can be removed to provide more resources for commercial trees. This resulted in even aged stand with fewer snags, gaps, and smaller lianas even decade's afterwards hence unsuitable habitat for this species. Lammertink (2004) shows that 85% density reduction of Checker-throated Woodpecker *Picus mentalis* in Kalimantan logged forest is correlated with quantity of timber removed. This probably indicates that the habitat condition in our study area is slightly better for this species than in logged forest in Kalimantan (2.0 birds/km$^2$ vs 1.2 birds/km$^2$).

Other bird species for which we were able to find densities from other studies also shared similar trend as in the hornbill and woodpecker comparison, i.e some species had higher density compared to density in logged or unlogged forest, while others had lower or similar density. The density for Argus pheasant *Argusianus argus* was 2.54 birds/km$^2$. This density is still within the range of densities from South-western Sumatra, 0.9-3.7 birds/km$^2$ (Winarni et al. 2009). This species prefers undisturbed forest (Winarni et al. 2009) and is very sensitive to hunting, but seems to be relatively tolerant of logging (Sozer et al. 1999). It seems that this species fares quite well in our study area. Compared with densities from logged forest in Sabah-Kalimantan (Mead 2008, Table 3.3), 10 species in our study had lower densities (e.g. Grey-cheeked Bulbul *Alophoixus bres*), three had similar densities (e.g. Scarlet-rumped Trogon *Harpactes* *duvaucelii*, and three had higher densities (e.g. Greater racket-tailed Drongo *Dicrurus paradiseus*). These again highlight variations in density which is possibly due to, for example, different disturbance regimes: Putz et al. (2001) concludes that different logging intensities in the tropics are creating great challenges for evaluating the effect of logging.

In summary, we added densities for 102 Sumatra secondary lowland forest birds. The mosaic habitat patches typical of selectively logged forest seems to support some group better and other less well. Through comparison between densities in our study area with available densities from other sites/islands, we highlighted the relative importance of secondary forest for bird conservation. Moreover, variations in densities between secondary forest across different sites or between secondary forest and unlogged forest were also examined. These variations show the importance to conduct studies on other sites, islands, or different habitat conditions. In addition, we also strongly encourage the use of sampling method that incorporate detection probabilities and the result presentation should include the coefficient of variation (or standard error) to enable statistical comparison between sites, habitats, and level of disturbances. Lastly, studies to show species persistence in longer term should be conducted to justify the long-term suitability of secondary forest for forest birds (Barlow et al. 2006).

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## Appendix 3.1.Bird species recorded, IUCN status, body size, guilds and density estimates

| [a]Grp | Family | Common name | Scientific name | [b]IUCN | [c]mass | [d]hb | [e]guild | [f]n | [g]D | [h]%CV | [i]95% CI | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | lower | upper |
| 1 | Accipitridae | Crested Serpent-eagle | *Spilornis cheela* | | large | G | dp | | | | | |
| 2 | Aegithinidae | Green Iora | *Aegithina viridissima* | NT | small | ETF | afgin | 126 | 44.0 | 10.4 | 35.9 | 53.9 |
| 3 | Alcedinidae | Banded Kingfisher | *Lacedo pulchella* | | medium | FS | mip | 21 | 2.8 | 1.2 | 2.7 | 2.9 |
| 4 | Alcedinidae | Rufous-collared Kingfisher | *Actenoides concretus* | NT | medlarge | FS | afginus | 7 | 1.3 | 0.6 | 1.2 | 1.3 |
| 5 | Alcedinidae | Blue-eared Kingfisher | *Alcedo meninting* | | small | ETF | mip | 7 | | | | |
| 6 | Alcedinidae | Rufous-backed Kingfisher | *Ceyx rufidorsa* | | small | FS | afginus | 5 | | | | |
| 7 | Alcedinidae | Black-backed Kingfisher | *Ceyx erithaca* | | small | FS | afginus | 3 | | | | |
| 8 | Bucerotidae | Black Hornbill | *Anthracoceros malayanus* | NT | large | ETF | afp | 28 | 2.9 | 16.7 | 2.1 | 4.1 |
| 9 | Bucerotidae | Rhinoceros Hornbill | *Buceros rhinoceros* | NT | large | ETF | afp | 27 | 1.2 | 28.0 | 0.7 | 2.1 |
| 10 | Bucerotidae | Helmeted Hornbill | *Rhinoplax vigil* | NT | large | ETF | afp | 14 | 0.4 | 24.6 | 0.2 | 0.7 |
| 11 | Bucerotidae | Bushy-crested Hornbill | *Anorrhinus galeritus* | | large | FS | afp | 13 | 4.6 | 48.7 | 1.7 | 12.2 |
| 12 | Bucerotidae | Wrinkled Hornbill | *Aceros corrugatus* | NT | large | ETF | afp | 10 | 0.7 | 37.3 | 0.3 | 1.6 |
| 13 | Bucerotidae | Wreathed Hornbill | *Aceros undulatus* | | large | ETF | afp | 7 | | | | |
| 14 | Bucerotidae | White-crowned Hornbill | *Aceros comatus* | NT | large | FS | afp | | | | | |
| 15 | Campephagidae | Black-winged Flycatcher-shrike | *Hemipus hirundinaceus* | | small | ETF | afgin | 23 | 7.1 | 19.3 | 4.8 | 10.5 |
| 16 | Campephagidae | Scarlet Minivet | *Pericrocotus flammeus* | | medium | ETF | afgin | 21 | 5.9 | 16.7 | 4.1 | 8.6 |
| 17 | Campephagidae | Lesser Cuckooshrike | *Coracina fimbriata* | | medium | ETF | afgin | 9 | | | | |
| 18 | Caprimulgidae | Large-tailed Nightjar | *Caprimulgus macrurus* | | medium | OS | npi | | | | | |
| 19 | Chloropseidae | Blue-winged Leafbird | *Chloropsis cochinchinensis* | | medium | ETF | nif | 54 | 16.8 | 8.1 | 14.3 | 19.7 |
| 20 | Chloropseidae | Greater Green Leafbird | *Chloropsis sonneratii* | | medium | ETF | nif | 17 | 4.7 | 24.5 | 2.8 | 7.9 |
| 21 | Chloropseidae | Lesser Green Leafbird | *Chloropsis cyanopogon* | NT | medium | ETF | nif | 15 | 5.5 | 33.0 | 2.8 | 11.0 |
| 22 | Columbidae | Thick-billed Green-pigeon | *Treron curvirostra* | | medlarge | ETF | af | 46 | 6.4 | 4.9 | 5.8 | 7.0 |
| 23 | Columbidae | Emerald Dove | *Chalcophaps indica* | | medlarge | ETF | tom | 37 | 2.9 | 22.3 | 1.8 | 4.5 |
| 24 | Columbidae | Green Imperial-pigeon | *Ducula aenea* | | large | FS | af | 3 | | | | |
| 25 | Columbidae | Mountain Imperial-pigeon | *Ducula badia* | | large | ETF | af | 1 | | | | |
| 26 | Coraciidae | Asian Dollarbird | *Eurystomus orientalis* | | medlarge | OS | si | 2 | | | | |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 27 | Corvidae | Slender-billed Crow | *Corvus enca* | | large | OS | dp | 16 | 1.4 | 36.5 | 0.7 | 3.0 |
| 28 | Corvidae | Crested Jay | *Platylophus galericulatus* | NT | medlarge | FS | afgin | 15 | 2.3 | 43.8 | 0.9 | 5.6 |
| 29 | Corvidae | Black Magpie | *Platysmurus leucopterus* | NT | large | FS | afgif | 12 | 2.0 | 30.5 | 1.0 | 3.7 |
| 30 | Cuculidae | Raffles's Malkoha | *Phaenicophaeus chlorophaeus* | | medium | ETF | afgin | 39 | 18.3 | 12.1 | 14.4 | 23.4 |
| 31 | Cuculidae | Indian Cuckoo | *Cuculus micropterus* | | medlarge | OS | afgin | 18 | 1.0 | 15.1 | 0.7 | 1.3 |
| 32 | Cuculidae | Plaintive Cuckoo | *Cacomantis merulinus* | | medium | G | afgin | 15 | 1.4 | 1.2 | 1.3 | 1.4 |
| 33 | Cuculidae | Drongo Cuckoo | *Surniculus lugubris* | | medium | ETF | afgin | 9 | | | | |
| 34 | Cuculidae | Short-toed Coucal | *Centropus rectunguis* | VU | large | FS | afgin | 8 | | | | |
| 35 | Cuculidae | Banded Bay Cuckoo | *Cacomanthis sonneratii* | | medium | ETF | afgin | 7 | | | | |
| 36 | Cuculidae | Hodgson's Hawk-cuckoo | *Cuculus fugax* | | medlarge | ETF | afgin | 7 | | | | |
| 37 | Cuculidae | Green-billed Malkoha | *Phaenicophaeus tristis* | | medlarge | ETF | afgin | 5 | | | | |
| 38 | Cuculidae | Black-bellied Malkoha | *Phaenicophaeus diardi* | NT | medium | ETF | afgin | 4 | 1.8 | 8.2 | 1.5 | 2.1 |
| 39 | Cuculidae | Chestnut-breasted Malkoha | *Phaenicophaeus curvirostris* | | large | ETF | afgin | 3 | | | | |
| 40 | Cuculidae | Rusty-breasted Cuckoo | *Cacomantis sepulcralis* | | medium | ETF | afgin | 2 | | | | |
| 41 | Cuculidae | Greater Coucal | *Centropus sinensis* | | large | OS | afgin | 2 | | | | |
| 42 | Cuculidae | Violet Cuckoo | *Chrysococcyx xanthorhynchus* | | small | ETF | afgin | 1 | | | | |
| 43 | Cuculidae | Himalayan Cuckoo | *Cuculus saturatus* | | medlarge | G | afgin | 1 | | | | |
| 44 | Dicaeidae | Orange-bellied Flowerpecker | *Dicaeum trigonostigma* | | small | ETF | nif | 81 | 96.1 | 12.6 | 74.9 | 123.4 |
| 45 | Dicaeidae | Plain Flowerpecker | *Dicaeum concolor* | | small | ETF | nif | 44 | 43.2 | 14.0 | 32.6 | 57.2 |
| 46 | Dicaeidae | Yellow-breasted Flowerpecker | *Prionochilus maculatus* | | small | ETF | afgif | 6 | | | | |
| 47 | Dicaeidae | Scarlet-backed Flowerpecker | *Dicaeum cruentatum* | | small | ETF | nif | 3 | | | | |
| 48 | Dicaeidae | Scarlet-breasted Flowerpecker | *Prionochilus thoracicus* | NT | small | ETF | afgif | 2 | 2.2 | 5.3 | 2.0 | 2.5 |
| 49 | Dicaeidae | Yellow-vented Flowerpecker | *Dicaeum chryssorheum* | | small | ETF | nif | 1 | | | | |
| 50 | Dicaeidae | Crimson-breasted Flowerpecker | *Prionochilus percussus* | | small | ETF | afgif | 1 | | | | |
| 51 | Dicruridae | Greater Racket-tailed Drongo | *Dicrurus paradiseus* | | medlarge | ETF | sgi | 122 | 21.5 | 14.9 | 16.0 | 28.8 |
| 52 | Eupetidae | Rail-babbler | *Eupetes macrocerus* | | medium | FS | tifi | 21 | 4.6 | 17.1 | 3.2 | 6.5 |
| 53 | Eurylaimidae | Black-and-yellow Broadbill | *Eurylaimus ochromalus* | NT | medium | ETF | sgi | 85 | 17.6 | 13.9 | 13.4 | 23.2 |
| 54 | Eurylaimidae | Asian Green Broadbill | *Calyptomena viridis* | NT | medium | FS | af | 24 | 4.0 | 26.8 | 2.3 | 6.8 |
| 55 | Eurylaimidae | Banded Broadbill | *Eurylaimus javanicus* | | medlarge | ETF | sgi | 18 | 3.0 | 10.4 | 2.4 | 3.8 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 56 | Eurylaimidae | Dusky Broadbill | *Corydon sumatranus* | | medlarge | ETF | sgi | 3 | | | | |
| 57 | Falcondiae | Black-thighed Falconet | *Microhierax fringillarius* | | medium | ES | ain | 1 | | | | |
| 58 | Hemiprocnidae | Whiskered Treeswift | *Hemiprocne comata* | | small | OS | si | | | | | |
| 59 | Irenidae | Asian Fairy-bluebird | *Irena puella* | | medium | ES | af | 43 | 20.6 | 10.5 | 16.7 | 25.4 |
| 60 | Meropidae | Red-bearded Bee-eater | *Nyctyornis amictus* | | medlarge | FS | si | 22 | 2.5 | 33.5 | 1.3 | 5.0 |
| 61 | Monarchidae | Black-naped Monarch | *Hypothymis azurea* | | small | ETF | si | 80 | 25.6 | 4.4 | 23.5 | 27.9 |
| 62 | Muscicapidae | Rufous-tailed Shama | *Trichixos pyrrhopygus* | NT | medium | FS | afgin | 82 | 13.5 | 10.6 | 11.0 | 16.7 |
| 63 | Muscicapidae | Grey-chested Jungle-flycatcher | *Rhinomyias umbratilis* | NT | small | FS | sgi | 36 | 6.7 | 5.5 | 6.0 | 7.5 |
| 64 | Muscicapidae | White-crowned Forktail | *Enicurus leschenaultii* | | medium | FS | tifi | 32 | 9.5 | 9.8 | 7.8 | 11.6 |
| 65 | Muscicapidae | Rufous-winged Philentoma | *Philentoma phyrrhopterum* | | small | FS | si | 24 | 17.3 | 18.3 | 11.9 | 25.1 |
| 66 | Muscicapidae | Pale Blue-flycatcher | *Cyornis unicolor* | | medium | ETF | si | 10 | 6.0 | 56.9 | 1.8 | 20.4 |
| 67 | Muscicapidae | Oriental Magpie-robin | *Copsychus saularis* | | medium | OS | afgin | 5 | | | | |
| 68 | Muscicapidae | White-rumped Shama | *Copsychus malabaricus* | | medium | ETF | afgin | 4 | | | | |
| 69 | Muscicapidae | Grey-headed Canary-flycatcher | *Culicicapa ceylonensis* | | small | FS | si | 2 | | | | |
| 70 | Muscicapidae | Large-billed Blue-flycatcher | *Cyornis caerulatus* | VU | small | FS | si | 2 | 0.8 | 7.2 | 0.7 | 1.0 |
| 71 | Muscicapidae | Malaysian Blue-flycatcher | *Cyornis turcosus* | NT | medium | ETF | si | 2 | 0.8 | 7.0 | 0.7 | 1.0 |
| 72 | Nectariniidae | Little Spiderhunter | *Arachnothera longirostra* | | small | G | nin | 236 | 164.7 | 8.9 | 137.4 | 197.5 |
| 73 | Nectariniidae | Purple-naped Sunbird | *Hypogramma hypogrammicum* | | small | ETF | nif | 43 | 25.2 | 12.1 | 19.7 | 32.1 |
| 74 | Nectariniidae | Ruby-cheeked Sunbird | *Anthreptes singalensis* | | small | ES | nif | 18 | 13.4 | 14.4 | 9.9 | 18.1 |
| 75 | Nectariniidae | Crimson Sunbird | *Aethopyga siparaja* | | small | G | nin | 14 | 14.6 | 35.6 | 6.9 | 30.7 |
| 76 | Nectariniidae | Plain-throated Sunbird | *Anthreptes malacensis* | | small | OS | nif | 14 | 3.2 | 41.6 | 1.3 | 7.6 |
| 77 | Nectariniidae | Plain Sunbird | *Anthreptes simplex* | | small | ETF | nif | 12 | 4.8 | 44.7 | 1.8 | 12.3 |
| 78 | Nectariniidae | Long-billed Spiderhunter | *Arachnothera robusta* | | medium | ETF | nin | 10 | 2.4 | 1.3 | 2.4 | 2.5 |
| 79 | Nectariniidae | Grey-breasted Spiderhunter | *Arachnothera affinis* | | medium | ETF | nif | 8 | | | | |
| 80 | Nectariniidae | Olive-backed Sunbird | *Nectarinia jugularis* | | small | OS | nif | 5 | | | | |
| 81 | Nectariniidae | Spectacled Spiderhunter | *Arachnothera flavigaster* | | medium | ETF | nin | 2 | | | | |
| 82 | Oriolidae | Black-hooded Oriole | *Oriolus xanthonotus* | | medium | ETF | afgif | 58 | 4.9 | 4.1 | 4.5 | 5.3 |
| 83 | Phasianidae | Great Argus | *Argusianus argus* | NT | large | FS | tom | 60 | 2.9 | 17.9 | 2.1 | 4.2 |
| 84 | Picidae | Buff-rumped Woodpecker | *Meiglyptes tristis* | | medium | ETF | afgin | 33 | 11.6 | 16.2 | 8.4 | 16.1 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 85 | Picidae | Crimson-winged Woodpecker | *Picus puniceus* | | medlarge | ETF | bgi | 25 | 3.6 | 15.4 | 2.6 | 4.9 |
| 86 | Picidae | Rufous Piculet | *Sassia abnormis* | | small | ETF | afginus | 19 | 12.4 | 17.1 | 8.7 | 17.6 |
| 87 | Picidae | Buff-necked Woodpecker | *Meiglyptes tukki* | NT | medium | ETF | bgi | 18 | 8.0 | 18.6 | 5.5 | 11.7 |
| 88 | Picidae | White-bellied Woodpecker | *Dryocopus javensis* | | large | ETF | bgi | 17 | 2.5 | 14.8 | 1.8 | 3.3 |
| 89 | Picidae | Maroon Woodpecker | *Blythipicus rubiginosus* | | medlarge | ETF | bgi | 14 | 5.2 | 34.6 | 2.6 | 10.7 |
| 90 | Picidae | Checker-throated Woodpecker | *Picus mentalis* | | medlarge | ETF | bgi | 13 | 2.0 | 0.7 | 2.0 | 2.1 |
| 91 | Picidae | Orange-backed Woodpecker | *Reinwardtipicus validus* | | medlarge | FS | bgi | 11 | 5.8 | 11.1 | 4.5 | 7.4 |
| 92 | Picidae | Grey-and-buff Woodpecker | *Hemicircus concretus* | | medium | ETF | bgi | 6 | | | | |
| 93 | Picidae | Rufous Woodpecker | *Celeus brachyurus* | | medlarge | ETF | bgi | 3 | | | | |
| 94 | Picidae | Olive-backed Woodpecker | *Dinopium rafflesii* | NT | medlarge | FS | bgi | 2 | 0.3 | 0.3 | 0.3 | 0.3 |
| 95 | Pittidae | Garnet Pitta | *Pitta granatina* | NT | medium | ETF | tifi | 6 | 1.9 | 23.8 | 1.2 | 2.9 |
| 96 | Pittidae | Javan Banded Pitta | *Pitta guajana* | | medlarge | ETF | tifi | 4 | | | | |
| 97 | Pittidae | Hooded Pitta | *Pitta sordida* | | medium | ETF | tifi | 3 | | | | |
| 98 | Psittacidae | Blue-rumped Parrot | *Psittinus cyanurus* | NT | medium | FS | af | 15 | 4.2 | 71.4 | 1.1 | 16.8 |
| 99 | Psittacidae | Blue-crowned Hanging-parrot | *Loriculus galgulus* | | medium | ETF | af | | | | | |
| 100 | Pycnonotidae | Spectacled Bulbul | *Pycnonotus erythropthalmos* | | small | ETF | afgif | 227 | 97.5 | 10.0 | 80.0 | 119.0 |
| 101 | Pycnonotidae | Hairy-backed Bulbul | *Tricholestes criniger* | | small | FS | afgif | 113 | 73.8 | 9.8 | 60.9 | 89.5 |
| 102 | Pycnonotidae | Cream-vented Bulbul | *Pycnonotus simplex* | | medium | ES | afgif | 87 | 64.7 | 17.0 | 46.3 | 90.5 |
| 103 | Pycnonotidae | Buff-vented Bulbul | *Iole olivacea* | NT | medium | ES | afgif | 83 | 44.0 | 13.6 | 33.7 | 57.6 |
| 104 | Pycnonotidae | Black-headed Bulbul | *Pycnonotus atriceps* | | medium | ES | afgif | 82 | 26.5 | 9.4 | 22.0 | 32.0 |
| 105 | Pycnonotidae | Yellow-bellied Bulbul | *Alophoixus phaeocephalus* | | medium | FS | afgif | 70 | 25.6 | 13.5 | 19.6 | 33.4 |
| 106 | Pycnonotidae | Olive-winged Bulbul | *Pycnonotus plumosus* | | medium | ES | afgif | 47 | 21.3 | 4.5 | 19.4 | 23.3 |
| 107 | Pycnonotidae | Grey-cheeked Bulbul | *Alophoixus bres* | | medium | FS | afgif | 36 | 9.7 | 6.4 | 8.6 | 11.1 |
| 108 | Pycnonotidae | Red-eyed Bulbul | *Pycnonotus brunneus* | | medium | ES | afgif | 27 | 8.9 | 14.6 | 6.6 | 12.0 |
| 109 | Pycnonotidae | Streaked Bulbul | *Ixos malaccensis* | NT | medium | ETF | afgif | 12 | 6.6 | 40.1 | 2.8 | 15.5 |
| 110 | Pycnonotidae | Puff-backed Bulbul | *Pycnonotus eutilotus* | NT | medium | FS | afgif | 6 | 3.2 | 32.5 | 1.7 | 6.2 |
| 111 | Pycnonotidae | Yellow-vented Bulbul | *Pycnonotus goavier* | | medium | G | afgif | 1 | | | | |
| 112 | Pycnonotidae | Black-crested Bulbul | *Pycnonotus melanicterus* | | medium | ETF | afgif | 1 | | | | |
| 113 | Ramphastidae | Blue-eared Barbet | *Megalaima australis* | | medium | G | af | 178 | 16.3 | 10.4 | 13.3 | 20.0 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 114 | Ramphastidae | Gold-whiskered Barbet | *Megalaima chrysopogon* | | large | ETF | afp | 69 | 2.7 | 10.2 | 2.2 | 3.3 |
| 115 | Ramphastidae | Yellow-crowned Barbet | *Megalaima henricii* | NT | medlarge | ETF | af | 60 | 4.0 | 11.2 | 3.2 | 5.0 |
| 116 | Ramphastidae | Red-crowned Barbet | *Megalaima rafflesii* | NT | medlarge | ETF | af | 48 | 1.9 | 6.4 | 1.7 | 2.2 |
| 117 | Ramphastidae | Brown Barbet | *Calorhamphus fuliginosus* | | medium | ETF | afgif | 43 | 25.4 | 20.6 | 16.8 | 38.5 |
| 118 | Rhipiduridae | Spotted Fantail | *Rhipidura perlata* | | small | FS | sgi | 6 | | | | |
| 119 | Rhipiduridae | Pied Fantail | *Rhipidura javanica* | | small | FS | sgi | 1 | | | | |
| 120 | Sittidae | Velvet-fronted Nuthatch | *Sitta frontalis* | | small | FS | bgi | 3 | | | | |
| 121 | Sturnidae | Hill Myna | *Gracula religiosa* | | large | G | af | 41 | 4.7 | 7.0 | 4.1 | 5.4 |
| 122 | Sylviidae | Dark-necked Tailorbird | *Orthotomus atrogularis* | | small | ES | afgin | 84 | 30.9 | 10.5 | 25.1 | 38.0 |
| 123 | Sylviidae | Rufous-tailed Tailorbird | *Orthotomus sericeus* | | small | ES | afgin | 31 | 7.8 | 20.8 | 5.1 | 11.8 |
| 124 | Sylviidae | Ashy Tailorbird | *Orthotomus ruficeps* | | small | ES | afgin | 4 | | | | |
| 125 | Sylviidae | Yellow-bellied Warbler | *Abroscopus superciliaris* | | small | ETF | afgin | 1 | | | | |
| 126 | Timaliidae | Ferruginous Babbler | *Trichastoma bicolor* | | medium | FS | afginus | 142 | 35.8 | 10.3 | 29.3 | 43.8 |
| 127 | Timaliidae | Chestnut-rumped Babbler | *Stachyris maculata* | NT | medium | ETF | afgin | 104 | 30.6 | 19.6 | 20.8 | 45.0 |
| 128 | Timaliidae | Chestnut-winged Babbler | *Stachyris erythroptera* | | small | ETF | afgin | 89 | 31.5 | 13.0 | 24.4 | 40.7 |
| 129 | Timaliidae | Sooty-capped Babbler | *Malacopteron affine* | | small | ETF | afgin | 87 | 34.5 | 13.6 | 26.4 | 45.0 |
| 130 | Timaliidae | Pin-striped Tit-babbler | *Macronous gularis* | | small | ETF | afginus | 84 | 12.6 | 12.8 | 9.8 | 16.3 |
| 131 | Timaliidae | Chestnut-backed Scimitar-babbler | *Pomatorhinus montanus* | | medium | FS | afgin | 76 | 11.0 | 7.2 | 9.5 | 12.6 |
| 132 | Timaliidae | Short-tailed Babbler | *Malacocincla malaccensis* | NT | medium | ETF | tifi | 69 | 20.4 | 13.5 | 15.6 | 26.6 |
| 133 | Timaliidae | Scaly-crowned Babbler | *Malacopteron cinereum* | | small | FS | afgin | 59 | 20.3 | 15.2 | 15.0 | 27.5 |
| 134 | Timaliidae | Brown Fulvetta | *Alcippe brunneicauda* | NT | small | FS | afgif | 54 | 9.4 | 5.9 | 8.3 | 10.6 |
| 135 | Timaliidae | Moustached Babbler | *Malacopteron magnirostre* | | small | ETF | afgin | 48 | 19.9 | 18.0 | 13.9 | 28.5 |
| 136 | Timaliidae | Black-capped Babbler | *Pellorneum capistratum* | | medium | ETF | tifi | 40 | 13.5 | 19.3 | 9.2 | 19.8 |
| 137 | Timaliidae | Fluffy-backed Tit-babbler | *Macronous ptilosus* | NT | small | ETF | afginus | 40 | 9.8 | 8.6 | 8.2 | 11.7 |
| 138 | Timaliidae | Rufous-crowned Babbler | *Malacopteron magnum* | NT | medium | FS | afgin | 38 | 10.1 | 9.3 | 8.3 | 12.2 |
| 139 | Timaliidae | Rufous-fronted Babbler | *Stachyris rufifrons* | | small | ETF | afginus | 30 | 11.8 | 6.3 | 10.4 | 13.4 |
| 140 | Timaliidae | White-chested Babbler | *Trichastoma rostratum* | NT | medium | ES | tifi | 16 | 5.5 | 22.0 | 3.5 | 8.7 |
| 141 | Timaliidae | Black-throated Babbler | *Stachyris nigricollis* | NT | medium | ETF | afginus | 16 | 2.6 | 25.5 | 1.5 | 4.4 |
| 142 | Timaliidae | Grey-headed Babbler | *Stachyris poliocephala* | | medium | FS | afginus | 13 | 5.4 | 28.0 | 3.0 | 9.9 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 143 | Timaliidae | Striped Wren-babbler | *Kenopia striata* | NT | small | FS | tifi | 6 | 1.5 | 15.2 | 1.1 | 2.0 |
| 144 | Timaliidae | Large Wren-babbler | *Turdinus macrodactylus* | NT | medium | FS | tifi | 3 | 0.7 | 15.1 | 0.5 | 1.0 |
| 145 | Timaliidae | White-necked Babbler | *Stachyris leucotis* | NT | medium | FS | afginus | 2 | 0.3 | 8.1 | 0.3 | 0.4 |
| 146 | Timaliidae | Abbott's Babbler | *Malacopteron abboti* | | medium | FS | afginus | 1 | | | | |
| 147 | Trogonidae | Scarlet-rumped Trogon | *Harpactes duvauceili* | NT | medium | FS | sgi | 52 | 4.5 | 3.8 | 4.1 | 4.8 |
| 148 | Trogonidae | Red-naped Trogon | *Harpactes kasumba* | | medlarge | FS | sgi | 21 | 4.6 | 14.8 | 3.4 | 6.3 |
| 149 | Trogonidae | Diard's Trogon | *Harpactes diardi* | NT | medlarge | FS | sgi | 18 | 2.3 | 23.5 | 1.4 | 3.8 |

[b] IUCN status (IUCN 2012): VU= vulnerable, NT=near threatened

[c] small – small species (weight < 20 g); medium – medium-sized (20-69 g); medlarge – medium-large (70-150 g); large – large (>150 g)

[d] Species were assigned to habitats used by Styring et al. (2011): forest specialists (FS), edge tolerant forest specialists (ETF); edge specialists (ES); open country species (OS); generalist (G)

[e] Feeding guilds are based on Lambert (1992) and Lambert and Collar (2002): dp=diurnal predator; npi= nocturnal predator; tifi= terrestrial insectivore of forest interior; afgin= arboreal foliage-gleaning insectivore; afginus=arboreal foliage-gleaning insectivore understory specialist; ain=aerial insectivore; bgi=bark-gleaning insectivore; sgi=sallying substrate-gleaning insectivore; si= sallying insectivore; afgif= arboreal foliage-gleaning insectivore–frugivore; afp= arboreal frugivore–predator; af=arboreal frugivore; mip=miscellaneous insectivore/piscivore; nif=nectarivore/insectifores/frugivore; nin=nectarivore/insectivore; tom=terrestrial omnivore.

[f] n=total observations (excluding flying)

[g] D= density estimate (birds/km$^2$)

[h] %CV the coefficient of variation of the estimate

[i] CI indicates the 95% confidence interval around the estimates (lower-upper)

# Chapter 4

## Bird densities in old vs young secondary lowland rainforest of Sumatra, Indonesia

Significant higher density of Chestnut-rumped Babbler *Stachyris maculata* in old secondary forest (top), while Puple-naped Sunbird *Hypogramma hypogrammicum* had higher density in young secondary forest (below).

## ABSTRACT

Comparing density estimates between habitat types differing in disturbance levels is helpful to quantitatively examine their relative importance for birds. Up to now, such comparisons are still few, particularly in global biodiversity hotspots such as the Indonesian Sundaic region. In this study, the densities of birds in old (canopy cover 71-100%) and young secondary forest (canopy cover < 40%) of the Harapan Rainforest Ecosystem Restoration concession in Sumatra were compared. We recorded a total of 146 bird species, and densities were calculated for 47 bird species (species recorded $\geq$ 10 times in each habitat type), including 10 globally near-threatened species. Density comparisons could be made for 33 species pairs, where 10 species had significantly higher densities in old secondary forest, and nine species had higher at young secondary forest, while the other 14 species showed no significant differences.  Species that are known to decline in logged forest had also lower density in young secondary forest, for example the Black-capped Babbler *Pellorneum capistratum* (21.6 birds/km$^2$ in old secondary forest and 7.1 birds/km$^2$ in young secondary forest). Vice versa, Purpe-naped Sunbird *Hypogramma hypogrammicum* and Fluffy-backed Tit-Babbler *Macronous ptilosus* with higher density in logged forest exhibited higher density in young secondary forest. However, not all species followed this pattern. For example, the Sooty-capped Babbler *Malacopteron affine,* although being logging sensitive, had higher density in young than old secondary forest (39 birds/km$^2$ vs 22 birds/km$^2$). Mosaics of degraded and unlogged forest patches, a typical condition of selectively logged forest, might have provided suitable habitat for these species.

In conclusion, not all bird species exhibited the density differences between old and young secondary forest that were expected due to their known susceptibility to logging, so more long-term monitoring is needed in a broader range of forest types to confirm patterns of bird species persistence in secondary forests of Sumatra.

**Keywords:** birds, rainforest, degraded lands, density comparison

## INTRODUCTION

Examining differences in fauna communities across different habitat types is an important approach to understand the variations across these habitat types (Peh et al. 2006, Styring et al. 2011). Using this approach one can identify relative importance of different habitat types on particular species or species group (e.g. Creswell et al. 1999, Barlow et al. 2007, Edwards et al. 2011), and species susceptibility to disturbance (e.g. Dale et al. 1994, Marsden 1998, Gray 2007, Waltert et al. 2004, Mallari et al. 2011). Knowledge on this can then be used to evaluate land management strategies for nature conservation. Moreover, this approach is particularly important in areas with high loss and alteration of forests through logging and agriculture, which represents major threats to tropical biodiversity (Hansen et al. 2013).

Sumatra is part of the Sundaic biodiversity hotspot (Sumatra, Peninsula Malaysia, Java, and Borneo Island) with an exceptionally rich fauna including numerous endemic bird, mammal, reptiles and amphibians (Myers et al. 2000, Sodhi et al. 2004). Moreover, from 228 lowland bird specialist (occur below 200 meter boundary) in Sumatra eight are considered to be threatened and 57 (25%) are near threatened (Wells 1985, BirdLife International 2013b). Undisturbed lowland forest (<200 m elevation) is now rare in the Sundaic region (Lambert and Collar 2002), particularly in Sumatra Island (Margono et al. 2012, Wilcove et al. 2013). A recent study reveals that 70% (75,400 km$^2$) of Sumatra's tropical forest area has been intensively cleared through 1990 to 2010, with additional 23,100 km$^2$ of primary forest in degraded condition and with logging as the main driver

(Margono et al. 2012). The primary forest cover loss and forest degradation are also slowing over the two decade periods, from 73,400 km$^2$ from 1990 to 2000, to 25,100 km$^2$ from 2000 to 2010. This is partly due to a greatly diminished resource base, particularly of lowland primary forests (Margono et al. 2012). Under this condition, many of near threatened species might change their status to threatened species. This might actually happen as most of the lowland areas are outside the existing protected area networks. In their evaluation of protected area networks in Sumatra, Gaveau et al. (2009) shows that allocation of forests for protected area is skewed toward highland, while lowland areas are mostly left unprotected. However, despite their degraded condition, secondary forests (i.e. selectively-logged primary forest) are generally thought to be worth protecting because they still retain high biodiversity values (e.g. Sodhi et al. 2005, Sekercioglu et al. 2007, Edwards et al. 2010) and are perhaps the only forest habitat left in lowland tropical forest landscapes. Preventing agricultural conversion of logged forests is essential to conserving the biodiversity of Sundaland forests (Wilcove et al. 2013).

No quantitative information (density estimate hereafter density) is available on the status of tropical forest birds in Sumatra's secondary forests, and also extremely limited for primary forest birds in the Sundaic region. Information on bird density can be used to assess global extinction risks (BirdLife International 2013b), and is important for conservation management authorities (Gaston et al. 2000, Gale and Thongaree 2006, Mallari 2009). Many Asian studies on tropical forest dependent birds have been conducted to examine the relative impacts of logging (e.g. Marsden 1998, Dunn 2004, Cleary et al. 2005, Sodhi et al. 2008), but none of these come from Sumatra and only few densities have been produced. Particularly for Sumatra, the few densities available are all from primary forest (Anggraini et al. 2000, Winarni et. al. 2009). In a recent study we presented global densities for 102 Sundaic lowland bird species from the Sumatran study area (Chapter 3), however without a comparison of densities between different habitat types. Comparing densities across different habitat characteristics can be used to assess bird responses to habitat changes and can provide advice for bird conservation and forest restoration (e.g. Mallari 2009).

In this study we conducted bird point-count surveys to provide reliable estimates of abundance of birds in two contrasting secondary lowland forests in Sumatra. Published studies on the impact of logging suggest that some bird species have a higher density in logged forest whereas others decline with logging (Marsden 1998, Mead 2008). We expected that the preference for old versus young secondary forest (or vice versa) would reflect the aversion or affinity for logged forests. We used non-metric multidimensional scaling to identify main habitat variables that correlate with bird species distribution. We expected that bird species that show higher density in old secondary forest are related to habitat variables that are typical for this forest types and vice versa. Our study provides new insight into species specific responses to habitat degradation, and thereby, a better understanding of suitable forest management practices for bird conservation.

## METHODS

*Study area*. Harapan Rainforest Ecosystem Restoration Concession (HRF, 984.5km$^2$) is the first ecosystem restoration concession in Indonesia (http://www.harapanrainforest.org). It covers two large selectively-logged primary forest that are located in Jambi (491.8 km$^2$) and South Sumatra Provinces (492.7 km$^2$), Indonesia. The concession's overall aim is to conserve and restore the forest to its original primary condition for the benefit of biodiversity, local traditional communities and ecosystem services. Logging ceased in 2006, and left a mosaic of secondary forest habitats in different stages of regeneration (Lee and Lindsell 2011). The HRF is a lowland site ranging in elevation from 30-120 m above sea level. Surveys were conducted in Jambi Province.

*Habitat surveys*. In this study we used 11 transects (each 2 km long, 11 data collection points/transect, each point was 200 m apart). These transects were placed to cover two general types of secondary forest: old secondary forest (5 transects) and young secondary forest (6 transects). Old secondary forest has a well-stratified structure from seedlings to trees, relatively high canopy cover (71-100%), and average tree diameter is > 20cm. Young secondary forest is dominated by shrub layer plants, and relatively low canopy cover (< 40%).

Habitat variables data within 25 m of each sampling point were collected. The following physical and structural variables were sampled (Lee and Lindsell 2011): (1) altitude using global positioning system, (2) slope using a clinometer (degree), (3) distance to water body (meter), (4) diameter at breast height (DBH, meter), tree height (meter), and species identity (*Macaranga* spp or not) for 10 nearest trees with DBH > 20 cm , (5) number of dead standing trees (DBH > 20 cm), (6) percentage of leaf litter cover in four 1 $m^2$ quadrats positioned randomly in each quarter, (7) canopy openness (using an array of 25 regularly spaced dots marked on a transparent Perspex sheet (30cm x 30cm, Brown et al. 2000) and (8) understory openness (by counting the number of visible dots arranged evenly in an 8 x 8 configuration on a 1m x 1m plastic sheet) in each quarter, (9) in each quarter, one observer stood holding a 1 meter stick perpendicular approximately at 1 m above the ground and turned slowly on the spot while counting the number of stems < 5 cm DBH the stick touched, which were classified as a sapling, liana, palm, ginger, rattan or bamboo. *Macaranga* spp. are relatively easy to identify in the field and common pioneer species in degraded forest with higher proportions in young secondary forest (Muslich 2010).

*Bird surveys.* We conducted bird point-transect surveys between April-June 2011, during the breeding season of most birds in Sumatra (van Marle and Voous 1988, Thiollay 1995). This method is a preferred method for surveying multi-species surveys in tropical forests (Bibby et al. 2000, Lee and Marsden 2008). Bird data were collected in the same sampling point where the habitat variables data were collected (i.e. 11 points per transect, 11 transects). Each point was spaced 200 m apart to maintain independent bird detection at consecutive points (Reynolds et al. 1980, Hutto et al. 1986). Surveys were conducted in the morning from 06:30 to 10:00 (10 minutes survey per point) to coincide with the peak period of bird activity (Lee and Marsden 2008). To reduce observer bias, bird surveys were conducted by the same observers for the whole period. At each point, the survey was conducted immediately after the observer arrived (without settling down period) and any birds detected moving away from around the survey point on the observer’s arrival was counted as being present during the count period (Lee and Marsden 2008). All perched birds or group were recorded along with number of individuals in the group, and horizontal distance from the survey point to the bird’s initial position (estimated using digital Rangefinder). Bird sound recordings were made per point to aid species identification by discussing with other bird experts and comparing with known bird recordings (e.g. from http://www.xeno.canto.org). Each transect was surveyed three times, if possible on three consecutive days (during the non-rainy day and no strong winds), otherwise on the next possible day. Whenever possible we rotated the daily order in which transects were visited.

*Statistical analysis.* We compared the value of 14 habitat variables between old and early secondary habitat. The differences between these habitats were tested with Kruskal-Wallis non-parametric ANOVA using R version 2.8.1 (R Development Core Team 2008).

We used the Chao 2 richness estimator to calculate total species richness as well as the completeness of our survey per habitat type. Chao 2 richness estimator is the best richness estimator (Walther and Moore 2005). Software EstimateS version 8 (Colwell 2006) was used. Samples were randomized 100 times. To compare cumulative species richness between old and young secondary forest we used the “c2cv” function with n=999 randomization in “rich” package (Rossi 2011). In this function species richness is computed as the cumulative over all samples, and compared by mean of a randomization test. Moreover, similarities of bird species composition among habitat types was quantified using Sørensen's similarity index (Magurran 2004), which is regarded as one of the most effective similarity measures (e.g. Southwood and Henderson 2000). Species accumulation curves were produced using "specaccum" function in "vegan" package (Oksanen et al. 2013).

In the bird density analysis, transect was taken as the sampling unit, and bird records from the three survey repetitions per transect were pooled, hence the total survey effort for each transect was 33 (11 points/transect times three survey repetitions per point-transect). Both aural and visual observations were combined. We used Distance v.6.0 (Thomas et al. 2010) to calculate bird densities for bird species that were recorded $\geq$ 10 times per habitat group. We calculated the densities for each habitat separately. All data were right-truncated at 50 m to remove any outlying records. This truncation approach aimed at improving model fit, and at reducing the likelihood of recording a bird outside the intended habitat type. Uniform, halfnormal, and hazard rate functions were tested for each species, and the model with lowest Akaike's Information Criterion (AIC) for a given set of data was selected as the best fit for those data (Buckland et al. 2001). Densities are presented as the number of birds per $km^2$ ± CV (coefficient of variation; the standard error of the density expressed as a percentage). To evaluate if there were overall differences of densities between old and young secondary forest an Exact Wilcoxon Rank test (Hothorn and Hornik 2013) was calculated. Moreover, for species where densities can be produced in both old and young secondary forest, we compared densities between these two habitats using Z-tests (Plumptre 2000). We used $\alpha$=0.05, Bonferroni-corrected for multiple comparisons ($\alpha$ /total number of comparison). This correction was also calculated to indicate possibility of obtaining false-positive results (type I errors), but we only used this as caution in interpretation of the results. The bird taxonomy in this study followed BirdLife International (2013a).

We conducted indirect gradient analysis by non-metric multidimensional scaling (NMDS, McCune and Grace 2002) to evaluate whether species that showed significant differences in density between old and young secondary forest were indeed correlated with habitat variables characterizing the habitat type in which they had higher density. The NMDS is commonly regarded as the most robust unconstrained ordination method in community ecology (Minchin 1987). This analysis was conducted on the presence-absence transect-species matrix. The habitat variables values were averaged at transect level. We used NMDS (R package vegan, Oksanen et al. 2013) to ordinate transect and species. We then superimposed computed vectors for the habitat variables onto the ordination diagrams. The significance of the fitted vectors was assessed using 1000 permutations of environmental variables. The goodness of fit statistic is the squared correlation coefficient $r^2$ (Oksanen et al. 2013). All analysis except for the density and Z test and Sørensen’s similarity index were conducted in R (R Development Core Team 2008).

## RESULTS

There were significant differences in most of the habitat variables measured between the two secondary forest types (but not for geographic variables, Table 4.1). Old secondary forest had significantly higher tree density and average tree height, and lower numbers of *Macaranga* spp. trees and dead-standing trees. This habitat type also had lower values for most of the understory related variables (i.e. understory openness, ginger, liana, and rattan density).

Table 4.1. Median values (and inter-quartile ranges) of habitat variables measured in old and young secondary forest in HRF. Differences between the two habitats were tested with a Kruskal-Wallis non-parametric ANOVA (*H*).

| | Old secondary forest | Young secondary forest | *H* |
|---|---|---|---|
| **Geographic** | | | |
| Altitude (m) | 78(20) | 76.5(19) | 0.5 |
| Slope (degree) | 12(22.7) | 16.25(13.9) | 1.6 |
| Distance to water body (m) | 0(0) | 0(0) | 0.3 |
| **Tree related variables** | | | |
| Tree density (trees/ha) | 188.4(79.7) | 132.6(105.5) | 7.5* |
| Mean tree height (m) | 23.6(4.27) | 19.2(4.17) | 19.7*** |
| Number of *Macaranga* spp. | 0(0) | 0(1) | 11.3** |
| Canopy openness | 3.5(3.25) | 3.75(4.12) | 0.4 |
| Number of dead standing tree | 0(1) | 1(2) | 4.1* |
| Basal area proportion (*1000) | 1.66(0.9) | 1.26(0. 9) | 9.4* |
| **Understory related variables** | | | |
| Understory openness | 5.7(8.5) | 9.4(10.6) | 3.9* |
| Ginger density$^{(1)}$ | 0(0) | 2(9.5) | 24.0 |
| Understory liana density $^{(1)}$ | 3(3) | 2(3) | 5.1* |
| Understory rattan density $^{(1)}$ | 0(0.5) | 0(0) | 1.6 |
| Sapling density $^{(1)}$ | 19(10) | 9(4.7) | 28.1*** |
| Leaf litter cover (%) | 0.9(0.05) | 0.9(0.24) | 44.8*** |

**Significant: *P < 0.05; **P < 0.001; ***P < 0.0001.** $^{(1)}$ average no of stems/m$^2$

We recorded 146 bird species (species recorded within 50 m of the point count, Appendix 4.1), 131 bird species recorded in old and 127 in young secondary forest. We found no significant difference of species richness between old and young secondary forest. The species accumulation curves (Figure 4.1) shows similarity between old and young secondary forest, also with high similarity in species composition (Sørensen similarity index=0.89). Based on the Chao 2 estimator, the expected total bird richness was 145.9 in old secondary forest and 139.2 in young secondary forest, which showed a survey completeness of approximately 90% at each habitat type. Nineteen species were only recorded in old secondary forest and 15 species only in young secondary forest, and all species were recorded < 10 times.

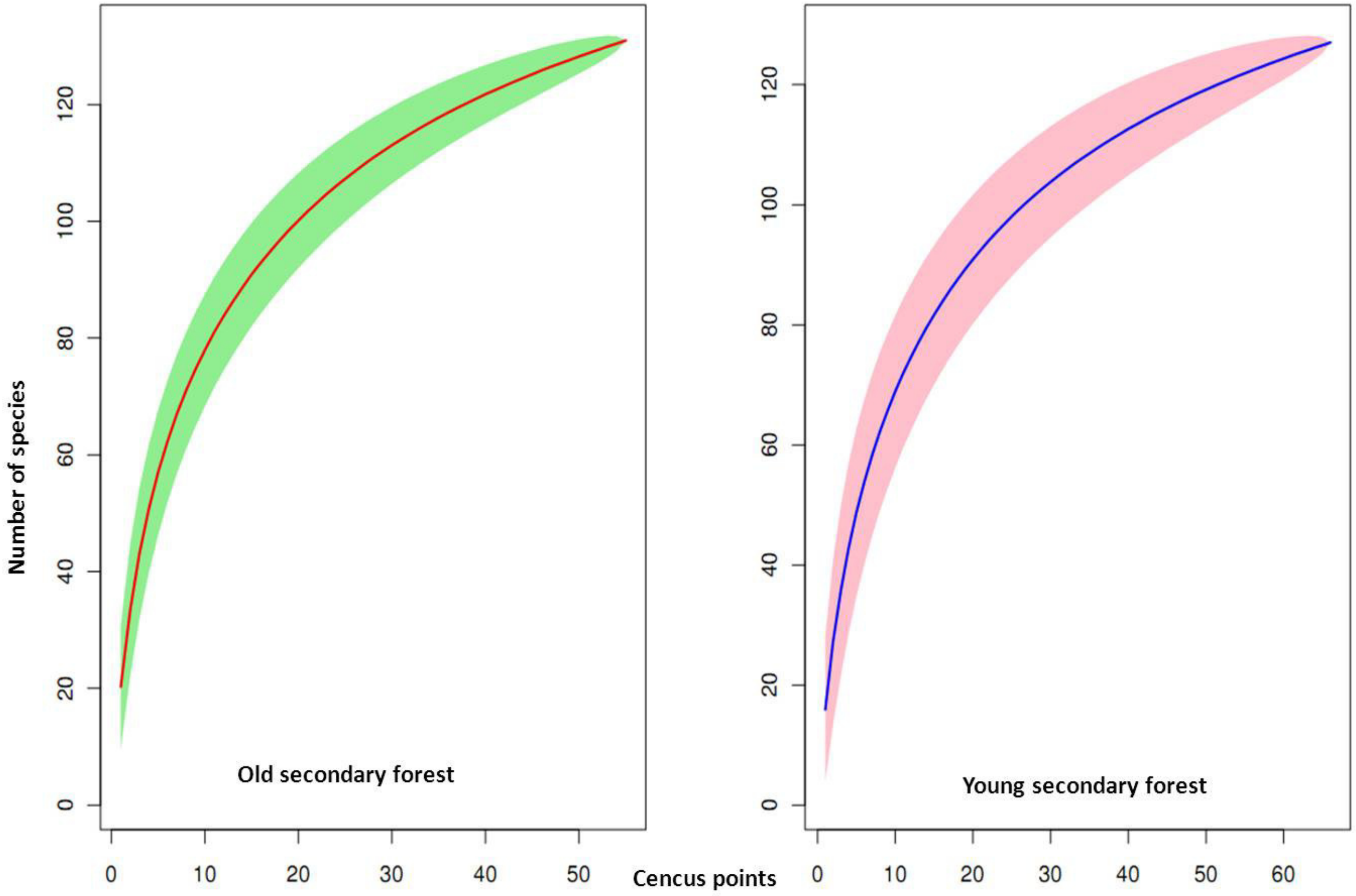


Figure 4.1. Species accumulation curves (±95% confidence intervals) for bird assemblages in old and young secondary forest.

Only 47 species were recorded ≥ 10 times at each habitat type, hence the densities were calculated for these species only. General comparison of densities from birds in old and young secondary forest indicated that there was no statistically significant difference in the median of densities between the old and young secondary forest (W=756, p=0.98). Table 4.2 shows the densities for the 47 species, including 33 species where we can compare the densities. Results from Z-test revealed a significant difference in densities between old and young secondary forest for 19 bird species (but only 11 after Bonferroni correction). Nine species had higher densities in young secondary forest (e.g. Fluffy-backed Tit-Babbler *Macronous ptilosus,* Sooty-capped Babbler *Malacopteron affine*), while densities for the other 10 species were higher in old secondary forest (e.g. Rufous-tailed Shama *Trichixos pyrrhopygus,* Greater Racket-tailed Drongo *Dicrurus paradiseus,* Black-capped Babbler *Pellorneum capistratum*). Densities for the remaining 11 bird species did not show significant differences (e.g. Asian Fairy-bluebird *Irena puella,* Black-and-yellow Broadbill *Eurylaimus ochromalus*). For the other 14 species (Table 4.2), comparison could not be made as densities could only be calculated in either only one of the two habitat types (e.g. Rufous-crowned Babbler *Malacopteron magnum* only in old secondary forest, and Pin-striped Tit-babbler *Macronous gularis* only in young secondary forest).

Tabel 4.2. Densities (km$^2$ with 95% Confidence Interval in brackets) for 47 lowland bird species in old and young secondary forest. Asterisks (*) indicate significance at $p < 0.05$, and Z test values (BOLD) indicate significant after applying Bonferroni correction, Z value > ± 3.16). The negative sign shows higher estimate for young secondary forest while positive sign shows higher estimate for old secondary forest. NT = Near-threatened.

| Species | IUCN 2013 | Old secondary forest | Young secondary forest | Z test |
|---|---|---|---|---|
| Yellow-bellied Bulbul *Alophoixus phaeocephalus* (sp1) | | 30.9 (24.9-38.4) | 16.1 (12.2-21.1) | **3.79*** |
| Hairy-backed Bulbul *Tricholestes criniger* (sp2) | | 112.4 (84.0-150.3) | 59.6 (35.9-98.7) | 2.41* |
| Green Iora *Aegithina viridissima* (sp3) | NT | 37 (30.4-45.2) | 27.6 (23.2-32.9) | 2.18* |
| Scaly-crowned Babbler *Malacopteron cinereum* (sp4) | | 23.1 (17.9-29.9) | 14.8 (11.3-19.3) | 2.42* |
| Chestnut-rumped Babbler *Stachyris maculata* (sp5) | NT | 35.5 (27.5-45.8) | 18 (13.9-23.4) | **3.48*** |
| Rufous-tailed Shama *Trichixos pyrrhopygus* (sp6) | NT | 16.2 (13.9-18.8) | 9 (7.3-11.1) | **4.97*** |
| Blue-winged Leafbird *Chloropsis cochinchinensis* (sp7) | | 19.3 (17.1-21.8) | 11.6 (10.2-13.1) | **5.91*** |
| Greater Racket-tailed Drongo *Dicrurus paradiseus* (sp8) | | 23.9 (20.9-27.4) | 15.4 (13.9-17.2) | **4.92*** |
| Short-tailed Babbler *Malacocincla malaccensis* (sp9) | NT | 24.7 (20.9-29.1) | 14.1 (11.2-17.9) | **4.19*** |
| Black-capped Babbler *Pellorneum capistratum* (sp10) | | 21.6 (17.3-27.0) | 7.1 (5.4-9.3) | **5.88*** |
| Blue-eared Barbet *Megalaima australis* (sp11) | | 14.7 (12.8-16.8) | 18.6 (16.1-21.6) | -2.48* |
| Brown Barbet *Calorhamphus fuliginosus* (sp12) | | 10.8 (9.2-12.7) | 32.4 (24.1-43.4) | **-4.66*** |
| Black-headed Bulbul *Pycnonotus atriceps* (sp13) | | 13.9 (11.9-16.2) | 36.1 (30.4-42.7) | **-7.09*** |
| Spectacled Bulbul *Pycnonotus erythropthalmos* (sp14) | | 64 (49.2-83.3) | 149.6 (117.3-190.9) | **-4.6*** |
| Olive-winged Bulbul *Pycnonotus plumosus* (sp15) | | 16.2 (12.7-20.7) | 25.2 (18.4-34.5) | -2.07* |
| Cream-vented Bulbul *Pycnonotus simplex* (sp16) | | 28.5 (24.1-33.9) | 75.1 (48.7-115.8) | -2.82* |
| Sooty-capped Babbler *Malacopteron affine* (sp17) | NT | 21.6 (16.8-27.7) | 38.6 (31.7-46.9) | **-3.75*** |
| Fluffy-backed Tit-babbler *Macronous ptilosus* (sp18) | NT | 8.5 (7.9-9.1) | 14.1 (10-19.9) | -2.44* |
| Purple-naped Sunbird *Hypogramma hypogrammicum* (sp19) | | 10.8 (9.9-11.7) | 28.6 (20.5-39.9) | **-3.81*** |
| Asian Fairy-bluebird *Irena puella* | | 14.7 (11.1-19.3) | 14.1 (11.7-17.0) | 0.26 |
| Grey-cheeked Bulbul *Alophoixus bres* | | 12.3 (9.7-15.7) | 9.6 (7.6-12-2) | 1.62 |
| Moustached Babbler *Malacopteron magnirostre* | | 18.5 (13.9-24.7) | 13.5 (9.4-19.5) | 1.49 |
| Raffles's Malkoha *Phaenicophaeus chlorophaeus* | | 13.1 (10.8-15.8) | 11.6 (9.5-14.0) | 0.95 |
| Plain Flowerpecker *Dicaeum concolor* | | 38.5 (28.1-52.8) | 31.3 (23.7-41.3) | 0.99 |
| Black-and-yellow Broadbill *Eurylaimus ochromalus* | NT | 16.2 (13.4-19.6) | 15.4 (12.3-19.3) | 0.36 |
| Buff-vented Bulbul *Iole olivacea* | NT | 33.9 (28.2-40.9) | 34.1 (22.4-51.9) | -0.03 |
| Dark-necked Tailorbird *Orthotomus atrogularis* | | 29.3 (25.2-34.1) | 31.2 (22.5-43.2) | -0.35 |
| Chestnut-winged Babbler *Stachyris erythroptera* | | 24.9 (17.3-35.9) | 28.3 (23.5-34.1) | -0.66 |
| Ferruginous Babbler *Trichastoma bicolor* | | 30.1 (25.6-35.4) | 34.7 (28.3-42.6) | -0.31 |
| Orange-bellied Flowerpecker *Dicaeum trigonostigma* | | 64.2 (43.7-94.3) | 95.9 (61.3-149.9) | -1.30 |
| Little Spiderhunter *Arachnothera longirostra* | | 128.3 (83.4-197.4) | 129.9 (93.2-181.2) | -0.05 |
| Black-naped Monarch *Hypothymis azurea* | | 27.8 (23.9-32.3) | 46.4 (27.8-77.4) | -1.54 |
| Rufous-winged Philentoma *Philentoma pyrrhopterum* | | 10.8 (8.7-13.4) | 15 (8.2-27.4) | -0.97 |
| Thick-billed Green-pigeon *Treron curvirostra* | | | 7.7 (7.4-8.1) | |
| Buff-rumped Woodpecker *Meiglyptes tristis* | | | 12.9 (11.1-14.9) | |
| Pin-striped Tit-babbler *Macronous gularis* | | | 17.4 (13.5-22.3) | |
| Rufous Piculet *Sassia abnormis* | | | 20.4 (10.9-38.4) | |
| White-crowned Forktail *Enicurus leschenaultii* | | | 9 (8.5-9.5) | |
| Brown Fulvetta *Alcippe brunneicauda* | NT | 18.5 (14.6-23.4) | | |
| Red-eyed Bulbul *Pycnonotus brunneus* | | 13.1 (12.1-14.2) | | |
| Rufous-crowned Babbler *Malacopteron magnum* | | 16.9 (11.9-24.1) | | |
| Rufous-tailed Tailorbird *Orthotomus sericeus* | | 8.5 (7.9-9.1) | | |
| Chestnut-backed Scimitar-babbler *Pomatorhinus montanus* | | 13.1 (9.8-17.6) | | |
| Rufous-fronted Babbler *Stachyris rufifrons* | | 20.8 (17.9-24.2) | | |
| Ruby-cheeked Sunbird *Anthreptes singalensis* | | 18.2 (3.6-92.2) | | |
| Crimson Sunbird *Aethopyga siparaja* | | 24.5 (16.2-37.1) | | |
| Grey-chested Jungle-flycatcher *Rhinomyias umbratilis* | NT | 14.7 (12.2-17.7) | | |

Nineteen species that showed significant difference in their density between old and young secondary forest were used in the non-metric multidimensional scaling (NMDS) to see whether, for example, species with high density in old secondary forest was also correlated with habitat variables typical of that forest type. The NMDS enabled us to plot transects and species in a two-dimensional species space (Figure 4.2; convergent solution found**,** two dimensions, stress= 0.16). Fitting environmental variables as vectors into this space revealed that average ginger density in the understory, average leaf litter cover, average sapling density, and average tree height were useful in explaining gradients (goodness-of-fit: ginger density, $r^2$=0.72, p=0.007; leaf litter cover, $r^2$=0.68, p=0.02; sapling density, $r^2$=0.71, p=0.01; tree height, $r^2$=0.72, p=0.008, understory openness, $r^2$=0.62, p=0.02). Species situated towards the left-lower part of the multidimensional scaling plot tend to occur in transects typical of old secondary forest with high average value for tree height, sapling density, and leaf litter cover. Examples are Chestnut-rumped Babbler *Stachyris maculata* (sp5) and Black-capped Babbler *Pellorneum capistratum* (sp10). On the left-upper part of the plot were species that also commonly observed in transect with high value in tree height, and sapling density but particularly in area with low understory openness, typical for old secondary forests. Examples are Yellow-bellied Bulbul *Alophoixus phaeocephalus* (sp1) and Short-tailed Babbler *Malacocincla malaccensis* (sp9). On the right-upper part of the plot were species that correlated with high understory openness such as Brown Barbet *Calorhamphus fuliginosus* (sp12), and Cream-vented Bulbul *Pycnonotus simplex* (sp16). Species situated towards right-lower right of the plot were correlated with high ginger density, which is also a typical characteristic of young secondary forest. Examples are Sooty-capped Babbler *Malacopteron affine* (sp17), and Purple-naped Sunbird *Hypogramma hypogrammicum* (sp19).

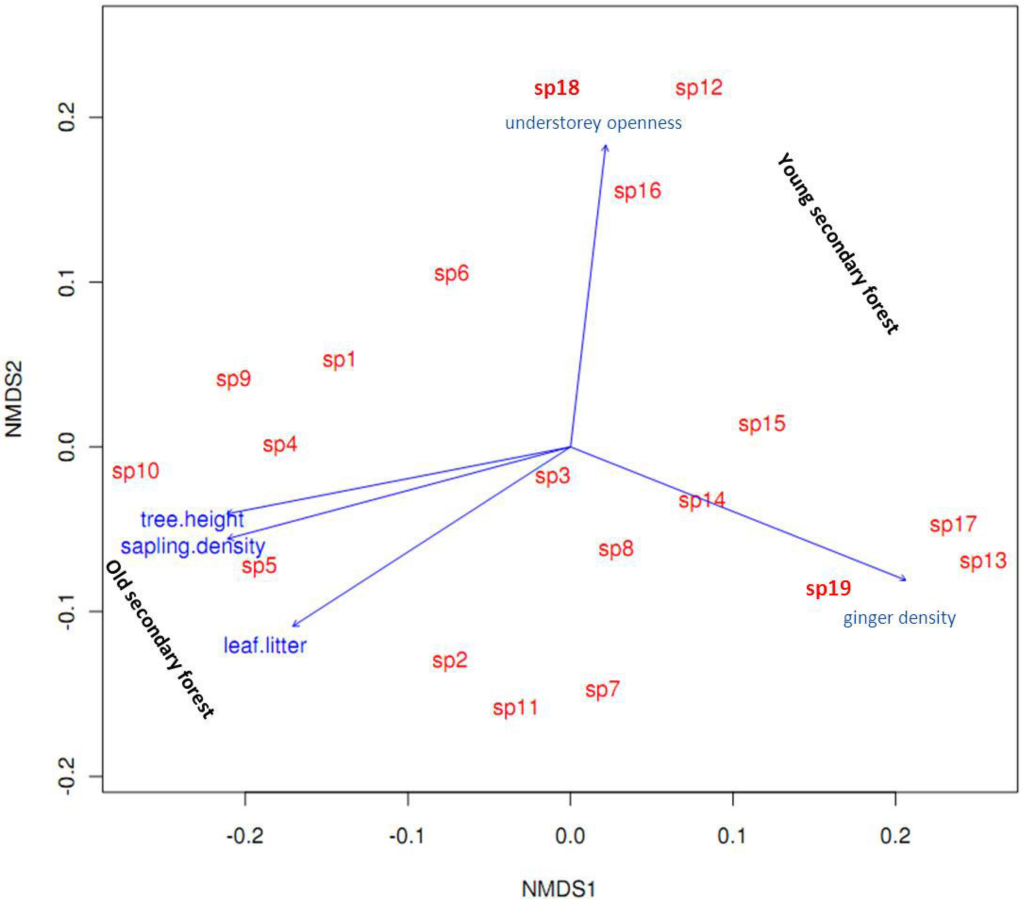
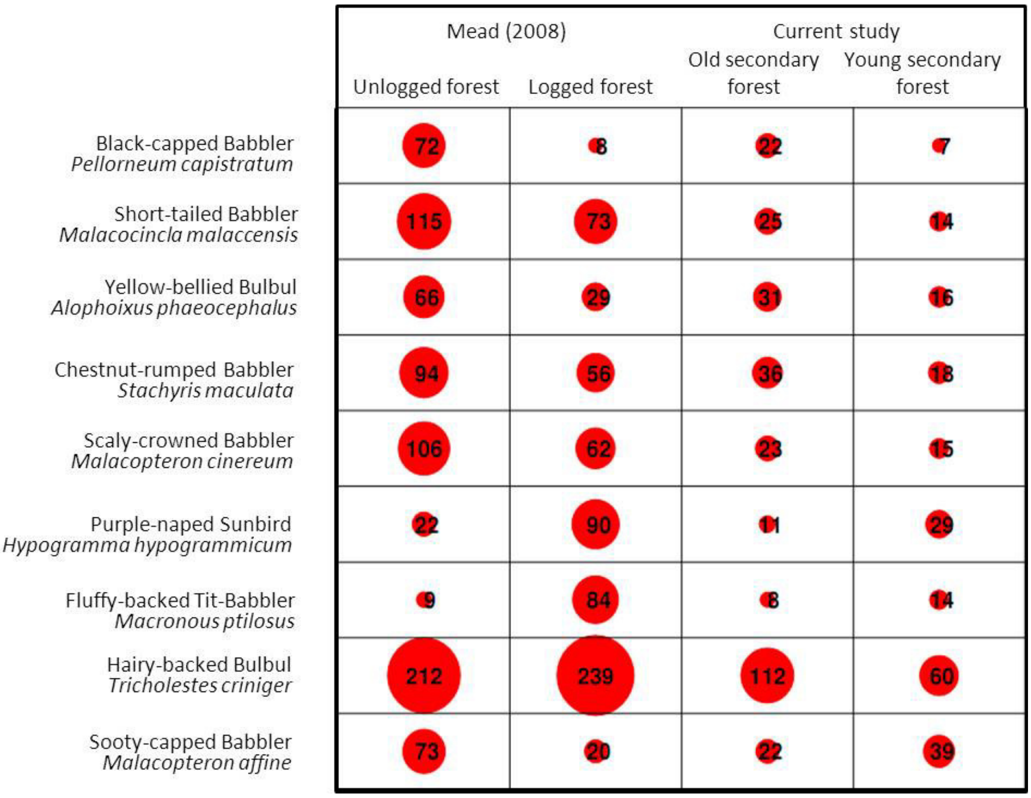


Figure 4.2. NMDS ordination biplots of bird species (e.g. sp1) with the habitat variables (blue text) superimposed. See Table 4.2 for definitions of bird species codes.

## DISCUSSION

We present bird density comparison between old and young lowland secondary forest in Sumatra. Bird density comparisons between different habitat disturbances have been rarely explored in Southeast Asia (Mead 2008, Marsden 1998) despite their potential benefits to identify quantitatively species specific response to disturbance. The current study add to this little explore topic, and the first that compare the density of individual bird species between two types of secondary forest, and adds to the limited knowledge on the quantitative response to disturbance of birds of the Sundaic region. Despite species richness was found to be a poor indicator of habitat change (Maas et al. 2009, Edwards et al. 2011), the species level could show the effect of habitat change. We present densities for 47, including 10 near-threatened species (BirdLife International 2013b). Where densities could be compared (33 species), 10 bird species had significantly higher densities in old secondary forest, nine bird species had higher densities in young secondary forest, while the other 14 species showed no significant differences. The responses of birds to age of secondary forest and habitat variables variation was complex, but still provides indication of disturbance. Overall, despite their degraded condition, these forests still maintained population of most lowland forest birds of Sumatra (64% of 228 lowland forest birds).



| | Mead (2008) | | Current study | |
|---|---|---|---|---|
| | Unlogged forest | Logged forest | Old secondary forest | Young secondary forest |
| Black-capped Babbler *Pellorneum capistratum* | 72 | 8 | 22 | 7 |
| Short-tailed Babbler *Malacocincla malaccensis* | 115 | 73 | 25 | 14 |
| Yellow-bellied Bulbul *Alophoixus phaeocephalus* | 66 | 29 | 31 | 16 |
| Chestnut-rumped Babbler *Stachyris maculata* | 94 | 56 | 36 | 18 |
| Scaly-crowned Babbler *Malacopteron cinereum* | 106 | 62 | 23 | 15 |
| Purple-naped Sunbird *Hypogramma hypogrammicum* | 22 | 90 | 11 | 29 |
| Fluffy-backed Tit-Babbler *Macronous ptilosus* | 9 | 84 | 8 | 14 |
| Hairy-backed Bulbul *Tricholestes criniger* | 212 | 239 | 112 | 60 |
| Sooty-capped Babbler *Malacopteron affine* | 73 | 20 | 22 | 39 |

Figure 4.3. Bird densities between unlogged and logged forest in Kalimantan (Mead 2008), and old secondary and young secondary forest in Sumatra (current study). The density for Fluffy-backed Tit-Babbler is from peripheral of unlogged and logged forest (Mead 2008), *see* text for the explanation.

Where possible, we relate our results to findings of other studies, but unfortunately, only one study in the Sundaic region (in Kalimantan) compares bird densities between unlogged and logged forest (Mead 2008). Species that have been found to decline in logged forest are also expected to show lower densities in young than in old secondary forest (and vice versa). Figure 4.3 shows the comparison of bird density between logged and unlogged forest (from Mead 2008), and between old and young secondary forest (this study). The density of Black-capped Babbler *Pellorneum capistratum* exhibited a 89% reduction in logged forest compared to that in unlogged forest. We found a similar trend with the density of this bird declining by 68% in young compared to old secondary forest. This species was commonly found in habitat with high values for tree height, sapling density, and leaf litter cover, which is typical for old secondary forest. These habitat variables were found to be significantly different between the two habitat types (Table 4.1), and significantly correlated with this species (Figure 4.2). This pattern held for five other bird species: Yellow-bellied bulbul *Alophoixus phaeocephalus* (48% decline in young forest), Scaly-crowned Babbler *Malacopteron cinereum* (35% decline), Chestnut-rumped Babbler *Stachyris maculata* (50% decline), and Short-tailed Babbler *Malacocincla malaccensis* (44% decline ). Two species have higher densities in logged forest than in primary forest: Fluffy-backed Tit-Babbler and Purple-naped Sunbird *Hypogramma hypogrammicum* (Figure 4.2). We also found a similar trend where densities for these species were 75%, and 164% higher in young than old secondary forest.

It is interesting to note that Mead (2008) finds Fluffy-backed Tit-Babbler to have lower density in logged forest. However, an opposite result is found when the density is compared between peripheral of unlogged and logged forest, which leads to the conclusion that this species is unaffected or even benefits from logging (Mead (2008). This species prefers undergrowth of secondary and selectively logged forest (Collar and Robson 2007), with a strong affinity to gaps and understory disturbance (Mead 2008). A study by Moradi et al. (2009) in Peninsula Malaysia shows that this species has higher density in the forest edge than in the forest interior. Similarly, this species has also been found to have lower abundance in selectively logged forest with high richness of lower story growth in Sabah, Borneo (Edwards et al. 2011).

The different trends emerging from comparing the density across different gradients of disturbance highlights the importance of more studies from different habitat gradients, which is currently lacking for most bird species in the Sundaic region. Secondary forest resulting from selectively logged forest is characterized by a mosaic of secondary forest patches in different stages of regenerations (Cleary et al. 2005, Putz et al. 2001) and contains also patches of unlogged forest (Mead 2008). This condition might favor some but not other species. For example in Kalimantan, Mead (2008) finds the density of Sooty-capped Babbler *Malacopteron affine* to be lower in logged forest. We found an opposite trend with this species having had 77% higher density in young than old secondary forest. This species prefers area with high density of trees and sapling, good midstorey cover, high litter abundance, and rarely occurs in areas with dense vine cover in the understory, and it avoids extensive gaps (Mead 2008). For the Hairy-backed Bulbul *Tricholestes criniger,* the story is the same but with a reverse trend. Mead (2008) shows higher density in logged forest. We found that this species had lower density in young than old secondary forest. This indicated that despite bulbul can do well in logged forest, it does decline where forest is severely degraded.

In this study, we compared densities between two different types of secondary forest. Quantitative comparison between different levels of disturbances are still very limited for Sundaic birds (Mead 2008, Moradi et al.

2009), especially in Sumatra. Species that decline after logging tend to also decline from old to young secondary forest. Moreover, species that decreased significantly in the young secondary forest can be used as indicator of forest recovery after disturbance. As selectively logged forests are often heterogeneous in structure and composition, e.g. due to small-scale differences in logging intensity and number of tree harvests (Putz et al. 2001, Cleary et al. 2005), more site specific studies are required to further enhance our understanding on how species respond to disturbance. The density information can be used to indicate habitat preferences. However, high density in particular habitats does not necessarily mean good habitat quality for that species (van Horne 1983). We suggested for temporal monitoring to be conducted to establish a better mechanistic understanding on species persistence in the secondary forest.

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Appendix 4.1. Abundance of all bird (point counts) sampled in old and young secondary forest. IUCN codes: NT= near-threatened, and VU = vulnerable.

| No | Family | Common name | Scientific name | Old secondary forest | Young secondary forest |
|---|---|---|---|---|---|
| 1 | Accipitridae | Crested Serpent-eagle | *Spilornis cheela* | | 1 |
| 2 | Aegithinidae | Green Iora | *Aegithina viridissima* | 40 | 41 |
| 3 | Alcedinidae | Blue-eared Kingfisher | *Alcedo meninting* | | 6 |
| 4 | Alcedinidae | Rufous-collared Kingfisher | *Actenoides concretus* | 4 | 3 |
| 5 | Alcedinidae | Black-backed Kingfisher | *Ceyx erithaca* | 3 | |
| 6 | Alcedinidae | Rufous-backed Kingfisher | *Ceyx rufidorsa* | 3 | 1 |
| 7 | Alcedinidae | Banded Kingfisher | *Lacedo pulchella* | 3 | 3 |
| 8 | Bucerotidae | Wrinkled Hornbill | *Aceros corrugatus* | 1 | 3 |
| 9 | Bucerotidae | Wreathed Hornbill | *Aceros undulatus* | 1 | 4 |
| 10 | Bucerotidae | Black Hornbill | *Anthracoceros malayanus* | 4 | 1 |
| 11 | Bucerotidae | Rhinoceros Hornbill | *Buceros rhinoceros* | 1 | 3 |
| 12 | Bucerotidae | Helmeted Hornbill | *Rhinoplax vigil* | | 1 |
| 13 | Bucerotidae | Bushy-crested Hornbill | *Anorrhinus galeritus* | 1 | 1 |
| 14 | Campephagidae | Lesser Cuckooshrike | *Coracina fimbriata* | 3 | 1 |
| 15 | Campephagidae | Black-winged Flycatcher-shrike | *Hemipus hirundinaceus* | 5 | 8 |
| 16 | Campephagidae | Scarlet Minivet | *Pericrocotus flammeus* | 7 | 6 |
| 17 | Chloropseidae | Blue-winged Leafbird | *Chloropsis cochinchinensis* | 27 | 17 |
| 18 | Chloropseidae | Lesser Green Leafbird | *Chloropsis cyanopogon* | 4 | 8 |
| 19 | Chloropseidae | Greater Green Leafbird | *Chloropsis sonneratii* | 9 | 2 |
| 20 | Columbidae | | *Ducula sp.* | | 3 |
| 21 | Columbidae | Thick-billed Green-pigeon | *Treron curvirostra* | 8 | 13 |
| 22 | Columbidae | Emerald Dove | *Chalcophaps indica* | 3 | 7 |
| 23 | Columbidae | Green Imperial-pigeon | *Ducula aenea* | 1 | 2 |
| 24 | Coraciidae | Asian Dollarbird | *Eurystomus orientalis* | 1 | |
| 25 | Corvidae | Crested Jay | *Platylophus galericulatus* | 3 | 2 |
| 26 | Corvidae | Black Magpie | *Platysmurus leucopterus* | 4 | 1 |
| 27 | Corvidae | Slender-billed Crow | *Corvus enca* | | 4 |
| 28 | Cuculidae | Rusty-breasted Cuckoo | *Cacomantis sepulcralis* | | 1 |
| 29 | Cuculidae | Banded Bay Cuckoo | *Cacomanthis sonneratii* | 2 | 3 |
| 30 | Cuculidae | Violet Cuckoo | *Chrysococcyx xanthorhynchus* | | 1 |
| 31 | Cuculidae | Hodgson's Hawk-cuckoo | *Cuculus fugax* | 3 | |
| 32 | Cuculidae | Drongo Cuckoo | *Surniculus lugubris* | 3 | |
| 33 | Cuculidae | Raffles's Malkoha | *Phaenicophaeus chlorophaeus* | 16 | 16 |
| 34 | Cuculidae | Chestnut-breasted Malkoha | *Phaenicophaeus curvirostris* | 1 | 1 |
| 35 | Cuculidae | Black-bellied Malkoha | *Phaenicophaeus diardi* | 3 | |
| 36 | Cuculidae | Green-billed Malkoha | *Phaenicophaeus tristis* | 1 | 4 |
| 37 | Cuculidae | Short-toed Coucal | *Centropus rectunguis* | 1 | |
| 38 | Cuculidae | Plaintive Cuckoo | *Cacomantis merulinus* | 1 | 2 |

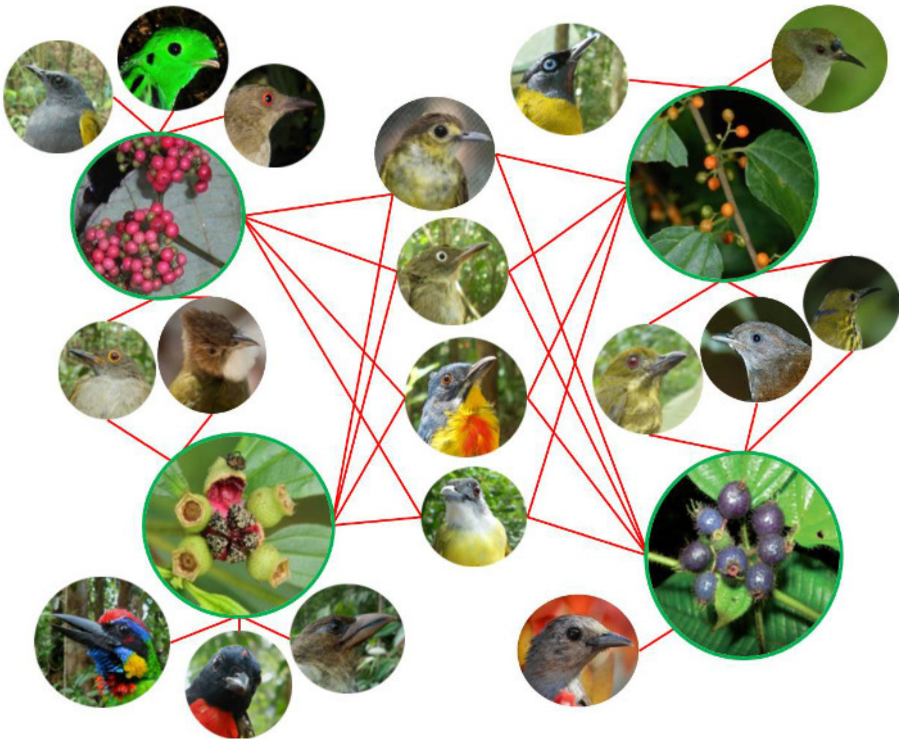
| | | | | | |
|---|---|---|---|---|---|
| 39 | Cuculidae | Indian Cuckoo | *Cuculus micropterus* | | 2 |
| 40 | Cuculidae | Greater Coucal | *Centropus sinensis* | | 1 |
| 41 | Dicaeidae | Yellow-vented Flowerpecker | *Dicaeum chryssorheum* | | 1 |
| 42 | Dicaeidae | Plain Flowerpecker | *Dicaeum concolor* | 26 | 15 |
| 43 | Dicaeidae | Scarlet-backed Flowerpecker | *Dicaeum cruentatum* | 2 | 1 |
| 44 | Dicaeidae | | *Dicaeum sp.* | 8 | 5 |
| 45 | Dicaeidae | Orange-bellied Flowerpecker | *Dicaeum trigonostigma* | 51 | 26 |
| 46 | Dicaeidae | Yellow-breasted Flowerpecker | *Prionochilus maculatus* | 5 | |
| 47 | Dicaeidae | Crimson-breasted Flowerpecker | *Prionochilus percussus* | | 1 |
| 48 | Dicaeidae | Scarlet-breasted Flowerpecker | *Prionochilus thoracicus* | 1 | 1 |
| 49 | Dicruridae | Greater Racket-tailed Drongo | *Dicrurus paradiseus* | 31 | 26 |
| 50 | Eupetidae | Rail-babbler | *Eupetes macrocerus* | 7 | 4 |
| 51 | Eurylaimidae | Dusky Broadbill | *Corydon sumatranus* | 2 | 1 |
| 52 | Eurylaimidae | Banded Broadbill | *Eurylaimus javanicus* | 3 | 7 |
| 53 | Eurylaimidae | Black-and-yellow Broadbill | *Eurylaimus ochromalus* | 17 | 20 |
| 54 | Eurylaimidae | Asian Green Broadbill | *Calyptomena viridis* | 8 | 3 |
| 55 | Irenidae | Asian Fairy-bluebird | *Irena puella* | 13 | 20 |
| 56 | Meropidae | Red-bearded Bee-eater | *Nyctyornis amictus* | 4 | 2 |
| 57 | Monarchidae | Black-naped Monarch | *Hypothymis azurea* | 35 | 33 |
| 58 | Muscicapidae | Malaysian Blue-flycatcher | *Cyornis turcosus* | 2 | |
| 59 | Muscicapidae | Pale Blue-flycatcher | *Cyornis unicolor* | 3 | 5 |
| 60 | Muscicapidae | White-rumped Shama | *Copsychus malabaricus* | 1 | 2 |
| 61 | Muscicapidae | Grey-headed Canary-flycatcher | *Culicicapa ceylonensis* | 1 | 1 |
| 62 | Muscicapidae | Large-billed Blue-flycatcher | *Cyornis caerulatus* | 1 | |
| 63 | Muscicapidae | Rufous-winged Philentoma | *Philentoma phyrrhopterum* | 12 | 10 |
| 64 | Muscicapidae | Grey-chested Jungle-flycatcher | *Rhinomyias umbratilis* | 19 | 2 |
| 65 | Muscicapidae | Rufous-tailed Shama | *Trichixos pyrrhopygus* | 20 | 12 |
| 66 | Muscicapidae | White-crowned Forktail | *Enicurus leschenaultii* | 7 | 14 |
| 67 | Muscicapidae | Oriental Magpie-robin | *Copsychus saularis* | 4 | |
| 68 | Nectariniidae | Ruby-cheeked Sunbird | *Anthreptes singalensis* | 12 | 5 |
| 69 | Nectariniidae | Plain Sunbird | *Anthreptes simplex* | 4 | 6 |
| 70 | Nectariniidae | Grey-breasted Spiderhunter | *Arachnothera affinis* | 4 | 3 |
| 71 | Nectariniidae | Spectacled Spiderhunter | *Arachnothera flavigaster* | 1 | 1 |
| 72 | Nectariniidae | Long-billed Spiderhunter | *Arachnothera robusta* | 5 | 1 |
| 73 | Nectariniidae | Purple-naped Sunbird | *Hypogramma hypogrammicum* | 14 | 25 |
| 74 | Nectariniidae | Crimson Sunbird | *Aethopyga siparaja* | 10 | 4 |
| 75 | Nectariniidae | Little Spiderhunter | *Arachnothera longirostra* | 112 | 106 |
| 76 | Nectariniidae | | *Arachnothera sp.* | 1 | |
| 77 | Nectariniidae | Plain-throated Sunbird | *Anthreptes malacensis* | 2 | 6 |
| 78 | Nectariniidae | Olive-backed Sunbird | *Nectarinia jugularis* | 1 | 4 |
| 79 | Oriolidae | Black-hooded Oriole | *Oriolus xanthonotus* | 7 | 5 |
| 80 | Phasianidae | Great Argus | *Argusianus argus* | 3 | 4 |
| 81 | Picidae | Maroon Woodpecker | *Blythipicus rubiginosus* | 8 | 3 |
| 82 | Picidae | Rufous Woodpecker | *Celeus brachyurus* | 1 | 3 |

| | | | | | |
|---|---|---|---|---|---|
| 83 | Picidae | White-bellied Woodpecker | *Dryocopus javensis* | 2 | 3 |
| 84 | Picidae | Grey-and-buff Woodpecker | *Hemicircus concretus* | 1 | 3 |
| 85 | Picidae | Buff-rumped Woodpecker | *Meiglyptes tristis* | 5 | 20 |
| 86 | Picidae | Buff-necked Woodpecker | *Meiglyptes tukki* | 5 | 7 |
| 87 | Picidae | Checker-throated Woodpecker | *Picus mentalis* | 4 | 3 |
| 88 | Picidae | | *Picus sp.* | 1 | 2 |
| 89 | Picidae | Crimson-winged Woodpecker | *Picus puniceus* | 1 | 7 |
| 90 | Picidae | Rufous Piculet | *Sassia abnormis* | 5 | 11 |
| 91 | Picidae | Olive-backed Woodpecker | *Dinopium rafflesii* | 1 | 1 |
| 92 | Picidae | Orange-backed Woodpecker | *Reinwardtipicus validus* | 4 | 7 |
| 93 | Pittidae | Garnet Pitta | *Pitta granatina* | 2 | 2 |
| 94 | Pittidae | Javan Banded Pitta | *Pitta guajana* | 1 | |
| 95 | Pittidae | Hooded Pitta | *Pitta sordida* | | 2 |
| 96 | Psittacidae | Blue-rumped Parrot | *Psittinus cyanurus* | 1 | 8 |
| 97 | Pycnonotidae | Buff-vented Bulbul | *Iole olivacea* | 37 | 37 |
| 98 | Pycnonotidae | Red-eyed Bulbul | *Pycnonotus brunneus* | 17 | 6 |
| 99 | Pycnonotidae | Olive-winged Bulbul | *Pycnonotus plumosus* | 19 | 26 |
| 100 | Pycnonotidae | Cream-vented Bulbul | *Pycnonotus simplex* | 37 | 45 |
| 101 | Pycnonotidae | Streaked Bulbul | *Ixos malaccensis* | 8 | 2 |
| 102 | Pycnonotidae | Spectacled Bulbul | *Pycnonotus erythropthalmos* | 76 | 97 |
| 103 | Pycnonotidae | Yellow-bellied Bulbul | *Alophoixus phaeocephalus* | 31 | 22 |
| 104 | Pycnonotidae | Black-headed Bulbul | *Pycnonotus atriceps* | 22 | 44 |
| 105 | Pycnonotidae | Puff-backed Bulbul | *Pycnonotus eutilotus* | 2 | 1 |
| 106 | Pycnonotidae | Hairy-backed Bulbul | *Tricholestes criniger* | 63 | 45 |
| 107 | Pycnonotidae | Grey-cheeked Bulbul | *Alophoixus bres* | 12 | 12 |
| 108 | Pycnonotidae | Yellow-vented Bulbul | *Pycnonotus goavier* | | 1 |
| 109 | Ramphastidae | Gold-whiskered Barbet | *Megalaima chrysopogon* | 1 | 7 |
| 110 | Ramphastidae | Yellow-crowned Barbet | *Megalaima henricii* | 7 | 3 |
| 111 | Ramphastidae | Red-crowned Barbet | *Megalaima rafflesii* | 3 | |
| 112 | Ramphastidae | | *Meiglyptes sp.* | 2 | |
| 113 | Ramphastidae | Brown Barbet | *Calorhamphus fuliginosus* | 13 | 15 |
| 114 | Ramphastidae | Blue-eared Barbet | *Megalaima australis* | 19 | 29 |
| 115 | Rhipiduridae | Pied Fantail | *Rhipidura javanica* | | 1 |
| 116 | Rhipiduridae | Spotted Fantail | *Rhipidura perlata* | 5 | |
| 117 | Sittidae | Velvet-fronted Nuthatch | *Sitta frontalis* | 3 | |
| 118 | Sturnidae | Hill Myna | *Gracula religiosa* | 2 | 5 |
| 119 | Sylviidae | Dark-necked Tailorbird | *Orthotomus atrogularis* | 39 | 24 |
| 120 | Sylviidae | Ashy Tailorbird | *Orthotomus ruficeps* | 1 | 3 |
| 121 | Sylviidae | Rufous-tailed Tailorbird | *Orthotomus sericeus* | 12 | 9 |
| 122 | Sylviidae | Yellow-bellied Warbler | *Abroscopus superciliaris* | 1 | |
| 123 | Timaliidae | White-chested Babbler | *Trichastoma rostratum* | 4 | 6 |
| 124 | Timaliidae | Short-tailed Babbler | *Malacocincla malaccensis* | 30 | 17 |
| 125 | Timaliidae | Black-capped Babbler | *Pellorneum capistratum* | 16 | 10 |
| 126 | Timaliidae | Sooty-capped Babbler | *Malacopteron affine* | 21 | 40 |

| | | | | | |
|---|---|---|---|---|---|
| 127 | Timaliidae | Moustached Babbler | *Malacopteron magnirostre* | 15 | 12 |
| 128 | Timaliidae | Chestnut-winged Babbler | *Stachyris erythroptera* | 22 | 36 |
| 129 | Timaliidae | Chestnut-rumped Babbler | *Stachyris maculata* | 31 | 20 |
| 130 | Timaliidae | Black-throated Babbler | *Stachyris nigricollis* | 4 | 2 |
| 131 | Timaliidae | Rufous-fronted Babbler | *Stachyris rufifrons* | 25 | 2 |
| 132 | Timaliidae | Pin-striped Tit-babbler | *Macronous gularis* | 9 | 22 |
| 133 | Timaliidae | Fluffy-backed Tit-babbler | *Macronous ptilosus* | 11 | 17 |
| 134 | Timaliidae | Striped Wren-babbler | *Kenopia striata* | 5 | |
| 135 | Timaliidae | Large Wren-babbler | *Turdinus macrodactylus* | 1 | 2 |
| 136 | Timaliidae | Abbott's Babbler | *Malacopteron abboti* | 1 | |
| 137 | Timaliidae | Scaly-crowned Babbler | *Malacopteron cinereum* | 20 | 18 |
| 138 | Timaliidae | Rufous-crowned Babbler | *Malacopteron magnum* | 15 | 9 |
| 139 | Timaliidae | Chestnut-backed Scimitar-babbler | *Pomatorhinus montanus* | 14 | 10 |
| 140 | Timaliidae | Brown Fulvetta | *Alcippe brunneicauda* | 21 | 8 |
| 141 | Timaliidae | White-necked Babbler | *Stachyris leucotis* | | 1 |
| 142 | Timaliidae | Grey-headed Babbler | *Stachyris poliocephala* | 3 | 6 |
| 143 | Timaliidae | Ferruginous Babbler | *Trichastoma bicolor* | 43 | 45 |
| 144 | Trogonidae | Diard's Trogon | *Harpactes diardi* | 4 | 1 |
| 145 | Trogonidae | Scarlet-rumped Trogon | *Harpactes duvaucelli* | 5 | 4 |
| 146 | Trogonidae | Red-naped Trogon | *Harpactes kasumba* | 4 | 4 |

# Chapter 5

## Frugivore bird-seed interaction networks and the restoration of old vs young secondary lowland rainforest in Sumatra



## ABSTRACT

Bird seed dispersal plays an important role in tropical forest regeneration. Information on which bird species is responsible for dispersing which plant species is crucial, but still limited, in particular for Southeast Asia, and also skewed towards large bird species. As more tropical forest landscapes are now dominated by secondary forests, where small to medium size birds dominate, which tend to be more resilient to disturbance, their role as seed dispersers becomes increasingly important. By examining fecal samples of birds collected by mist-netting in 12 Harapan Rainforest locations (Sumatra, Indonesia), we quantified the rarely explored bird-seed interaction networks worldwide for old vs young secondary forests.  We captured 58 bird species (298 individuals) from May to June 2012 and collected fecal samples with seeds from 20 plant species and from 22 bird species (132 bird individuals).  We found that the bird-seed dispersal networks in the study area were dominated by generalist dispersers with 16 bird species had at least two seed species in their fecal samples. Bird species from the Pycnonotidae (bulbuls) dominated the bird-seed network. In both the old and young secondary forests, network level parameters (e.g. connectance, H2’) were similar, but different species were important:  Yellow-bellied Bulbul *Alophoixus phaeocephalus* had the highest interaction strength in old secondary forests, but was replaced by Cream-vented Bulbul *Pycnonotus simplex* in young secondary forests. For the birds, fruits of *Melastoma malabatrichum* had the highest strength value in old secondary forest, but replaced by *Trema canabina* in young secondary forest. In general, bird density was positively related to the number of interactions and the number of seed species found in fecal samples. In conclusion, we here provide much evidence for the important role of common birds (such as the bulbul species) as seed dispersers and vice versa, the significant importance of small fleshy multi-seed fruit species (and also several weed species) for frugivore birds, but we still need a better understanding of the relative role of bird and plant species and their spatio-temporal variation to reliably characterize bird-seed interaction networks and to improve management practices in rainforest restoration projects.

**Keywords:** avian frugivore, plant-frugivore networks, seed dispersal, tropical forest

## INTRODUCTION

Bird seed dispersal plays an important role in forest regeneration (e.g. Corlett 1998b, Corlett and Hau 2000) and maintenance of plant diversity in tropical forests (e.g. Terborgh et al. 2002). About 90% of tropical trees and shrubs produce fleshy fruits that are adapted for consumption by vertebrates (Howe and Smallwood 1982, Howe 1986, Jordano 2000), and 48 plant families have been recorded in the diets of frugivore birds in Southeast Asia (Snow 1981). Human disturbance had been shown to disturb animal-mediated seed dispersal, where the number of seed removed decreased as forest disturbance increased, particularly in forest disturbed by hunting and logging activities (Markl et al. 2012).

Levey et al. (2002) proposes research priorities including the relative contribution of different frugivore species for seed removal and deposition (Lambert 2002, Pizo 2002), and how these are influenced by anthropogenic forest disturbance (Kaplin and Lambert 2002). Despite the relatively good understanding of the impact of logging on frugivore birds in Southeast Asia, our understanding of plant species selection by birds is still too limited to identify the seed dispersal role of frugivore bird assemblages (Corlett 1998, Sankamethawee et al. 2011), and studies are mostly skewed towards large frugivore species (e.g. Kinnaird 1998, Kitamura et al. 2004, Savini et al. 2009, but *see* Sankamethawee et al. 2011, Poonswad et al. 1998, Kitamura et al. 2002, and Kitamura et al. 2005). Due to the negative effect of logging on large birds (Cleary et al. 2007), hence small-medium size birds may play an important role in shaping the future of forest composition after degradation. Understanding which bird species are responsible for dispersing what plant species through examining bird fecal samples can provide insight into bird seed dispersal in degraded tropical forest (Corlet and Hau 2000). Moreover, some of the most damaging invasive plants can be dispersed by frugivores, hence basic understanding on the importance of weed species in plant-frugivore interaction can be used to devise appropriate eradication or control program, particularly in area where weed species already become important part of the network (Gosper et al. 2005, Buckley et al. 2006, Wescott and Dennis 2006, Wescott et al. 2008). In addition, network approach has been widely used to investigate plant-bird interaction network (e.g. Sankamethawee et al. 2012, Schleuning et al. 2012) but study to compare interaction networks between different habitat types has been rare (Menke et al. 2012).

Avian diets can be assessed by using observations at fruiting trees and or collection of fecal samples. The combination of these two data sources is effective for identifying species interactions between plants and frugivores (Wheelwright et al. 1984, Silva et al. 2002, Sankamethawee et al. 2011). In this study we investigated how tropical plant-frugivore networks change along two disturbances gradients (old vs young secondary forest). We identified plant-species interactions through examining bird fecal samples from frugivore birds capture using mist-nets, with a focus on which bird species dispersed which plant species. Examining bird fecal samples will not directly tell where exactly the seeds might come from and where they might have been dispersed, because the location where the bird is captured is not necessarily where seeds would have been eaten or deposited. We compared bird fecal samples between old and young secondary forests. Bulbuls are the most common frugivore group in tropical Asia (Sanitjan and Chen 2009, Sankamethawee et al. 2011). They can tolerate degraded landscapes (Corlett and Hau 2008). We expected that this group will play important role (i.e. consume many fruits and many fruit species), but species specific responses to habitat disturbance can play a role (for example, some species cannot tolerate highly degraded forest). In addition, the mutualistic bird-seed network in primary forest and in disturbed forest is dominated by generalist dispersers (Corlett 1998, Sankamethawee et al. 2011, Menke et al. 2012). We expected that this will also be true in our study area. In this study, we focus on-bird-seed interaction networks and their potential contribution to forest restoration and weed invasion.

The study was conducted in Harapan Rainforest, the first ecosystem restoration concession in Indonesia. This ex-logged forest covers 984.55 km$^2$. The commercial logging ceased 2006. Previous logging activities have left a mosaic of secondary forest habitats of different stages of regeneration: high, medium and low secondary forest (Lee and Lindsell 2011), which are typically characterizing ex-logged forest (Putz et al. 2001).

## METHODS

*Survey methodology.* Fecal samples were collected from frugivores birds caught with mist nets. Frugivore birds were defined loosely as bird that feeds mainly or partly on fruits. Mist nets were conducted between May-June 2012 in two secondary forest types, old and young. Old secondary forest is characterized by higher tree density, higher average tree height, and lower numbers of *Macaranga* trees and dead- trees (*see* Chapter 4).

At each forest type we had six net locations and each location was at least 1 km apart from each other. Nets were opened between 08.00 and 17.00. Mist nets become less effective after five days of use (Whittaker 1972). A mist-netting study in Harapan Rainforest indicated that bird capture rate declined already after the second and third day (Fangyuan Hua, *pers. comm.*), hence we only conducted mist netting for two consecutive days per location. Nine mist nets were used (6 nets each, which were 15 m long and 2.6 m high, and 3 nets each with length 11 m long and 2.6 m high) with a total length of 123 m. Two heights of net placement were used: high nets consisted of four nets with the lower part of the net being 5-6 meter above the ground, and the 5 low nets at least 2 meter above the ground. The high net set up was used to capture mid-storey frugivore birds. The high nets were set up using rig system, which is suitable for capturing sub-canopy and canopy birds (Whittaker 1972), while the low net was erected using bamboo poles. The low net set up was used to capture frugivore birds that forage in the understory utilizing food resources from shrub species such as *Clidemia hirta*.

Each frugivore bird captured was placed in a paper bag for 15 to 60 minutes (Corlett 1998a) and then released (whether they defecated or not) after banded with numbered metal bands. Each bag was used only once. Gape width was also measured for furgivore bird species captured. All fecal samples collected were then examined for evidence of seeds. In each fecal sample, we used forceps to separate all seeds from the sample and identified them as precisely as possible. Unknown seeds that could not be identified were described according to morphospecies for consistent tallying among samples. During the mist netting period, we also looked for potential fruiting trees and collected fruits, seeds and leaves for identification. We matched the collected seeds from fruits found around the net locations and from fecal samples to assist in identifying the seed species identity. All non-frugivore birds captured were not banded and only noted. The bird taxonomy in this study followed BirdLife International taxonomy (BirdLife International 2013). To make generalization of fruit seed types found in the bird fecal samples, all seed species identified were grouped based on their general fruit characteristics (hereafter fruit-seed type): fruit type (fleshy, berry, or capsule) and number of seeds per fruit (single or multiple). Moreover, we also grouped the seed species into two main groups: weed species and non-weed species, in order to understand how well weed species are integrated into the existing interaction networks.

*Analysis.* Quantitative seed dispersal network were based on the analysis of fecal samples from birds. Interaction frequency was quantified as the number of fecal samples containing at least one intact seeds of each plant species. For example, 12 fecal samples were collected from bird species X and contained a total of 3 seed species (A, B and C). Seed A was found in 10 fecal samples, seed B in 12 fecal samples, and seed C in 2 fecal samples. Based on this, the interaction frequency between bird species X and seed A, B and C would be 10, 12 and 2, respectively.

We constructed two types of seed dispersal networks. The first one was a network that combined data from old and young secondary forest. This overall network was used to provide general overview of seed dispersal network in the secondary forest. The second one was a habitat specific network, i.e. network in old versus young secondary forests. Comparison between these two networks was aimed to show potential impact of habitat degradation on seed dispersal network.

For both network types (i.e. combined and habitat specific networks), the following network parameters were calculated:

1. at network level we calculated:
    1. Link per species (mean number of interaction per-species)
    2. Shannon interaction diversity, a measure of the number of interactions and the evenness of their frequency distribution (Dormann et al. 2013).
    3. Connectance, a measure of network complexity (Dunne et al. 2002).
    4. $H_2$’, a measure of overall level of specialization. The more selective a species, the larger is $H_2$’ for the network (Bluthgen et al. 2006).
2. at species-level we calculated:
    1. Species specialization (d'), a measure of how specialized a given species is in relation to what resources are on offer (Bluthgen et al. 2006). This value is suitable for cross-network comparison (Dormann

2011).

2. Interaction strength, a measure of how important a species in a network (Dormann et al. 2013).

The d' and $H_2$’ values are scale-independent and provide a meaningful indices to characterize specialization on the level of single species and the entire network (Bluthgen et al. 2006). All these network parameters were calculated using the bipartite package (Dormann et al. 2013).

We conducted simple linear regressions to test the relationship of bird species density to the number of interactions per disperser and the number of seed species found in fecal samples per disperser. For this analysis, the density estimates for each bird seed dispersers were derived from a previous study (Chapter 3). To test whether there were differences in frequency distribution of interactions for each fruit-seed type between old and young secondary forest, we conducted Pearson's Chi-squared test. The relative importance of fruit-seed type was assessed by removing one at the time fruit-seed type from the contingency table and the changes in p-value were assessed. For example, in the complete contingency table we had number of interactions for four fruit-seed types for old and young secondary forest. We first calculated the Chi-square value for this complete data set. After that, we removed the number of interactions for fleshy multi-seed fruit from the contingency table, calculate the Chi-square value, and then compared it with the Chi-square value from the complete data set. The lower p-value compared to p-value from complete data set will indicate the relative importance of the fruit-seed type that were removed.

For all statistical analysis we used R 2.15.2 (R Development Core Team 2012). To analyze bird-plant interaction networks we used the ‘bipartite’ package (Dormann et al. 2009, Dormann et al. 2013) with ‘gplots’ package for additional graphical presentation (Warnes et al. 2009).

## RESULTS

We captured a total of 298 individual birds (58 species), and collected fecal samples from 164 individuals (25 species, Appendix 5.1). From the 164 fecal samples collected, 132 samples (22 bird species) contained seeds. Table 5.1 summarized information on the bird species with seeds in their fecal samples. Seeds recovered from the fecal samples were identified, when possible, until species level. From the 20 seed morphospecies, 19 could be identified until species or genus level (Table 5.2). Only two seed species were from large fleshy-fruit (fruit size > 20 mm).

From a total of 204 interactions recorded (i.e. bird-seed interactions, Figure 5.1), four bird species from Pycnonotidae family had the highest number of interaction: Yellow-bellied Bulbul *Alophoixus phaeocephalus* (43 interactions), Hairy-backed Bulbul *Tricholestes criniger* (37 interactions), Cream-vented Bulbul *Pycnonotus simplex* (35 interactions), and Spectacled Bulbul *Pycnonotus erythropthalmos* (28 interactions). These were also species that had the highest number of seed species in their fecal samples (13, 8, 13, 11, respectively).

Table 5.1. The frugivore-birds in the tropical secondary forest

| Family | Common name | Scientific name | code | [1]Guild | [2] Body size class | [3] Gape class | [4]N | Sample contained seeds | Total plant species | [5]Density (birds/km$^2$) |
|---|---|---|---|---|---|---|---|---|---|---|
| Chloropseidae | Blue-winged Leafbird | *Chloropsis cochinchinensis* | chlo.coch | nif | medium | M | 1 | 1 | 1 | 16.8 |
| Dicaeidae | Plain Flowerpecker | *Dicaeum concolor* | dica.conc | nif | small | S | 2 | 2 | 1 | 43.2 |
| Dicaeidae | Yellow-breasted Flowerpecker | *Prionochilus maculatus* | prio.macu | afgif | small | S | 6 | 5 | 3 | 6.5 |
| Dicaeidae | Crimson-breasted Flowerpecker | *Prionochilus percussus* | prio.perc | afgif | small | S | 12 | 11 | 6 | 6.8 |
| Dicaeidae | Scarlet-breasted Flowerpecker | *Prionochilus thoracicus* | prio.thor | afgif | medium | S | 2 | 1 | 1 | 2.2 |
| Eurylaimidae | Asian Green Broadbill | *Calyptomena viridis* | caly.viri | af | medium | L | 2 | 2 | 2 | 4 |
| Irenidae | Asian Fairy-bluebird | *Irena puella* | iren.puel | af | medium | L | 1 | 1 | 2 | 20.6 |
| Nectariniidae | Plain Sunbird | *Anthreptes simplex* | anth.simp | nif | small | S | 2 | 2 | 1 | 4.8 |
| Nectariniidae | Purple-naped Sunbird | *Hypogramma hypogrammicum* | hypo.hypo | nif | small | S | 9 | 3 | 3 | 25.2 |
| Pycnonotidae | Grey-cheeked Bulbul | *Alophoixus bres* | alop.bres | afgif | medium | M | 1 | 1 | 2 | 9.7 |
| Pycnonotidae | Yellow-bellied Bulbul | *Alophoixus phaeocephalus* | alop.phae | afgif | medium | M | 22 | 22 | 13 | 25.6 |
| Pycnonotidae | Buff-vented Bulbul | *Iole olivacea* | iole.oliv | afgif | medium | M | 1 | 1 | 3 | 44 |
| Pycnonotidae | Streaked Bulbul | *Ixos malaccensis* | ixos.mala | afgif | medium | M | 1 | 1 | 1 | 6.6 |
| Pycnonotidae | Black-headed Bulbul | *Pycnonotus atriceps* | pycn.atri | afgif | medium | M | 2 | 1 | 2 | 26.5 |
| Pycnonotidae | Red-eyed Bulbul | *Pycnonotus brunneus* | pycn.brun | afgif | medium | M | 5 | 5 | 4 | 8.9 |
| Pycnonotidae | Grey-bellied Bulbul | *Pycnonotus cyaniventris* | pycn.cyani | afgif | medium | M | 5 | 5 | 2 | NA |
| Pycnonotidae | Spectacled Bulbul | *Pycnonotus erythropthalmos* | pycn.eryt | afgif | small | M | 19 | 18 | 11 | 97.5 |
| Pycnonotidae | Cream-vented Bulbul | *Pycnonotus simplex* | pycn.simp | afgif | medium | M | 22 | 20 | 13 | 64.7 |
| Pycnonotidae | Hairy-backed Bulbul | *Tricholestes criniger* | tric.crin | afgif | small | M | 25 | 25 | 8 | 73.8 |
| Ramphastidae | Brown Barbet | *Calorhamphus fuliginosus* | calo.fuli | afgif | medium | L | 1 | 1 | 1 | 25.4 |
| Ramphastidae | Red-crowned Barbet | *Megalaima rafflesii* | mega.raff | af | medlarge | L | 2 | 2 | 3 | 1.9 |
| Timaliidae | Brown Fulvetta | *Alcippe brunneicauda* | alci.brun | afgif | small | M | 4 | 4 | 2 | 9.4 |

1. Guild classification based on (Lambert 1992): nif (nectarivores/insectivores/frugivores), tom (terrestrial omnivores), afgif (arboreal foliage-gleaning insectivores/frugivores, af (arboreal frugivores).
2. Body size class, data from (Dunning 2008) and classified based on Lambert (1992): small (weight < 20 gram), medium (weight 20-69 gram), medium-large (weight 70-150 gram).
3. Gape class based on classification by Moran et al. (2004): S small (< 1.0 cm), M medium (1.0-1.5 cm), L large (> 1.5 cm) .
4. N: total number of individual captured
5. Density estimates were derived from Chapter 3

Table 5.2. Plant species identified from seeds in the fecal samples collected (only for seeds that could be identified until minimum genus level).

| Family | Species | Species code | [1]Fruit characteristics | [2]Weed species |
|---|---|---|---|---|
| Melastomataceae | *Bellucia axinanthera* | bell.axin | Berry multi seed | No |
| Melastomataceae | *Clidemia hirta* | clid.hirt | Berry multi seeds | Yes |
| Euphorbiaceae | *Mallotus paniculatus* | mall.pani | Capsule multi seed | No |
| Melastomataceae | *Pternandra cordata* | pter.cord | Capsule multi seed | No |
| Phyllanthaceae | *Glochidion laevigata* | gloc.laev | Capsule multi seed | No |
| Asteraceae | *Clibadium surinamense* | clib.suri | Fleshy multi seed | Yes |
| Leeaceae | *Leea indica* | leea.ind | Fleshy multi seed | No |
| Melastomataceae | *Melastoma malabathricum* | mela.mala | Fleshy multi seed | Yes |
| Moraceae | *Ficus sp.* | ficus.sp | Fleshy multi seed | No |
| Rubiaceae | *Psychotria viridis* | psyc.viri | Fleshy multi seed | No |
| Verbenaceae | *Callicarpa petandra* | call.peta | Fleshy multi seed | No |
| Cannabaceae | *Trema canabina* | trem.cana | Fleshy single seed | No |
| Celastracea | *Salacia chinensis* | sala.chin | Fleshy single seed | No |
| Euphorbiaceae | *Bridelia sp.* | bridl.sp | Fleshy single seed | No |
| Lamiaceae | *Vitex vestita* | vite.vest | Fleshy single seed | No |
| Melastomataceae | *Memecylon pauciflorom* | meme.pauc | Fleshy single seed | No |
| Phyllanthaceae | *Antidesma sp.* | anti.sp | Fleshy single seed | No |
| Rhizophoraceae | *Gynotroches axillaris* | gyno.axil | Fleshy single seed | No |
| Ulmaceae | *Gironiera nervosa* | giro.nerv | Fleshy single seed | No |

[1] Slik (2009), Lok et al. (2011) , [2] Tjitrosemito et al. 1986

Four seed species were found in fecal samples with > 20 bird individuals (Figure 5.1): *Callicarpa petandra* (33 interactions), *Melastoma malabatrichum* (32 interactions), *Trema canabina* (24 interactions), and *Clidemia hirta* (23 interactions). These four seed species were also found in fecal samples from many bird species (i.e. consumed by 10, 10, 10, 8 bird species, respectively) compared to other seed species (Figure 5.1).

Table 5.3. Parameters at network level

| Parameters | Seed dispersal network | | |
|---|---|---|---|
| | Combined | Old | Young |
| Number of bird species | 25 | 15 | 20 |
| Number of seed species | 20 | 12 | 17 |
| Link per species | 2.02 | 1.50 | 1.91 |
| Connectance (complexity) | 0.19 | 0.23 | 0.22 |
| Shannon interaction diversity | 4.15 | 3.45 | 3.88 |
| $H_2$' (specialization) | 0.24 | 0.22 | 0.28 |

**Bird:** *Chloropsis cochinchinensis* (chlo.coch), *Dicaeum concolor* (dica.conc), *Prionochilus maculatus* (prio.macu), *Prionochilus percussus* (prio.perc), *Prionochilus thoracicus* (prio.thor), *Calyptomena viridis* (caly.viri), *Irena puella* (iren.puel), *Anthreptes simplex* (anth.simp), *Hypogramma hypogrammicum* (hypo.hypo), *Alophoixus bres* (alop.bres), *Alophoixus phaeocephalus* (alop.phae), *Iole olivacea* (iole.oliv), *Ixos mala*ccensis (ixos.mala), *Pycnonotus atriceps* (pycn.atri), *Pycnonotus brunneus* (pycn.brun), *Pycnonotus cyaniventris* (pycn.cyani), *Pycnonotus erythropthalmos* (pycn.eryt), *Pycnonotus simplex* (pycn.simp), *Tricholestes criniger* (tric.crin), *Calorhamphus fuliginosus* (calo.fuli), *Megalaima rafflesii* (mega.raff), *Alcippe brunneicauda* (alci.brun).
**Plant:** *Antidesma* sp. (anti.sp), *Bellucia axinanthera* (bell.axin), *Bridelia* sp. (bridl.sp), *Callicarpa petandra* (call.peta), *Clibadium surinamense* (clib.suri), *Clidemia hirta* (clid.hirt), *Ficus* sp. (ficus.sp), *Gironiera nervosa* (giro.nerv), *Glochidion laevigata* (gloc.laev), *Gynotroches axillaris* (gyno.axil), *Leea indica* (leea.ind), *Mallotus paniculatus* (mall.pani), *Melastoma malabathricum* (mela.mala), *Memecylon pauciflorom* (meme.pauc), *Psychotria viridis* (psyc.viri), *Pternandra cordata* (pter.cord), *Salacia chinensis* (sala.chin), *Trema canabina* (trem.cana), *Vitex vestita* (vite.vest).

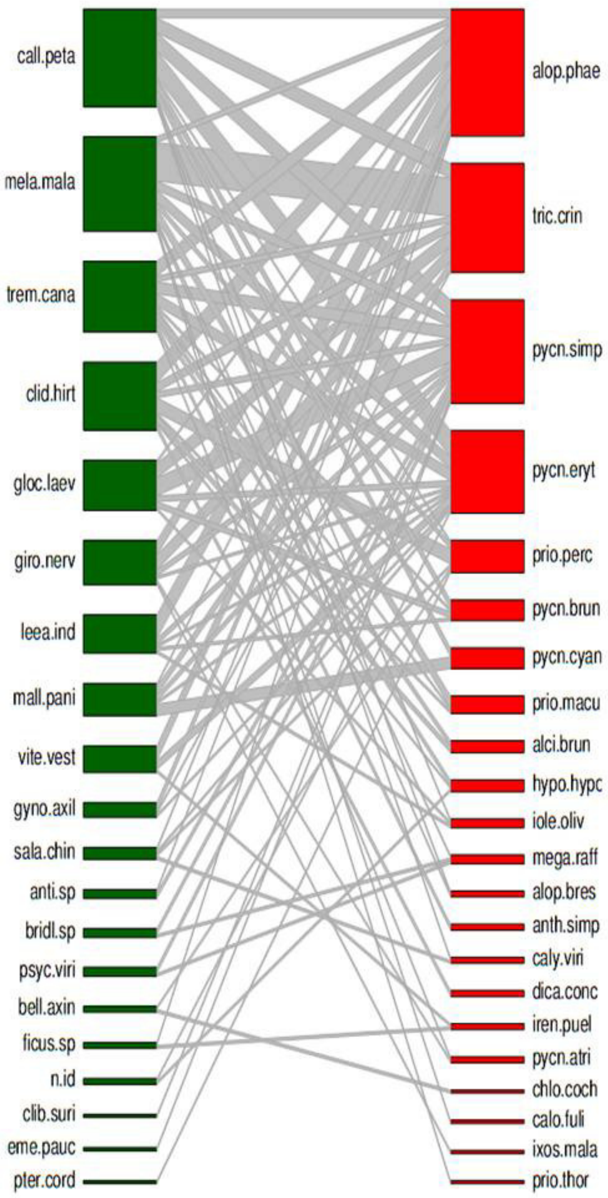


Figure 5.1. Bird-seed network showing bird species (red), seed species (green, fecal samples from the respective bird species) and the frequency of their interaction in between.

In the combined network (Figure 5.1), we found that bird density was a significant predictor for the number of interactions in the network ($R^2$=0.45, p=0.0017) and the number of seed species found per bird species ($R^2$=0.42, p=0.001122). The comparison between old and secondary forest (Appendix 5.2) revealed similarity in complexity (i.e. connectance value), link per species, $H_2$’ value, and Shannon diversity value (Table 5.3). Moreover, networks at old and young secondary forest dominated by highly generalized seed dispersers (low d' value, Figure 5.2). However, the species’ interaction strength (i.e. how important a species is in a network) revealed a slightly different pattern (Figure 5.3). In the combined network (Figure 5.3a) Cream-vented Bulbul (strength=5.35) and Yellow-bellied Bulbul (strength=4.003) had the highest strength value. In old secondary forest these two species still were the most important dispersers, with Yellow-bellied Bulbul exhibiting a strength value of 5.01 and Cream-vented Bulbul of 1.79. However, this pattern changed in young secondary forest with Cream-vented Bulbul (4.36) and Spectacled Bulbul (2.87) having the highest strength value.

From the plant side in combined networks two species had the highest strength value (Figure 5.3b): *Melastoma malabatrichum* (4.3) and *Trema canabina* (3.2). However, when examined the network at each secondary forest type, *Melastoma malabatrichum* and *Clidemia hirta* had the highest strength value in old secondary forest, 3.9 and 3.3, respectively. In the young secondary forest, *Trema canabina, Callicarpa petandra,* and *Melastoma malabatrichum* had the highest strength value, 2.9, 2.7, and 2.2, respectively.

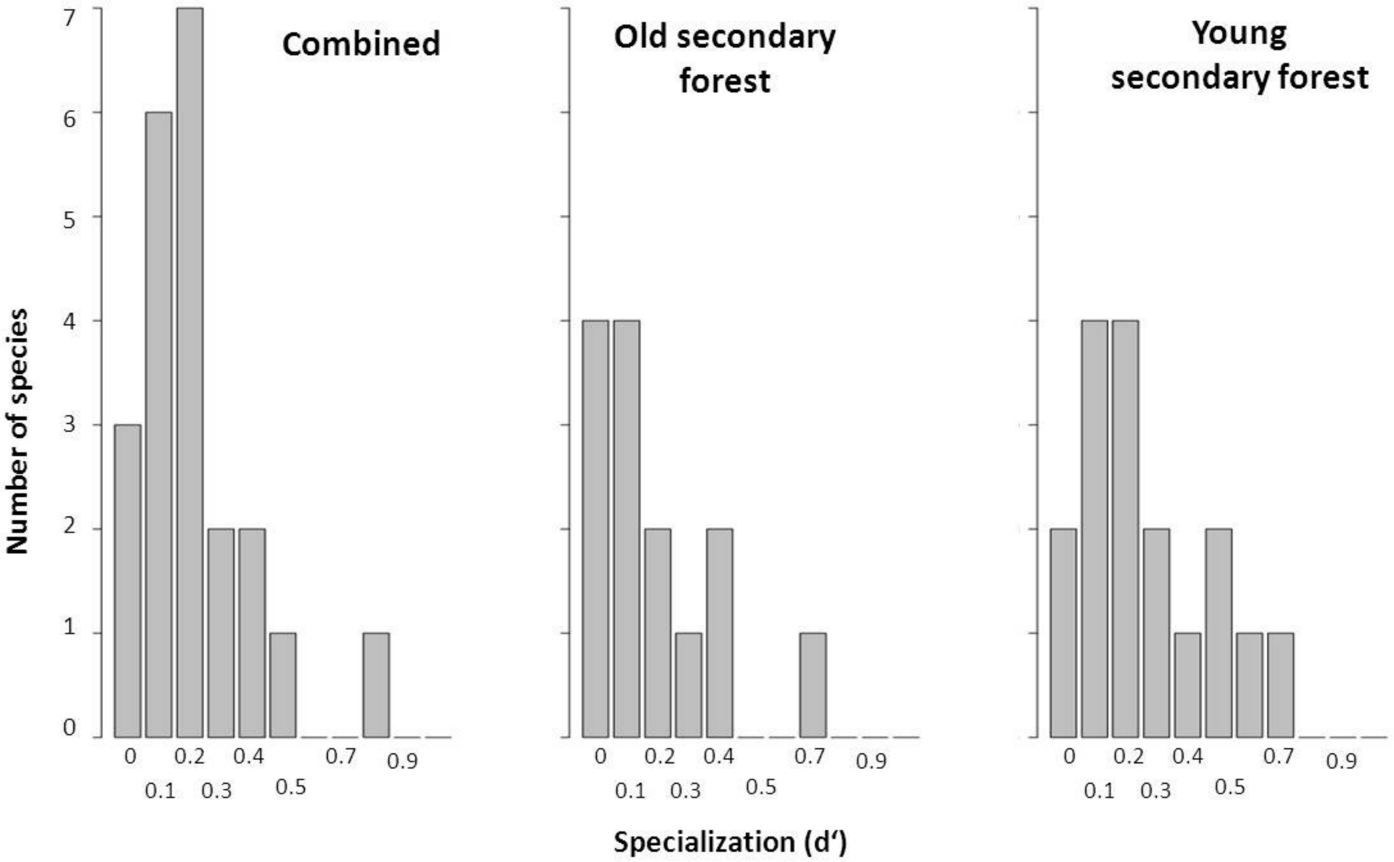


Figure 5.2. Patterns within seed dispersal networks in old secondary forest (A) and young secondary forest (B). Bars show the number of species in each category (label '0' defines 0.00 < d' < 0.05, etc.)

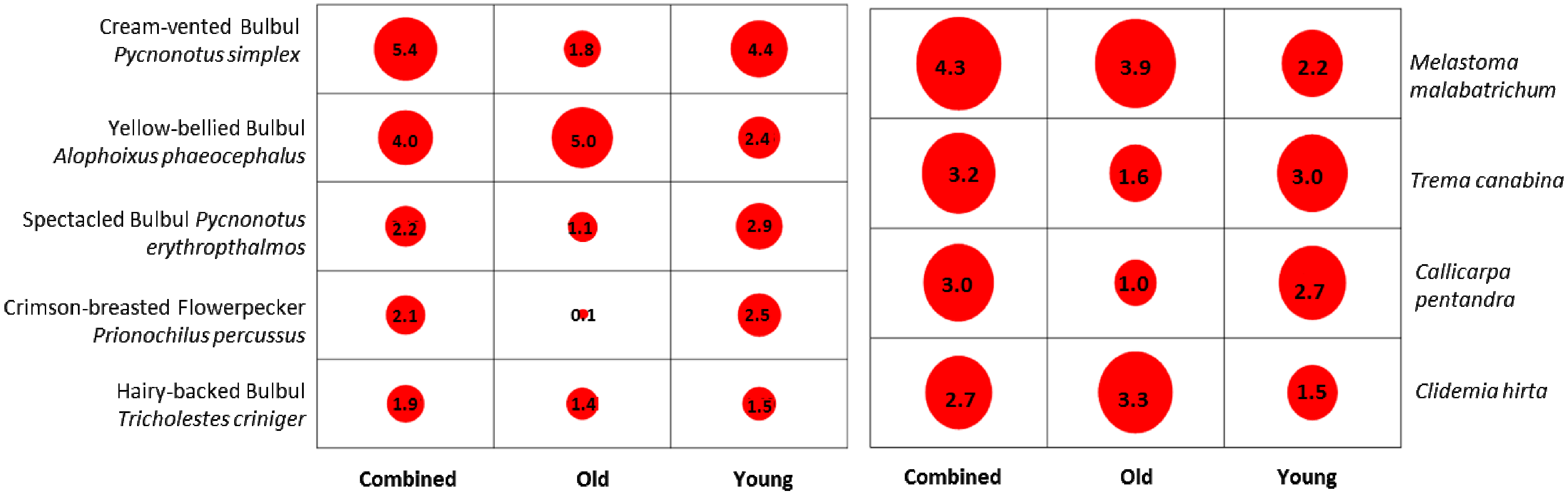


Figure 5.3. Interaction strength patterns within bird-seed dispersal networks for bird species (left) and seed species (right). Species with higher strength value at each network (i.e. combined, old and young secondary forest). Number represented the strength values.

Grouping seed species identified based on fruit characteristics showed that fleshy multi-seed fruits had higher proportion of interaction in combined network (Figure 5.4). Interactions with capsule multi-seeds fruits were only recorded in young secondary forest, hence Chi-square test to compare differences in the frequency of interaction with fruit-seed types between old and young secondary forest were only conducted for three fruit-seed types (i.e. fleshy multi-seed, fleshy single-seed, berry multi-seed. Comparing the complete contingency table revealed a significant difference in the number of interactions between old and young secondary forest ($X^2$ =13.98, p=0.0009). Removing the fruit-seed type one at the time and compare the p-value with the p-value from the complete data set shown the stronger significant importance of fleshy multi-seed type that distinguished the two secondary forest types (i.e. removal of this type resulted in non-significant difference in the frequency of interactions between old and young secondary forest, $X^2$ without fleshy multi-seed = 0.55, p=0.45). The removal of other fruit-seed types were still resulted in the significant differences between old and young secondary forest as long as fleshy multi-seed still in the data set.

Three species were categorized as weed species: *Clidemia hirta, Melastoma malabathricum,* and *Clibadium surinamense*. Examining the number of interaction for weed vs non weed-species between old and young secondary forest (Figure 5.5) showed that 31 out of 69 interactions in old secondary forest were with weed species while only 25 interaction out of 135 in young secondary forest.

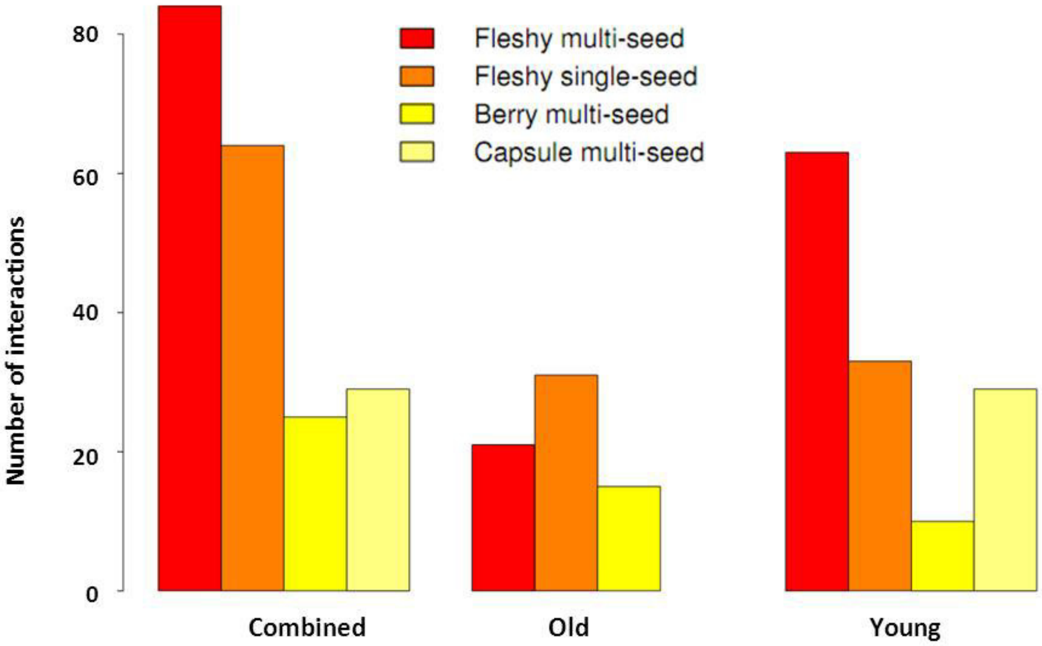


Figure 5.4. Number of interactions per fruit type.

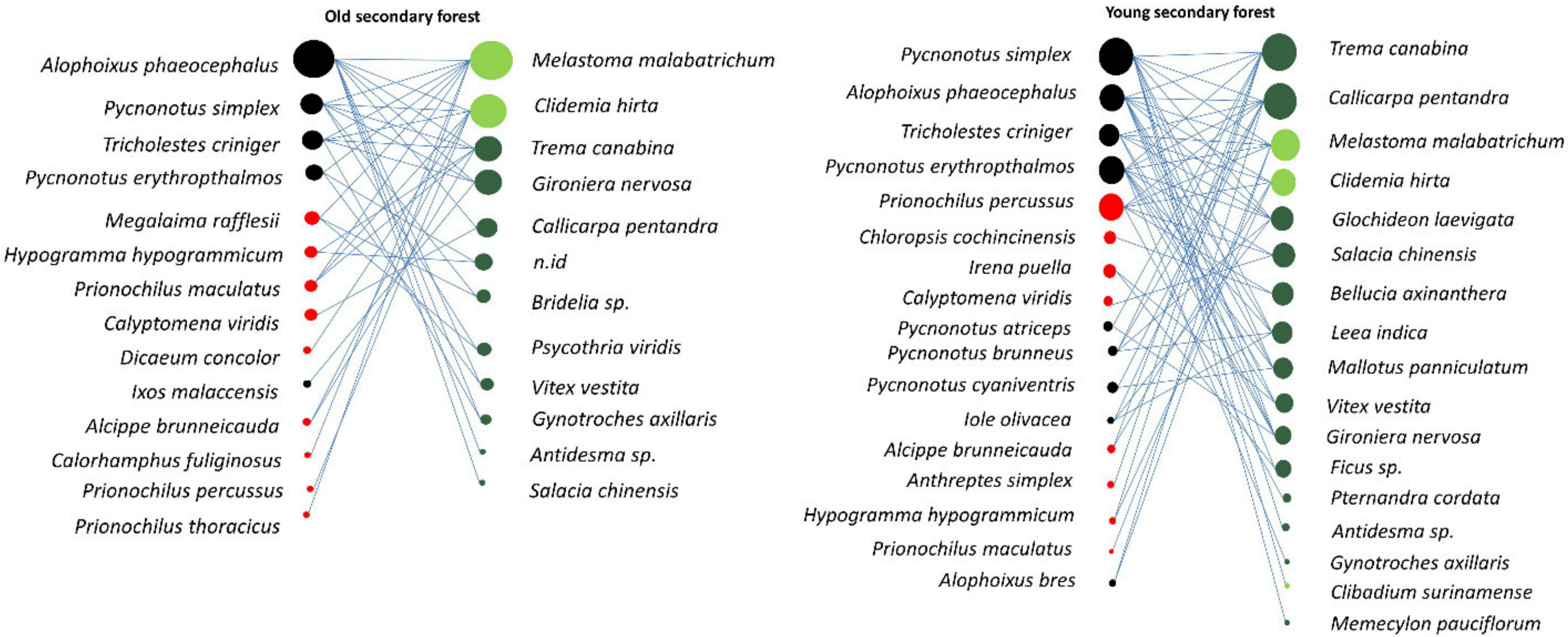


Figure 5.5. Bird-fruit interaction networks: (black) bulbul species, (red) other bird species, (light green) weed species, (dark green) non weed species. The size of the circle is proportional to the interaction strength of a species.

## DISCUSSION

In this study, we focused on a quantitative bird-seed interaction networks in the secondary lowland tropical forest of Sumatra. This is one of very few studies worldwide that investigate quantitative differences in bird-seed interaction networks between two habitat gradients. Mutualistic plant–animal interactions analyze using a network approach can provide understanding on the importance of dispersers or plant species in a particular habitat type which cannot be assessed using single pairwise interaction. We found that bird-seed interaction networks were dominated by generalist species (Figure 5.2). Despite similarity of some network level parameters (e.g. H2', connectance) between old and young secondary forest, there were strong differences at the level of species identity (i.e. the species interaction strength), which can be linked to differences in bird species density. Results of our seed dispersal network can also help in understanding management of weed invasion particularly in knowing what suites of dispersers exist, what species they are spreading (e.g. Buckley et al. 2006, Wescott and Dennis 2006, Wescott et al. 2008), and how important they are for frugivore birds (Gosper et al. 2005, Spotswood et al. 2012). Moreover, our results can also be used to decide important fruiting plant that can be planted to attract frugivores and increase seed rain in degraded forest (Corlet and Hau 2000, Martinez-Garza and Howe 2009, Cole et al. 2010, Sansevero et al. 2011).

Generally, specialization in the tropical plant-frugivore network has been shown to be low (Bluthgen et al. 2008, Schleuning et al. 2011, Schleuning et al.

2012, Menke et al. 2012). We found similar trends with specialization at network level and species level being similar between old and young secondary forest. Low specialization means that the network consists of bird species interacting with several plant species. In other words, fruiting plants are dispersed by a suite of frugivore species (Orians et al. 1996). Hence, losing any one disperser species may be of minor importance and only very heavy disturbance that simultaneously impacts multiple dispersers could have long-term consequence on plant population dynamics (Orians et al. 1996, Wilson and Traveset 2000).

Our study focused on seed dispersal by small to medium size birds up to the medium forest stratum. At this stratum level, partial frugivores (species that use other major food resources beside fruits, *sensu* Kissling et al. 2007) have been shown to have generalized fruit choice (Schleuning et al. 2011). In our networks, species with the highest strength values were birds from the Pycnonotidae (bulbuls). Various bulbul species are dominant or important frugivores and seed dispersers in the open, secondary and primary forest throughout the Oriental region (Corlett 1998, Kitamura et al. 2002, Sankamethawee 2012). Their relatively wide gape width (10-15 mm) for their size permits them to consume a wide range of fruits (Corlett 1998b, this study). These species can be considered as partial frugivores as they also consume insects (Cortlett and Hau 2000). This diet flexibility is a possible reason for some species from this group to better persist in the degraded forest (Lambert 1992, Chapter 4).

Our combined bird-seed network supports the observation that species with higher density are more likely to interact with several plant species (Bascompte and Jordano 2007, Sanitjan and Chen 2009, Vazquez et al. 2009, Sankamethawee et al. 2011). Limited information on density estimates for birds prevented us to analyze in much detail features of old versus young secondary forest. However, based on available density information, the shift in species importance between networks in old and young secondary forest was presumably related to differences in species density. For example, Yellow-bellied Bulbul *Alophoixus phaeocephalus* had highest number of interaction (22 interactions) and density (30.9 birds/km$^2$, Chapter 4) in in old secondary forest, but not in young secondary forest (21 interactions, 16.1 birds/km$^2$). On the other hand, Cream-vented Bulbul *Pycnonotus simplex* had the highest number of interactions (25 interactions) and density (75.1 birds/km$^2$) in young secondary forest but not in old secondary forest (10 interactions, 28.5 birds/km$^2$). The decrease of Yellow-bellied Bulbul density in degraded forest may have been related to the relatively higher reliance on insect prey than in other bulbul species and the fact that it mainly forages in the understory (Mead 2008). Food resource availability (Wong 1986, Hussin 1994, Burke and Nol 1998, Zanette et al. 2000) and change in microclimatic condition (Pearson 1977, Karr and Freemark 1983, Johns 1986, Hussin 1994) have been proposed as two factors that cause decline for understory birds. Population size of key dispersers has been shown to positively correlate with seed dispersal function (e.g. McConckey and Drake 2006), hence population size that maintains their ecological function should be identified and maintained for the continuation of this service (McConckey et al. 2012).

From the plant perspective, the change in the dominance of the disperser species between old and young secondary forest did not appear to have a significant influence. However, we still have limited understanding of the effectiveness of each seed disperser species. Disperser effectiveness depends, in a complex way, on the number of seeds per defecation, patterns of movement within and between habitats, preferred defecation position, and some further factors (Corlett 1998b). Whether a bird is a major seed disperser depends on whether frugivory, seed removal, seed deposition, or recruitment is the key and most sensitive process (Carlo and Yang 2011). This means that disperser with low participation in the network could be still effective disperser. Nevertheless, our study provides strong evidence for the importance of bulbul species for seed removal (they were not captured just under the canopy of fruiting trees), and to a certain extent seed deposition.

Understanding the role of each species for the dispersal of particular invasive seed plant species can be very useful in weed management (Buckley et al. 2006, Wescott and Dennis 2006, Wescott et al. 2008), particularly when weed species has been well integrated into the frugivore bird-seed interaction network (e.g. Spotswood et al. 2012, Heleno et al. 2013) hence their removal might affect the frugivore bird community (Buckley et al. 2006). *Clidemia hirta* is an invasive plant to Indonesia (Takashi and Mikami 2008), categorized as weed species (along with *Melastoma malabatricum* and *Clibadium surinamense*, Tjitrosemito et al. 1986) and has been recorded to invade undisturbed tropical forest (Peters 2001), while the invasion is related to soil disturbance by wild pigs (Fujinuma and Harrison 2012). Abundance of this invasive weed still increases even in area with less soil disturbance by wild pigs (i.e. 1 km from the forest edge), although soil disturbance, and also light availability, have been shown to be essential for the establishment of *Clidemia hirta* (Peters 2001). We found this species to have higher strength value (and to interact with eight bird species) in old than young secondary forest, indicating the importance of this plant for frugivore community in old secondary forest. Fruit consumption increases with relative abundance of plant species growing in a particular area (Lefevre 2008). The mosaic habitat conditions with high variability of canopy openings in our study area might have provided suitable conditions for this invasive weed species. The higher interaction frequency in old secondary forest might be also related to three forest specialist birds that consumed this weed, particularly the Brown Fulvetta *Alcippe brunneicauda*. The Brown Fulvetta is an arboreal foliage-gleaning insectivore (Lambert and Collar 2002) and forest specialist species (Styring et al. 2011), which tolerates secondary and logged forest (BirdLife International 2013), and has already been recorded to consume fruits (Sankamethawee et al. 2012). This species is presumably the most important disperser of *Clidemia hirta* into the less degraded forest. However, further studies are required to proof this assumption, e.g. by looking at movement rate and dispersal distance (Wescott and Dennis 2006).

In forest restoration, birds play important role in delivering seeds into degraded forest area (e.g. Corlett and Hau 2000, Lamb et al. 2005). Bird loss leads to cessation of dispersal of native seeds from intact to degraded forests, thus promoting only passive regeneration of degraded forests (Caves et al. 2013). Plant species that are found to be consumed by many bird species can be planted in heavily degraded forest to attract many bird species, which can increase plant species diversity in the degraded forest (Wunderle Jr. 1997). This is an important ecological process in the tropics, where animal seed dispersal is the dominant mode of dispersal (Howe and Smallwood 1982). Several fruit tree species that were identified in our study can be planted in a mixture of trees to attract birds to degraded forest (Vieira et al. 1994, Clark et al. 2004). Particularly important were seeds from fleshy multi-seed fruits that had high number of interaction with dispersers in the young than in old secondary forest. For example, seeds from *Leea indica* (woody or herbaceous, 1-6 m tall) had been found in fecal samples from five bird species (all from the family Pycnonotidae). This species can be found in back mangroves, secondary forests, primary forests in the lowlands and wet ridges up to 1,700 m in altitude. Lok et al. (2011) shows that by obtaining cuttings of the parent plant, production of sexually mature plants is faster than that sown by seed. Planting this species in degraded forest can possibly attract visitation of bulbuls to increase seed rain under this tree species (see also e.g. Wunderle Jr. 1997, Slocum and Horvitz 2000).

In conclusion, this study provides the first quantitative bird-seed interaction networks from secondary tropical forest in Southeast Asia, which also has been rarely explored worldwide. Despite similar networks between old and young secondary forest, we found differences in the species' importance. More studies to understand how human disturbance influences frugivory or seed dispersal are needed to clarify the important role that animal-mediated seed dispersal can play in tropical forest communities (e.g. with respect to restoring degraded sites or predicting weed invasion). More information on seasonal variation and more direct observations (which bird species visit and consume certain plant species) would help to improve restoration management. Moreover, bird species that played an important role in our study area might turn out to be actually inefficient dispersers when more details of their seed deposition behavior and seedling recruitment are known. Nevertheless, we provided here much evidence for the important role of particular birds (here the bulbul species) as seed dispersers and vice versa, the importance of small fleshy multi-seeded plant species for frugivore birds in the secondary forest.

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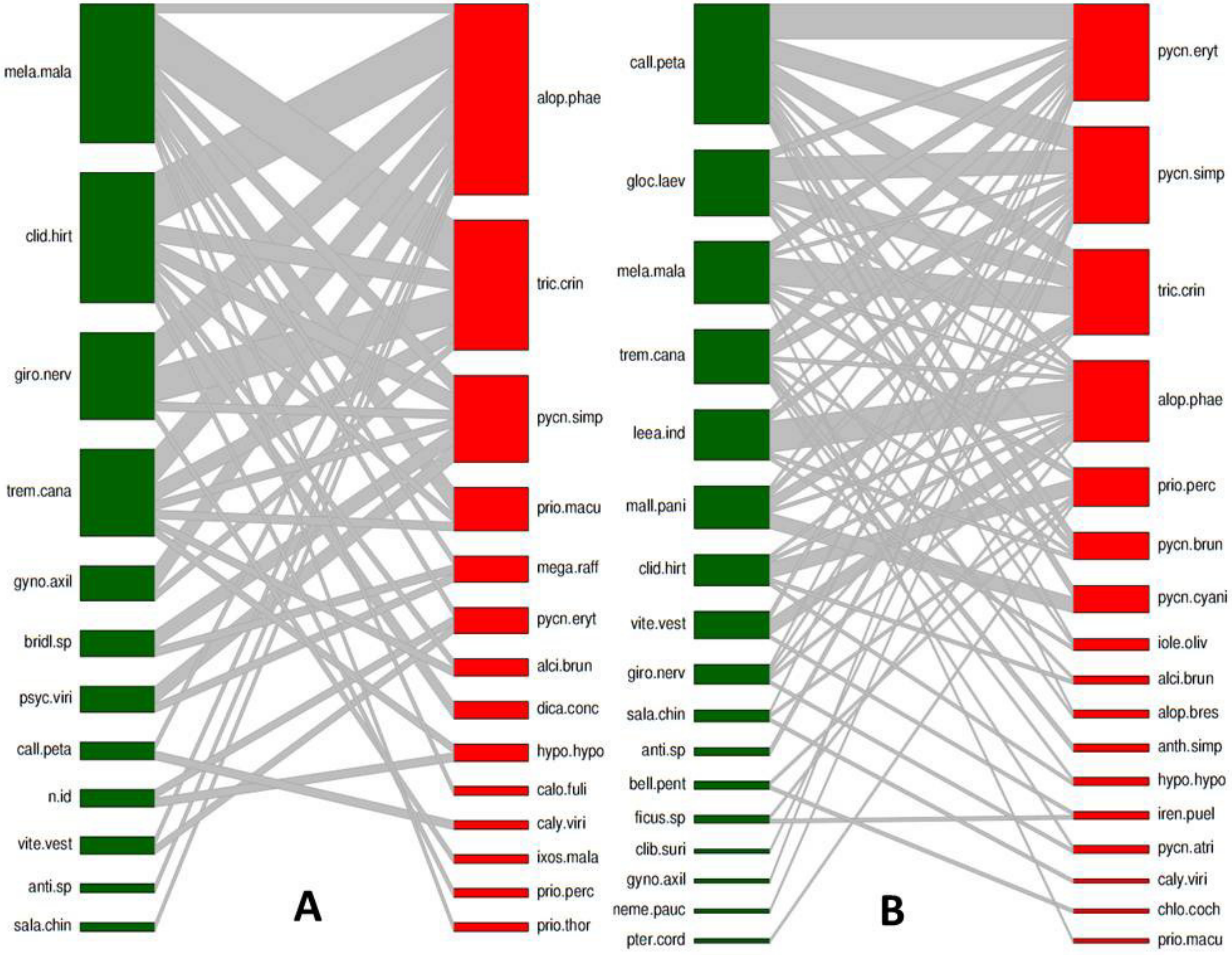
Appendix 5.1. Bird species captured and fecal samples (number in brackets) collected during the mist-net surveys.

| Family | Common name | Scientific name | Old secondary forest | Young secondary forest | Total |
|---|---|---|---|---|---|
| Aegithinidae | Green Iora | *Aegithina viridissima* |  | 1 | 1 |
| Alcedinidae | Rufous-collared Kingfisher | *Actenoides concretus* | 1 | 1 (1) | 2 |
| Alcedinidae | Blue-banded Kingfisher | *Alcedo euryzona* | 1 |  | 1 |
| Alcedinidae | Blue-eared Kingfisher | *Alcedo meninting* | 1 | 2 | 3 |
| Alcedinidae | Rufous-backed Kingfisher | *Ceyx rufidorsa* | 6 | 7 | 13 |
| Apodidae | Silver-rumped Spinetail | *Rhaphidura leucopygialis* |  | 1 | 1 |
| Chloropseidae | Blue-winged Leafbird | *Chloropsis cochinchinensis* |  | 1 (1) | 1 |
| Columbidae | Emerald Dove | *Chalcophaps indica* |  | 8 (5) | 8 |
| Dicaeidae | Plain Flowerpecker | *Dicaeum concolor* | 2 (2) |  | 2 |
| Dicaeidae | Flowerpecker | *Dicaeum sp.* |  | 1 | 1 |
| Dicaeidae | Yellow-breasted Flowerpecker | *Prionochilus maculatus* | 5 (5) | 1 (1) | 6 |
| Dicaeidae | Crimson-breasted Flowerpecker | *Prionochilus percussus* | 3 (2) | 10 (10) | 13 |
| Dicaeidae | Scarlet-breasted Flowerpecker | *Prionochilus thoracicus* | 1 (2) |  | 1 |
| Dicruridae | Greater Racket-tailed Drongo | *Dicrurus paradiseus* |  | 1 | 1 |
| Eurylaimidae | Asian Green Broadbill | *Calyptomena viridis* | 1 | 1 | 2 |
| Irenidae | Asian Fairy-bluebird | *Irena puella* |  | 1 (1) | 1 |
| Monarchidae | Black-naped Monarch | *Hypothymis azurea* | 2 | 1 | 3 |
| Muscicapidae | Large-billed Blue-flycatcher | *Cyornis caerulatus* | 1 | 1 | 2 |
| Muscicapidae | Malaysian Blue-flycatcher | *Cyornis turcosus* | 1 |  | 1 |
| Muscicapidae | White-crowned Forktail | *Enicurus leschenaultii* | 2 |  | 2 |
| Muscicapidae | Rufous-winged Philentoma | *Philentoma phyrrhopterum* | 2 | 1 | 3 |
| Muscicapidae | Grey-chested Jungle-flycatcher | *Rhinomyias umbratilis* | 11 (8) | 2 (2) | 13 |
| Muscicapidae | Rufous-tailed Shama | *Trichixos pyrrhopygus* | 2 | 1 | 3 |
| Nectariniidae | Plain Sunbird | *Anthreptes simplex* |  | 2 (2) | 2 |
| Nectariniidae | Little Spiderhunter | *Arachnothera longirostra* | 5 | 23 | 28 |
| Nectariniidae | Long-billed Spiderhunter | *Arachnothera robusta* | 1 |  | 1 |
| Nectariniidae | Purple-naped Sunbird | *Hypogramma hypogrammicum* | 3 (3) | 6 (6) | 9 |
| Picidae | Buff-necked Woodpecker | *Meiglyptes tukki* | 1 | 3 | 4 |
| Picidae | Checker-throated Woodpecker | *Picus mentalis* |  | 1 | 1 |
| Picidae | Banded Woodpecker | *Picus mineaceus* |  | 1 | 1 |
| Picidae | Rufous Piculet | *Sassia abnormis* | 2 | 10 | 12 |
| Pycnonotidae | Grey-cheeked Bulbul | *Alophoixus bres* |  | 1 (1) | 1 |
| Pycnonotidae | Yellow-bellied Bulbul | *Alophoixus phaeocephalus* | 13 (14) | 9 (8) | 22 |
| Pycnonotidae | Buff-vented Bulbul | *Iole olivacea* |  | 1 (1) | 1 |

| | | | | | |
|---|---|---|---|---|---|
| Pycnonotidae | Streaked Bulbul | *Ixos malaccensis* | 1 (1) | | 1 |
| Pycnonotidae | Black-headed Bulbul | *Pycnonotus atriceps* | | 2 (2) | 2 |
| Pycnonotidae | Red-eyed Bulbul | *Pycnonotus brunneus* | | 5 (5) | 5 |
| Pycnonotidae | Grey-bellied Bulbul | *Pycnonotus cyaniventris* | | 5 (5) | 5 |
| Pycnonotidae | Spectacled Bulbul | *Pycnonotus erythropthalmos* | 4 (2) | 17 (17) | 21 |
| Pycnonotidae | Cream-vented Bulbul | *Pycnonotus simplex* | 8 (8) | 14 (14) | 22 |
| Pycnonotidae | Hairy-backed Bulbul | *Tricholestes criniger* | 12 (12) | 13 (13) | 25 |
| Ramphastidae | Brown Barbet | *Calorhamphus fuliginosus* | 1 (1) | | 1 |
| Ramphastidae | Red-crowned Barbet | *Megalaima rafflesii* | 2 (2) | | 2 |
| Rhipiduridae | Spotted Fantail | *Rhipidura perlata* | 1 | | 1 |
| Sylviidae | Dark-necked Tailorbird | *Orthotomus atrogularis* | | 1 | 1 |
| Sylviidae | Arctic Warbler | *Phylloscopus borealis* | | 1 | 1 |
| Timaliidae | Brown Fulvetta | *Alcippe brunneicauda* | 3 (3) | 1 (1) | 4 |
| Timaliidae | Sooty-capped Babbler | *Malacopteron affine* | | 1 | 1 |
| Timaliidae | Scaly-crowned Babbler | *Malacopteron cinereum* | 9 | 3 | 12 |
| Timaliidae | Moustached Babbler | *Malacopteron magnirostre* | 2 | 3 | 5 |
| Timaliidae | Rufous-crowned Babbler | *Malacopteron magnum* | 1 | 1 | 2 |
| Timaliidae | Black-capped Babbler | *Pellorneum capistratum* | 2 | | 2 |
| Timaliidae | Chestnut-backed Scimitar-babbler | *Pomatorhinus montanus* | 1 | 1 | 2 |
| Timaliidae | Chestnut-rumped Babbler | *Stachyris maculata* | 8 | | 5 |
| Timaliidae | Grey-headed Babbler | *Stachyris poliocephala* | | 1 | 1 |
| Timaliidae | Rufous-fronted Babbler | *Stachyris rufifrons* | 1 | | 1 |
| Timaliidae | Ferruginous Babbler | *Trichastoma bicolor* | 1 | 2 | 3 |
| Timaliidae | White-chested Babbler | *Trichastoma rostratum* | 1 | 3 | 4 |

Appendix 5.2. Bird-seed network (A: old secondary forest, B: young secondary forest) showing bird species (red), seed species (green, fecal samples from the respective bird species) and the frequency of their interaction in between.



**Bird:** *Chloropsis cochinchinensis* (chlo.coch), *Dicaeum concolor* (dica.conc), *Prionochilus maculatus* (prio.macu), *Prionochilus percussus* (prio.perc), *Prionochilus thoracicus* (prio.thor), *Calyptomena viridis* (caly.viri), *Irena puella* (iren.puel), *Anthreptes simplex* (anth.simp), *Hypogramma hypogrammicum* (hypo.hypo), *Alophoixus bres* (alop.bres), *Alophoixus phaeocephalus* (alop.phae), *Iole olivacea* (iole.oliv), *Ixos malac*censis (ixos.mala), *Pycnonotus atriceps* (pycn.atri), *Pycnonotus brunneus* (pycn.brun), *Pycnonotus cyaniventris* (pycn.cyani), *Pycnonotus erythropthalmos* (pycn.eryt), *Pycnonotus simplex* (pycn.simp), *Tricholestes criniger* (tric.crin), *Calorhamphus fuliginosus* (calo.fuli), *Megalaima rafflesii* (mega.raff), *Alcippe brunneicauda* (alci.brun).

**Plant:** *Antidesma* sp. (anti.sp), *Bellucia axinanthera* (bell.axin), *Bridelia* sp. (bridl.sp), *Callicarpa petandra* (call.peta), *Clibadium surinamense* (clib.suri), *Clidemia hirta* (clid.hirt), *Ficus* sp. (ficus.sp), *Gironiera nervosa* (giro.nerv), *Glochidion laevigata* (gloc.laev), *Gynotroches axillaris* (gyno.axil), *Leea indica* (leea.ind), *Mallotus paniculatus* (mall.pani), *Melastoma malabathricum* (mela.mala), *Memecylon pauciflorom* (meme.pauc), *Psychotria viridis* (psyc.viri), *Pternandra cordata* (pter.cord), *Salacia chinensis* (sala.chin), *Trema canabina* (trem.cana), *Vitex vestita* (vite.vest).

# SUMMARY

Secondary tropical rainforest (i.e. selectively logged primary forest) has been shown to contain high biodiversity, worth to be protected from further degradation. Particularly for Indonesia, lowland rainforest remnants have not been appropriately covered in the current protected area networks, while their number is rapidly declining. As many lowland forest areas have been converted to other land-use types (e.g. oil palm plantation), lowland secondary forests are still worth to be protected. In 2004, the Government of Indonesia issued a new regulation that allowed ex-logged forest to be managed for the purpose of ecosystem restoration. Under this license, logging is not permitted within the concession area and all the activities implemented are aimed towards restoring the forest ecosystem. As the effects of forest restoration will turn out only many years after the implementation of forest restoration activities, understanding the current conservation value of the secondary forest is important. Despite relatively good knowledge on the impact of logging on biota, there is still limited understanding of how animals use different restoration and succession phases of the secondary forest and their potential ecosystem services.

In this study, we looked at bird community structure, the birds' seed dispersal, and bird densities in the secondary forest of the Harapan Rainforest Concession, Jambi-South Sumatra Province, Indonesia, between 2011 and 2012. This is the first ecosystem restoration concession in Indonesia, and covers approximately 980 $km^2$ of secondary lowland rainforest in different stages of regeneration.

The first study (Chapter 2) documents how bird species richness of different functional groups responds to habitat variation at three different spatial scales (from point-count to transect level). From this study we established an understanding that different species richness groups responded to different sets of forest characteristics, which reflected their respective ecological traits. Most of the bird species groups were affected by the understory, particularly benefitting from rattan density in the understory. The results from this study indicate how habitat variables at different spatial scales can be managed to assist the recovery of negatively impacted bird groups.

The second study (Chapter 3) presents the first density estimates for many of South-east Asia lowland forest birds. We calculated density estimates for 102 bird species which include 41 globally endangered bird species. Bird density estimates provide insight how the current densities deviate from former studies. However, there appears to be variation in density estimates across different locations, which might reflect differences in habitat condition and anthropogenic pressure. This variation highlights the importance of site specific density estimates as baseline for measuring success in forest restoration activities. Due to paucity of information, more studies are needed to provide better understanding of variation of bird density over time and space, particularly in Southeast Asia.

The third study (Chapter 4) looks at differences in density of birds between two contrasting secondary forest types, old and young secondary forest. We expected that species that declined in logged forest would also have lower density in early secondary forest (and vice versa). This pattern was indeed found for several, but not all species. The mosaic of degraded and relict forest patches in the study area, a typical feature of selectively logged forests, might provide suitable habitat for species that have been found to be negatively affected by logging. We need more long term studies to further our understanding of species persistence in the secondary forest.

The last study (Chapter 5) focuses on seed dispersal by birds through examining fecal samples. We found that seed dispersal networks in the study area were dominated by generalist dispersers. At the network level, the calculated parameters were similar between old and young secondary forest. However, at the species level species, bird species that were important in old secondary forest were not important in young secondary forest (and *vice versa*). Disperser abundance was affected by this shift. Plant-bird interaction patterns can be also used to explain how weed species can establish inside forest areas. Further studies need to be conducted to evaluate seasonal variations and to quantify bird-seed dispersal networks.

In conclusion, densities of birds and bird community structure in the secondary lowland rainforest of Sumatra were affected by forest characteristics at different spatial scales, which influenced also the birds' seed dispersal and thereby, their contribution to forest regeneration. We provide here detailed information on the forest use patterns of birds as a basis for improved restoration management practices.

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