Structure and tree diversity of lowland limestone forest on Seram Island, Indonesia

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Abstract

There have previously been very few studies of forests on Seram Island in the Eastern Indonesian archipelago and none before on lowland limestone primary forests. The COLUPSIA project on collaborative land use planning has therefore chosen Seram as one of two project sites. The objective of the COLUPSIA project is to establish collaborative and equitable land use planning. In order to achieve its objective the COLUPSIA project aims to improve understanding of traditional resource management and how it interacts with governmental systems, as well as enhancing knowledge about tropical landscapes and ecosystem services.

The aim of this study was to contribute to the COLUPSIA project through describing lowland limestone forest on Seram Island in respect to (1) forest structure, (2) tree species richness and (3) tree species composition. We set up 5 plots, each of 0.2 ha, at one site, Mawalai, and collected data on tree variables (tree diameter ≥10 cm) as well as for some other life forms and environmental data. I made comparisons both within the Mawalai site and between sites, where I compared data from the Mawalai site with two 1 ha plots that were already set up at one site each, within the same forest type.

Results varied depending on scale; tree species composition differed between some plots within one site, but much more between different sites where groupings per site were clear in NMS ordinations. Forest structure, in terms of diameter and stem density, differed between sites. A combination of the two, basal area, also varied within site. Species richness differed between one less species rich site (one 1 ha plot, 59 species) and the two other, more species rich sites (one 1 ha plot, 96 species and five 0.2 ha plots, 95 species), but did not differ significantly within the Mawalai site.

Spatial distance and the amount of surface rock cover might explain a large portion of the variation seen both in between sites and between plots within site. It is however not possible to distinguish between the two in this study since they correlate and the rock cover gradient is insufficient. As one of few studies on limestone forest in Malesia this is also an example of what tree species might occur there. The distributions of tree species found in the study, based on a small sample, varied; some species have distributions towards New Guinea and Australia, others have Western distributions and some are restricted to the near region.

Keywords: Indonesia, limestone, the Moluccas, Seram, tree diversity, tropical rain forest

Populärvetenskaplig sammanfattning

Tropisk regnskog är kanske det mest artrika ekosystemet och samtidigt ett av de minst
Tropisk regnskog är kanske det mest artrika ekosystemet på jorden och samtidigt ett av de
minst kända. Det finns många platser som sällan eller aldrig studerats och den höga artri-
kedomen försvårar för ekologiska studier eftersom många av arterna är okända. I Indonesi-
ens övärld har ekologiska studier främst gjorts på de stora öarna medan det på ön Seram, i
östra delen av landet, bara har genomförts ett fåtal studier. Seram är speciell eftersom en
stor del av ön består av kalk, något som är ovanligt, och eftersom avskogningen inte har
varit så stor där än. Tropisk skog på kalkmark är ofta mindre produktiv och har inte stude-
rats särskilt mycket. Det finns exempel på några studier av skog på kalkmark på öar i Syd-
ostasien, men ingen har tidigare gjorts av låglänt skog på kalkmark på Seram.

Ett större tvärvetenskapligt projekt (COLUPSIA) som arbetar för att främja gemensam
markanvändningsplanering använder Seram som ett av två studieområden. Ett mål med
projektet är att testa metoder som kan användas för att olika parter som berörs ska kunna
vara delaktiga i planeringen av hur mark används. För att nå projektmålen så behövs mer
information om både traditionell resurshantering och statliga styrsystem. Det behövs sam-
tidigt en ökad kunskap om marken som planeringen berör: de tropiska landskapen och de-
ras ekosystemtjänster.

Syftet med min studie var att bidra till COLUPSIA -projektet genom att beskriva låglänt
naturskog på kalkmark på ön Seram. Det gjorde jag med avseende på (1) skogens struktur,
(2) trädartsrikedom och (3) trädartssammansättning. Tillsammans med fältassistenter från
den närmsta byn mätte jag diameter och höjd på träd och samlade in löv för att träden skul-
le kunna artbestämmas. För att försöka förstå vad sammansättningen av trädarter påverkas
av så samlade jag även in information av några olika miljöfaktorer (t ex andel mark täckt
av sten, markens lutning, förekomst av vatten). Sedan jämförde jag de data som jag samlat
in med data från två andra områden som redan studerats inom ramarna för COLUPSIA -
projektet.

Det visade sig att både geografiskt avstånd och mängden ytlig sten skulle kunna förklara
en stor del av variationen i trädartsammansättning både mellan olika om-råden och inom
samma område. Artrikedomen var generellt hög men lägre i ett område (en yta 1 ha, 59
trädarter) än i de två andra områdena (en yta 1 ha, 96 trädarter och fem ytor á 0,2 ha, 95
trädarter). Det är viktigt att veta hur variationen inom en skogstyp ser ut vid markanvänd-
ningsplanering. Det kan t ex gälla utvärdering av hur mycket kol som lagras i olika delar
av skogen (t ex för REDD+). Det kan också handla om i vilka delar av skogen som det finns
flest arter, något som kan vägas in vid prioritering av områden vid naturvårdsplanering. På
grund av den dåliga kunskapen är också den grundläggande beskrivningen av trädartsam-
mansättningen av intresse.

Nyckelord: biodiversitet, Indonesien, kalkmark, Moluckerna, Seram, tropisk regnskog, träd

Contents

1 Introduction

Around the world our environment is being degraded, and in tropical areas deforestation is still high. Along with disappearing tropical forests, the ecological services that they provide are also lost or deteriorated. The last decades forest cover in Indonesia has decreased drastically (see e.g., Laumonier et al., 2010, UNEP/GRID-Arendal, 2007), with forests being converted to other types of land use in many parts of the country. From 2000 to 2005 Indonesia contributed to an estimated 12.8% of the world's clearings of humid tropical forest, making it the second largest contributor after Brazil (Hansen et al., 2008). This habitat loss affects biodiversity in an area where species richness and endemism are among the highest in the world per unit area (Sodhi and Brook, 2006). The Wallacea region[1] in the Eastern part of the Indonesian archipelago has been pointed out as one of 25 biodiversity hotspots worldwide (Myers et al., 2000). At the same time natural resource management is difficult to implement in Indonesia due to both insufficient ecological and social data and inadequate systems of governance. The lack of stakeholder involvement in land use planning and natural resource policy making further enhances the difficulties; the realities of people affected by the policies and plans are not recognized.

Against this background the Collaborative Land Use Planning for Sustainable Institutional Arrangements (COLUPSIA) project was initiated. The COLUPSIA project is funded by the European Union, CIRAD (Centre de coopération internationale en recherche agronomique pour le développement), CIFOR (Center for International Forestry Research) and TELAPAK (environmental nongovernmental organization). The project is working at provincial and district level for two different sites in Indonesia: the Kapuas Hulu regency in West Kalimantan and the Maluku Tengah regency on Seram Island in the Moluccas in Eastern Indonesia. The

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[1] The term Wallaceae is commonly used when referring to the islands of Sulawesi, the Lesser Sunda Islands, the Moluccas and East Timor.

purpose is to establish "collaborative and equitable LUP [Land Use Planning] leading to the design and testing of new institutional arrangements, environmental policies and pro-poor financing instruments based on more secure land tenure and community rights" (Laumonier, 2010). In order for the project purpose to be achieved it is important to reach a better understanding of traditional systems for resource management as well as government systems and what priorities and perceptions communities have concerning resource management. Equally important is for the project to develop scientific knowledge of poorly known tropical landscapes, forests and the services that they can bring to societies.

To monitor the environment, ecological mapping of the vegetation has for long been recognized as one of the most useful scientific tools available (Küchler and Zonneveld, 1988). Along with other types of spatial information vegetation maps can also be part of a broader management scheme to identify the importance of different ecosystem services in a landscape context (Yapp et al., 2010). The CO-LUPSIA project aims to use vegetation maps and associated ecological data as a basis for land use planning and natural resource management. The project is completing a vegetation map of Seram (Figure 2), for which it needs comprehensive information on every vegetation type.

On Seram Island limestone formations are covering a large area and they stretch from sea level to 3000 m elevation, a rather unique situation in the tropics. In comparison with other rain forest types, forests on limestone have received little attention. Together with deforestation such as logging and fires, quarrying and mining are major threats to limestone flora and fauna (Kiew, 1991, Clements et al., 2006). The lack of knowledge about tropical limestone ecosystems impedes conservation efforts and while habitats are lost so are our prospects to learn from them.

Since there are very limited studies on limestone vegetation in Indonesia (Laumonier, 1997) and only one previous survey of limestone vegetation on Seram Island, for mountain forest (Edwards et al., 1990, 1993), the COLUPSIA project aims to study limestone vegetation in detail. My study is part of this more comprehensive limestone vegetation survey.

1.1 Aim

The overall aim of this study was to contribute to the ecological and biological baseline data for Seram Island in the Moluccas, Indonesia that the COLUPSIA project will establish. More specifically the aim was to describe the forest struc-

ture, tree species richness and tree species composition of lowland primary forest on limestone in the buffer zone between a national park and a nearby rural area with settlements. Three research questions were posed and investigated:

Are there any differences in

- forest structure
- tree species richness
- tree species composition

within and among sites of lowland primary forests on limestone?

2 Material and methods

2.1 Study area

The study area is on the Seram Island in Maluku, Eastern Indonesia. As the second largest island in Maluku Seram covers an area of 17 429 km^2 (Monk et al., 1997). Seram is part of a continental fragment originating from the Australian plate, it emerged about 3 to 5 Ma and has been isolated from larger land masses since then (Audley-Charles, 1987, 1993). The island is mountainous, with its highest peak just over 3000 m, but it is non-volcanic. Seram has a geological composition of mostly raised sedimentary and metamorphic rocks; a considerable part of it being limestone (Audley-Charles et al., 1979, Edwards et al., 1993). At the center of the island, stretching out towards the coasts, is the Manusela National Park of 189,000 ha (Monk et al., 1997).
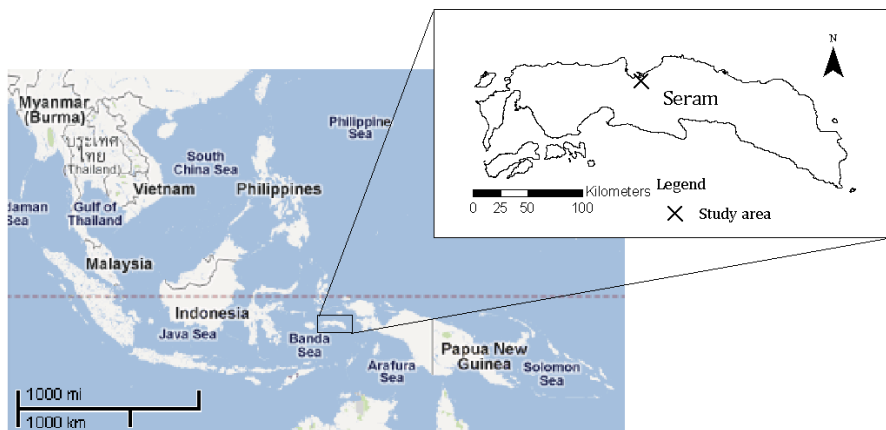

Figure 1. Seram Island with studied area marked. Map of Southeast Asia from Google Maps (Europa Technologies et al., 2011).

As part of the Wallacea region, the fauna of Seram shows mixed origins; both from New Guinea-Australia and Asia (George, 1987). Different groups of animals show different distributional patterns. The division between Asian and Australasian flora is similarly complex; some groups of plants have their distribution center on the Sahul continental shelf (Australia and New Guinea) and others on the Sunda continental shelf (Western Indonesia, Malaysia and northward), but ranges overlap (Whitmore, 1984). There are also taxa that can be found throughout the Malesian region and some that have a bicentric distribution and can be found both to the West and to the East, but not in central Sulawesi or much of Maluku in the central part of the region (Dransfield, 1987).

The climate on Seram is tropical ever wet. Fontanel and Chantefort (1978) describes all of Seram below 1000 m elevation as having hot bioclimates (mean temperature of the coldest month $> 20^0$C). Yearly precipitation (P, mean annual rainfall) on the island varies from 2000 mm to over 3000 mm, with some limited areas receiving less rain. The north coast is slightly less humid when compared to the south coast, but no area of the island is described as having any dry month (dry month, $p < 2T$ where T, mean temperature in ^{0}C and p, precipitation in mm) (Fontanel and Chantefort, 1978), though Schmidt and Ferguson (1951) considered there to be one or a few dry months (dry month $p < 60$ mm, data from the 1920's and 1930's), except for in the very wet south-central part.

The study area was located in lowland primary limestone forest in between the Masihulan village and the Manusela National Park on the Northern side of Seram Island, in the Central Seram Regency. Masihulan is a village of about 460 people that moved there about 10 years ago from its former location nearer the sea (Karlsson, 2011), but there have been gardens in the area for longer. The land that surrounds Masihulan has a variety of vegetation types due to different land use and geology (Figure 2). To the west the Masihulan area borders to the Manusela National Park, while to the north the area in between Masihulan and nearby Sawai village consist mostly of mixed gardens. There is also primary forest as well as secondary and logged-over forest nearby (Figure 2). In the study area there is some limited extraction of valuable timber trees.
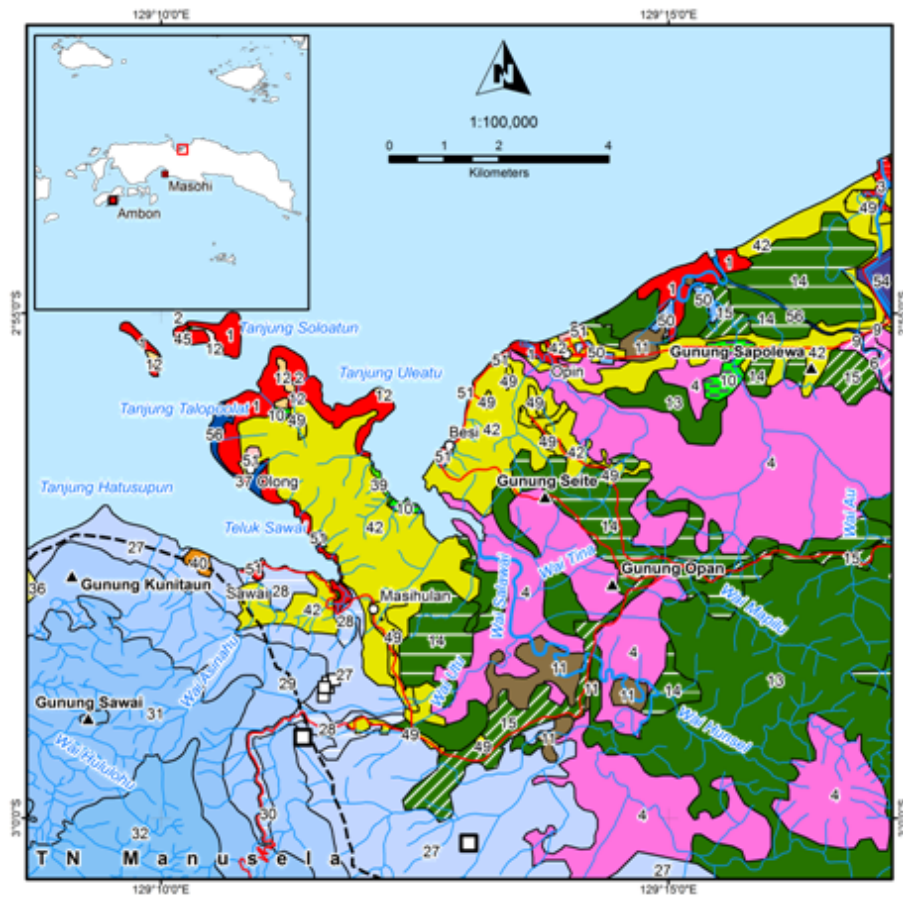
2.2   Study plots

The COLUPSIA project aims to examine 4 ha of forest for each of six elevation classes (0-300 m, 300-800 m, 800-1300 m, 1300-1800 m, 1800-2300 m, 2300-

2800 m), and had already established one 1 ha plot at each of four elevations (100 m, 300 m, 500 m, 800 m) in primary forest on limestone before my study. This study in the Mawalai area was done in order to add another 1 hectare to the study of lowland (< 300 masl = meter above sea level) limestone primary forest and to further examine variability within this forest type. To encompass more spatial variation we divided the one hectare sample area at the Mawalai site into 5 plots of 0.2 ha each, spread out over an area of about 10 ha. The already existing plots for lowland primary forest over limestone are 1 ha at Wai Onye (100 masl) to the Southeast and 1 ha at Lok Wae Utu (300 masl), on the border of the Manusela National Park (Figure 2). The three sites are 0.5 to 2.5 km apart.

Selection of the 5 plots was made based on stratified sampling with the following criteria: 1) < 300 masl, 2) limestone, 3) primary forest, 4) general slope < 15^0, 5) no big permanent water courses (> 2 m width), 6) no large disturbed areas. Laumonier and coworkers in the COLUPSIA project chose the general area where sampling took place using satellite images, topographical and geological maps (criteria 1-3). Within that general area, at Mawalai, we considered criteria 4, 5 and 6 in the field. Three plots were sized 100 m × 20 m and placed in a gentle slope with the long side following the elevation contour line. Two plots were sized 50 m × 40 m, since it was not possible to fit a wider design without passing gullies, rivers, steep ground or large naturally disturbed areas. We laid out four plots in a slope with about 50 m (45 m the closest) in between them: plot 1 highest up and plot 3, 4 and 5 downhill from it in that order. Plot 2 was laid out about 50 m downhill from plot 1, but to the South since it was difficult to fit all plots along the same slope with the above criteria. The direction of each plot and its position along the elevation contour line was then adjusted for depending on the local topography. The elevations of the plots are between 200 and 300 masl (Table 2). We divided the plots into subplots of 10 m × 10 m (Figure 3) using ropes, and recorded some general plot data (Table 1).

Table 1. List of the recorded elements with a short description of the method used and where it was done. Existing data refer to data collected by others in the COLUPSIA project on the Lok Wae Utu and Wai Onye sites.

Recorded elements	Method	Where
Alluvial code	Visual: 0-no water, 1-occasional small stream (< 2 m wide), 2-permanent small stream (< 2 m wide), 3-occasional standing water	Mawalai: each subplot Lok Wae Utu: 50 of 100 subplots Wai Onye: 50 of 100 subplots
Aspect	Compass direction of slope	Mawalai: each subplot Lok Wae Utu: 50 of 100 subplots Wai Onye: 50 of 100 subplots
Surface rock cover	Estimating in % of subplot surface	Mawalai: each subplot Lok Wae Utu: 50 of 100 subplots Wai Onye: 50 of 100 subplots
Other life forms than trees	Counts	Mawalai: half of every other subplot
Slope	Clinometer, steepest direction of subplot, in degrees	Mawalai: each subplot Lok Wae Utu: 50 of 100 subplots Wai Onye: 50 of 100 subplots
Soil depth	Auger, in centimeter	Mawalai: twice in every other subplot, once in each half
Tree diameter	Diameter at reference height (drh), in centimeter to nearest 1 cm estimated with a measuring tape	Mawalai: all trees ($\geq$ 10 cm) within plots
Tree crown projection	Measure crown radius in four directions, in meter to nearest 0.5 m	Mawalai: all trees ($\geq$ 10 cm) within plots
Tree height	Haga altimeter, in meter to nearest 1 m	Mawalai: all trees ($\geq$ 10 cm) within plots
Tree height 1st bransch	Haga altimeter, in meter to nearest 1 m	Mawalai: all trees ($\geq$ 10 cm) within plots
Tree position	Estimating using subplot grid (x,y) from plot corner, in meter to nearest 1 m	Mawalai: all trees ($\geq$ 10 cm) within plots Wai Onye: existing data, all trees ($\geq$ 10 cm) within plots Lok Wae Utu: existing data, all trees ($\geq$ 10 cm) within plots
Tree species name	Collected species samples for identification at Bogor herbarium	Mawalai: all trees ($\geq$ 10 cm) within plots Wai Onye: existing data, all trees ($\geq$ 10 cm) within plots Lok Wae Utu: existing data, all trees ($\geq$ 10 cm) within plots

Legend

Plot size
- ☐ 0.2 ha plot
- ◻ 1 ha plot
- ● Village
- ○ Hamlet
- ▲ Mountain
- ── Main Road
- ── River
- ⬚ Manusela National Park

Vegetation class
- 1, Mangrove
- 2, Logged-over or depleted mangrove
- 3, Back mangrove and nipa swamp
- 4, Fresh water swamp forest
- 6, Overlogged forest or very depleted fresh water swamp forest
- 9, Swamp grassland or fernland
- 10, Secondary regrowth swamp forest (Belukar rawa)
- 11, Sago swamp
- 12, Coastal (beach) forest
- 13, Lowland forest (< 300 m)
- 14, Logged over lowland forest_ depleted
- 15, Overlogged lowland forest_ very depleted
- 27, Lowland Limestone forest formation (< 300 m)
- 28, Logged over lowland limestone forest formation_depleted
- 29, Hill Limestone forest formation (300 - 800 m)
- 30, Logged over hill limestone forest formation_depleted
- 31, Submontane Limestone forest formation (800 - 1300 m)
- 32, Lower montane Limestone forest formation (1300 - 1800 m)
- 36, Grassland (Natural)
- 37, Grassland
- 39, Secondary regrowth forest (Belukar tua)
- 40, Savanna
- 42, Mixed Garden
- 45, Coconut plantation
- 49, Food crop field (including ladang)
- 50, Irrigated paddy field
- 51, Settlement
- 54, Shrimp pond
- 56, Water body

Figure 2. Draft ecological vegetation map of study area, Central Seram, Indonesia (Setiabudi and Laumonier). The white squares represent plots where data for this study was collected. Three sites: 5 0.2 ha plots at Mawalai, 1 ha plot on the boarder of the Manusela National Park at Lok Wae Utu and 1 ha plot further Southeast at Wai Onye.

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Table 2.   General information about Mawalai 0.2 ha plots.

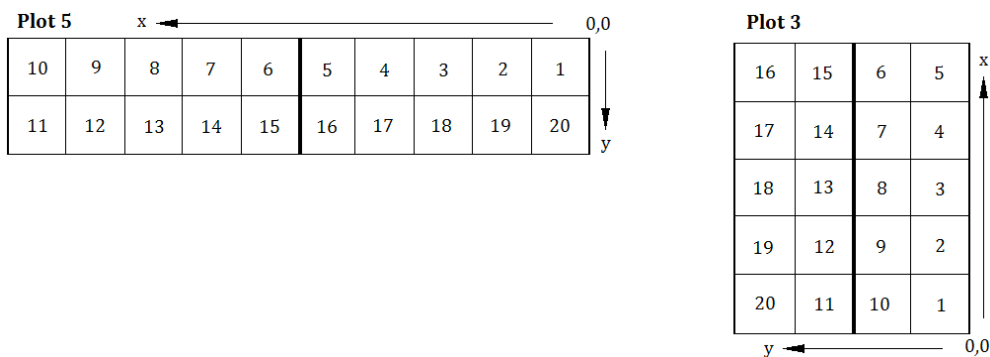| Plot number	1	2	3	4	5
Design (m × m)	100 × 20	50 × 40	50 × 40	100 × 20	100 × 20
Drainage	Well drained	Mostly well drained	Well drained	Well drained	Well drained
Elevation (masl)	260	210	250	240	230
Geology	Limestone	Limestone	Limestone	Limestone	Limestone
GPS co-ordinates (X(0), Y(0))	S 02^{0}58.704' E 129^{0}11.607'	S 02^{0}58.792' E 129^{0}11.600'	S 02^{0}58.706' E 129^{0}11.643'	S 02^{0}58.654' E 129^{0}11.644'	S 02^{0}58.629' E 129^{0}11.705'
Location in the terrain	Midslope	Midslope on small ridge	Midslope on small ridge	Midslope	Midslope
Orientation of centerline	220^0	340^0	230^0	140^0	185^0
Slope (aspect)	10^0 (SE)	8^0 (SSE)	4^0 (NE)	12^0 (N)	8^0 (E)

Figure 3. Examples of plot division into subplots for the two different plot designs: plot 5 (100 m × 20 m) and plot 3 (50 m × 40 m). The thick line indicates the centerline of the plot and plots are orientated with the upper part uphill. The outer corner of subplot 1 is the point X(0), Y(0) of the plot.

2.3 Sampling methods

2.3.1 Forest structure

Trees

All live trees in each Mawalai plot, with a diameter at reference height (drh) ≥ 10 cm and that had some part of the stem within the plot, were tagged and described regarding: diameter, height, height of first branch, tree crown projection, position in relation to a zero point at one corner of the plot, and subplot identity.

We measured diameter at 1.3 m height or if the buttress was taller or if low stem-parts had abnormities, 30 cm above that. For a few trees too large to climb to measure diameter, the diameter was estimated using already measured trees as reference. Total tree height and height of first branch measurements were made using a Haga altimeter. This was done in two measurements; at the first measurement, $\alpha 1$, height from eye-level to the top of the tree was measured and at the second measurement, $\alpha 2$, height from eye-level to the base of the tree. The two measurements were then added to give the height of the tree or similarly to give the height of the first branch for those measurements (αHb). Where needed, for an accurate distance to the tree, slope was adjusted for in field.

Tree crown projection was based on the radius of the crown in four directions from the center of the tree base to the outer limit of the crown (Figure 3). The area of the crown projection was then calculated using the general equation for the area of an ellipse, $A = \frac{1}{4}\pi(a_1 + b_1)(a_2 + b_2)$, where a_1, b_1, a_2 and b_2 are the four radii (a_1+b_1 and a_2+b_2 the two diameters) measured. If the crown was not situated above the base of the tree (i.e. leaning), the two directions that best fitted the direction of the leaning stem were measured from the center of the base of the tree (one recorded as minus) and the other two were measured half way in between them. Radii were measured in the directions of the centerline of the plot and perpendicular to it. If a tree outside the plot had a crown that extended into the plot then this crown was not measured, but if a tree inside the plot boundary had a crown that extended outside the plot then this part of the crown was included in the crown projection.
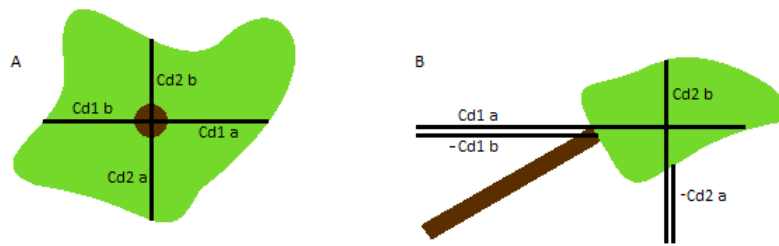
Figure 4. Crown projection measurements of trees seen from above. The four different denominations are for each measured radius, where Cd = Crown diameter and 1 or 2 the two diameters. Radius Cd2 b was measured uphill in relation to the general slope of the plot. Measurements were made along the directions of the subplot boundaries.

Other life forms

We collected data for vegetation other than trees with drh ≥ 10 cm from every other subplot (Table 2). These subplots were divided into halves by a rope stretched between two opposite corners and we collected data from the lower half (Figure 4). The number of each of the following life forms was recorded for every surveyed sub-plot: pole trees, saplings, shrubs, palms, pandans, ferns, rattans, woody climbers, vascular epiphytes and dead standing trees (Table 3).

Table 3. Forest structure components recorded in subplots and criteria for their inclusion. H = height, Φ = diameter, m = meter, m (m/plant) = total length of rattan, adding the lengths of each individual

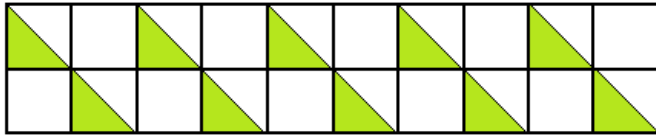| Life form	Criteria
Pole trees	h > 4 m, Φ < 10 cm
Saplings	0.5 m < h < 4 m
Shrub	h > 1.5 m
Palm	h > 4 m
Palm	h < 4 m
Pandan	h > 4 m
Pandan	h < 4 m
Fern	h < 1.5 m
Rattan	m (m/plant)
Woody climber	Φ > 5 cm
Woody climber	Φ < 5 cm
Vascular epiphyte	Visible from the ground
Dead standing trees	Φ > 10 cm (Φ < 10 cm)

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Figure 5. An example of the division of subplots into halfs at the Mawalai site. The shaded area indicates where data were collected on life forms other than trees with dbh >10 cm. Two measurements of soil depth were made: one in the shaded half and another in the corresponding white half.

2.3.2 Physical aspects

For every other subplot at the Mawalai site plots, we measured soil depth once in each half of the subplot at a representative point, using an auger. If soil was deeper than one meter, depth was recorded as > 100 cm. I estimated the amount of visible rock cover (i.e. rocky area not covered by soil or trees) for every subplot at the Mawalai site and for half of the subplots (50 out of 100) at the Wai Onye and Lok Wai Utu sites. When surface rock was < 25% it was estimated to the nearest 1%, when surface rock was ≥ 25% it was estimated to the nearest 5%.

The slope of each subplot at the Mawalai site and half of the subplots at the Wai Onye and Lok Wai Utu sites was measured using a clinometer and its aspect was recorded. For the same subplots occurrence of streams was recorded in the following categories: no stream (0), occasional stream (1), permanent small stream, < 2 m wide (2), and occasional still water (4). Presence of a permanent path through the subplots was recorded, if yes (1) and if no (0).

2.3.3 Tree species collection and identification

The species of trees were recorded for trees, within plots, with a diameter > 10 cm. If known, local names of trees were recorded with the help of field assistants from the area. Herbarium samples (leaves and fruits/flowers if present) were collected, and voucher specimens were sent to the herbarium in Bogor for identification. Vouchers are kept at the CIFOR office in Bogor.

2.3.4 Existing data for comparison

Mawalai data were compared with data from the two 1 ha plots that the COLUPSIA project had already establish in lowland primary forest on limestone: Lok Wae Utu and Wai Onye. Existing data for the Lok Wae Utu plot include crown projection, tree diameter, tree position and scientific names of tree species for trees ≥ 10 cm. Way Onye plot data include tree diameter, tree position and scientific names of tree species for trees ≥ 10 cm.

2.4 Data analysis

I have compared forest structure variables, species richness and species composition within the Mawalai site and between three sites: Lok Wae Utu, Mawalai and Wai Onye.

2.4.1 Forest structure

Variables of forest structure were analyzed using Minitab 16 Statistical Software (Minitab Inc., 2009) for basic statistics, such as means and standard errors of means, as well as graphical representation of data. Most of the variables, including diameter, height, height of first branch and tree density, were found to have non-normal distributions. Due also to difficulties in satisfactory transforming some of the data sets to normal distribution, I used non-parametric tests instead. The non-parametric Mood's Median test, using Minitab 16, was chosen since it is considered "robust against outliers" (Minitab Inc., 2009). Tree distribution maps were made in ArcMap 10 using collected spatial data and calculated basal area (BA). Basal area, the area covered by tree stems, was calculated based on recorded diameters for every tree: $BA = (Diameter\ /\ 2)^2 \times \pi$. Relative dominance was calculated as (Species total BA) / (Total BA) (see e.g., Mueller-Dombois and Ellenberg, 2002).

2.4.2 Species richness

Species richness as well as species densities of plots and sites were compared using sample based rarefaction curves. Species richness can then be compared for different numbers of individuals and species density can be compared at the same area sampled (Gotelli and Colwell, 2001), i.e. here at total number of individuals for each plot or site where sampled area is the same. Rarefaction was performed in EstimateS 8.2.0 (Colwell, 2009) and graphical representation of the results was made in Minitab 16 (Minitab Inc., 2009). The rarefaction was based on sample data as advised by Gotelli and Colwell (2001) to account for some patchiness in species distribution. Sample units used were 10 m × 10 m subplots. For the rarefaction graphs I chose the numbers of individuals for the x-axis to make both comparisons of species richness and species density possible. When confidence intervals are not overlapping, species richness is significantly different between samples (Colwell et al., 2004).

2.4.3 Species composition

In order to visualize the relationships between tree species composition of sample units grouped by site or plot, I used Nonmetric Multidimensional Scaling (NMS) in the PC-ORD 5 package (McCune and Mefford, 1999). NMS has been recommended for ecological community data (McCune and Grace, 2002). The sample units in the ordinations were either 0.04 ha subplots or 0.2 ha plots. For the NMS default settings were used with autopilot mode and "slow and thorough" for speed and thoroughness. Distance measure was Sorensen (Bray-Curtis) and starting configurations were random. When running NMS in PC-ORD the program recommends a number of dimensions for a best solution. The recommendation is based on the highest number of dimensions where the last added dimension has decreased final stress by at least 5 units (McCune and Grace, 2002). Stress is a measure of dissimilarity between the results in n-dimensions and results in a reduced number of dimensions. For two of the ordinations 3 dimensions were recommended and for one ordination a 2-dimensional solution was considered sufficient.

Species data sets were first reduced by removing all species that were only present in one of the analyzed samples (plot or subplot). For species data of all three sites, two different data sets were analyzed: 15 0.2 ha plots and 75 0.04 ha subplots, respectively. A separate ordination was made for only species data from the Mawalai site with 25 0.04 ha subplots. The following steps were taken before NMS was performed on species data:

1. For each species the number of 10 m × 10 m subplots where the species was present within a 0.2 ha / 0.04 ha plot was added. This frequency was divided by the total number of 10 m × 10 m subplots within a 0.2 ha plot (i.e. 20) or a 0.04 ha subplot (i.e. 4).
2. The PC-ORD arcsine square root transformation was performed on the data set, as recommended for proportion data (Sokal and Rohlf, 1995).
3. A matrix of environmental data was entered as crude data of counts, averages and codes for the plots or subplots corresponding to the species matrix.

The resulting graphs are joint plots with environmental variables larger than chosen cutoff values for r^2 as arrows in species space. R^2 is amount of correlation between the environmental variables and a combination of all axes in the graphical solution. The arrow is the hypotenuse of correlation between the environmental variable and the axes (McCune and Mefford, 1999).

To make comparisons of plots' species composition within the Mawalai site and among the three sites, the Multi-response Permutation Procedures (MRPP) was used since it does not require assumptions of data distributions (McCune and Grace, 2002). MRPP was performed on the same data set as described above for 0.04 ha subplots with groupings for plots (Mawalai, within site comparison) or site (between sites com parison). Default settings were used so that distance measured used was Sorensen (Bray-Curtis) with weighting of groups set to the recommended n / sum(n). Pairwise comparisons were made and distance matrix was rank transformed. T is a measure of difference between groups. A, the agreement within groups, is regarded as fairly high in community ecology if $A > 0.3$ (McCune and Grace, 2002).

In order to see if there were species that were frequent and abundant but more so in one particular site, I used the Indicator Species Analysis (ISA) (Dufrene and Legendre, 1997) in PC-ORD 5 (McCune and Mefford, 1999). The Indicator Value (IV) is a combination of species abundance and species frequency where a high value indicates a frequent and abundant species that also has a high exclusiveness, i.e. it occurs mostly in just one group. The same species data set as for the NMS analysis was used where all species that only occurred once in a 0.04 ha subplot were excluded. Statistical significance was tested using ISA's randomization test with default settings with 4999 number of runs.

3 Results

The results are divided into three parts, one for each question posed. All parts are further divided in two sections. In the first section a within site comparison is made between 5 plots of 0.2 ha spread out in an area of about 10 ha. In the second section three sites within the same forest type, 0.5 to 2.5 km apart, are compared.

3.1 Forest structure

Differences in forest structure depended on spatial scale. There were no significant differences for tree variables between plots within the Mawalai site, but considerable differences in diameter size and density between sites.

3.1.1 Mawalai – within site comparisons

The only measured forest structure variable that differed more between some plots at the Mawalai site was the amount of rattan. Large differences can also be seen in total basal area.

Trees

The tree variables for Mawalai are summarized in Table 4. Using the Mood's Median test for differences in between sample medians, no significant differences ($p < 0.05$) were found for the Mawalai 0.02 ha plots in regard to diameter, tree height, height of first branch or tree density.

For each of the five 0.2 ha plots, and for all together, the distribution of diameter follows an L-shape (Figure 6). Plot 1 has more trees with diameter 20 cm to 30 cm and plot 4 has a more spread out distribution with some very thick stems. Both plot 2 and plot 5 have gaps since they lack trees with a diameter of 60-80 cm.

Table 4. Forest structure for five (1-5) 0.2 ha plots at Mawalai, Central Seram, Indonesia. 'All' is for all the five plots together.

Forest structure	1	2	3	4	5	All
Total number of trees	91	92	93	74	88	438
Total number of species	38	42	43	28	40	95
Mean tree density (no. trees 0.01 ha^{-1})	4.6±0.3	4.7±0.5	4.7±0.5	3.7±0.3	4.4±0.4	4.4±0.2
Tree density (no. trees ha^{-1})	455	460	465	370	440	438
Mean height (m)	21.7±0.9	21.7±0.9	23.7±1.2	24.8±1.7	20.9±1.0	22.5±0.5
Mean height 1st branch (m)	13.4±0.7	11.8±0.7	13.2±0.9	12.3±1.1	10.8±0.7	12.3±0.4
Mean drh (cm)	25.7±1.7	24.9±1.9	25.5±1.7	27.4±3.2	21.6±1.6	24.9±0.9
Basal area (m^{2}ha^{-1})	33.3	34.3	33.5	43.3	23.3	33.5
Crown projection area (m^{2}ha^{-1})	16313	21815	18223	17559	14998	17782

All above measurements are for trees ≥ 10 cm drh. Where appropriate the standard error of mean is noted.
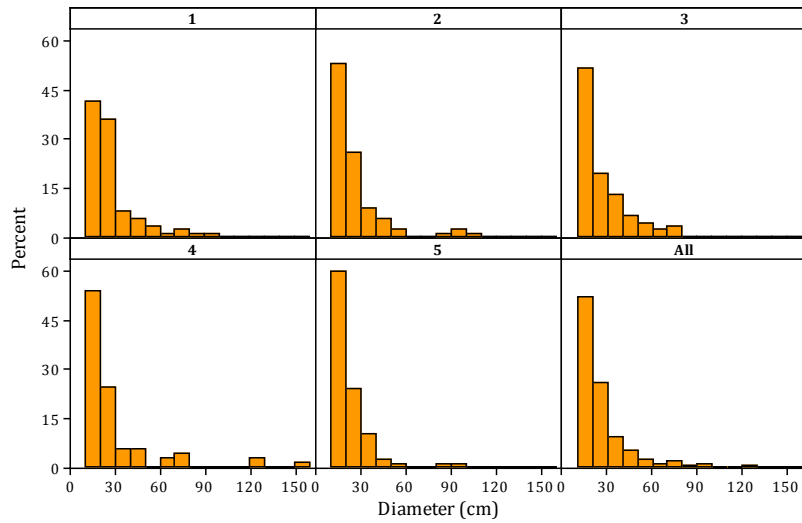

Figure 6. Mawalai diameter distribution, Central Seram, Indonesia. Graphs for the diameter distribution of 0.2 ha plots 1-5 on separate panels and the 6th panel, 'All', for the five Mawalai plots together. Diameter classes are of 10 cm and distribution is showed as a percentage of totals (per plot or all respectively).

Table 5. The distribution of total crown projection area for different height categories of trees at the Mawalai site (5 0.2 ha plots), Central Seram, Indonesia. Means are per tree within height category.

Height category	Number of trees	Crown projection area (%)	Mean crown projection area $\pm$ SE (m^2)
0-10	10	2.3	9.7 $\pm$ 2.9
10-20	200	45.7	20.4 $\pm$ 1.1
20-30	140	32.0	34.7 $\pm$ 2.2
30-40	56	12.8	58.6 $\pm$ 5.4
40-50	20	4.6	131.3 $\pm$ 22.1
50-60	4	0.9	138.0 $\pm$ 22.9
60-70	8	1.8	286.5 $\pm$ 56.4
All	438	100.0	40.6 $\pm$ 2.7

For all plots at the Mawalai site, trees are mostly 10 m to 30 m high and the first branches of trees mostly 5 m to 20 m above the ground (Appendix 2). Almost half of the total crown projection area (45.7%) is from trees 10 m to 20 m high (Table 5). At each plot some trees are much higher than the average canopy. The emergent trees (> 40 m high) are few, but have very large crowns. These high trees often have sparse foliage with few very large branches.

Other life forms

Data for other life forms are summarized in Appendix 3. They are characterized by high variation within plots. All of the variables in Appendix 3 have been tested for differences between plots, using the nonparametric Mood's Median Test in Minitab 16. There were no differences between sites except for meters of rattan (p = 0.005). Plot 2 and plot 5 differ most in rattan medians, where plot 2 has more rattan than plot 5 (Figure 7).
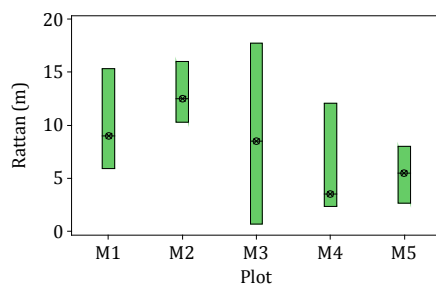

Figure 7. Length of rattan in meters. The medians and 95% confidence intervals of 0.01 ha subplots' rattan length per 0.2 ha plots at the Mawalai site, Central Seram, Indonesia. Round symbol is median. All confidence intervals overlap except those of plot 2 and plot 5.

3.1.2 Lok Wae Utu, Mawalai and Wai Onye – between sites comparisons

The three sites differed in the measured forest structure variables. While the Mawalai site was less dense but had on average larger tree diameters, the Wai Onye site was considerably more dense but with smaller trees. The Lok Wae Utu site ranked number two both in density and tree diameter. A Mood's Median test shows that there are significant differences ($p < 0.001$) between diameter and tree density medians of the three sites. Two graphs (Figure 8) show the medians with 95% confidence interval.

Table 6. Forest structure and taxonomic data for three sites, with 1 ha sampled in each, Central Seram, Indonesia. 'All' is for all three sites together, i.e. 3 ha.

Forest structure	Lok Wae Utu	Mawalai	Wai Onye	All
Total number of trees (stems)	555 (555)	438 (438)	648 (657)	1641
Total number of species	96	95	59	149
Number of families	33	34	27	40
Number of genus	69	74	46	98
Mean tree density (n 0.01 ha^{-1})	5.6 ± 0.2	4.4 ± 0.2	6.5 ± 0.2	5.5 ± 0.1
Mean drh (cm)	21.3 ± 0.7	24.9 ± 0.9	18.6 ± 0.5	21.2 ± 0.4
Basal area (m^{2}ha^{-1})	31.0	33.5	26.5	30.6
Crown projection area (m^{2}ha^{-1})	12449	17782	-	-

All above measurements are for trees ≥ 10 cm drh. Where appropriate the standard error of mean is noted. Number of families and number of genus include only those identified to that level. Total number of species include also those that have only morphologically been determined a separate species. Diameter and basal area have been calculated based on stems ≥ 10 cm drh; trees are considered as individuals and some tree individuals have several stems.
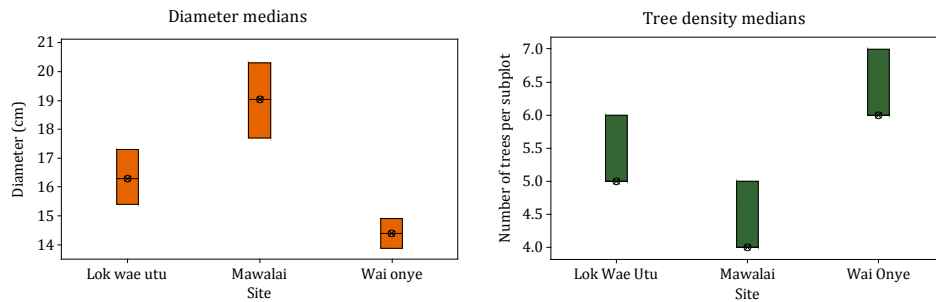

Figure 8. Boxplots with diameter and tree density medians for three sites and their 95% confidence intervals, Central Seram, Indonesia. None of the confidence intervals for diameter medians overlap. The confidence intervals for tree density medians go back to back. The round symbols indicate the median.

3.2 Species richness

There were no significant differences in species richness between plots within the same site. There were however significant differences between one less species rich site and the two other, more species rich, sites. A list with preliminary species identification is found in Appendix 7.

3.2.1 Mawalai – within site comparisons

There were no significant differences between the plots either in terms of species richness or species density (Figure 9). The plots at the Mawalai site all had overlapping confidence intervals for their sample-based rarefaction curves. Four of the plots had very similar curves, but plot 4's rarefaction curve was slightly lower. Overall, confidence intervals were wide.
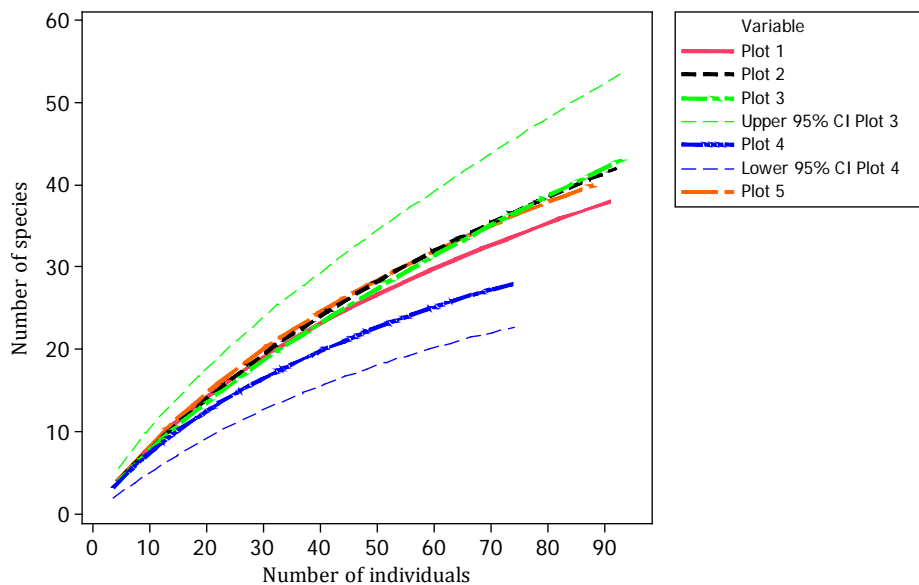

Figure 9. Sample-based rarefaction curve for tree species (trees ≥ 10 cm drh) at the Mawalai site, Central Seram, Indonesia. Curves are for 5 plots of 0.2 ha each and the highest and lowest confidence intervals (CI). Other CI:s have been omitted for clarity. All CI:s overlap, though the rarefaction curve for plot 4 is at the lower end.

3.2.2 Lok Wae Utu, Mawalai and Wai Onye – between sites comparisons

The Wai Onye site was found to be significantly less species rich as well as less species dense than the Lok Wae Utu and Mawalai sites (Figure 10). The rarefaction curves for the Mawalai and the Lok Wae Utu sites are similar in shape and

their confidence intervals overlap. The rarefaction curve for the Wai Onye site is considerably lower and flatter than the other two and its confidence intervals do not overlap with those of the other two curves, except for at a very low number of trees. Both species density, comparing the species numbers at the endpoints of the rarefaction curves, and species richness, comparing the numbers of species for a set number of trees, is lower for the Wai Onye site.
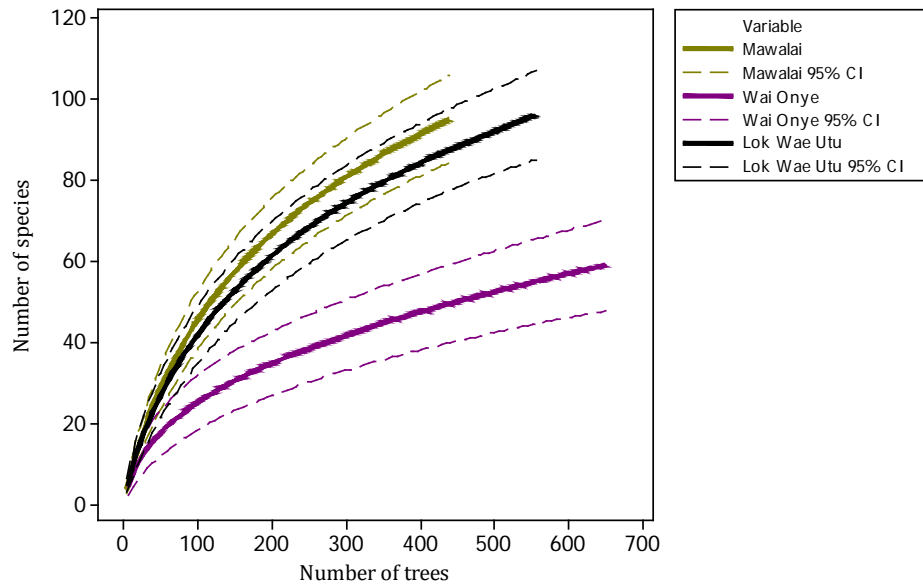

Figure 10. Sample rarefaction curves for tree species (trees ≥ 10 cm drh) in lowland primary limestone forest, Central Seram, Indonesia. The three sites are: Mawalai (5 0.2 ha plots), Lok Wae Utu (1 1 ha plot) and Wai Onye (1 1 ha plot). Based on samples of 10 m × 10 m within plots. CI = Confidence interval.

3.3   Species composition

Species composition differed between the three sites, and also when comparing some of the 0.2 ha plots at the same site. At both scales distance and amount of surface rock correlate with the differences seen.

3.3.1   Mawalai – within site comparisons

In all plots many tree species occur with only one individual (Figure 11). Plot 3 has most species with just one individual, while plot 4 is distinguished by having fewer species with only one individual. Plot 4 also has the lowest total number of

species (Table 4). Table 7 lists the two most abundant (highest number of individuals) and most dominant (largest basal area) species for the Mawalai plots.

The most abundant and most dominant species at the Mawalai site are *Gymnacranthera paniculata*, *Alangium javanicum* and *Palaquium amboinense* (Table 7; Table 9). Often, though, the most dominant species are not particularly frequent: a few very big trees contribute to a large portion of total basal area (Table 7). Many of the emergent trees (trees $\geq$ 40 m high) are similarly infrequent trees (Appendix 4), reflecting the overall picture of the rainforest. Several of the emergent trees are also dominant in terms of local basal area (Table 7), but since each species is infrequent they are less dominant over larger areas (Table 9).

Table 7. The two most abundant or dominant species for 0.2 ha plots (1-5) at the Mawalai site, Central Seram. Fr: Species contribution to total number of trees, per plot. BA: species contribution to plot total basal area. Bold numbers are species that rank number 1 or 2 for that category.

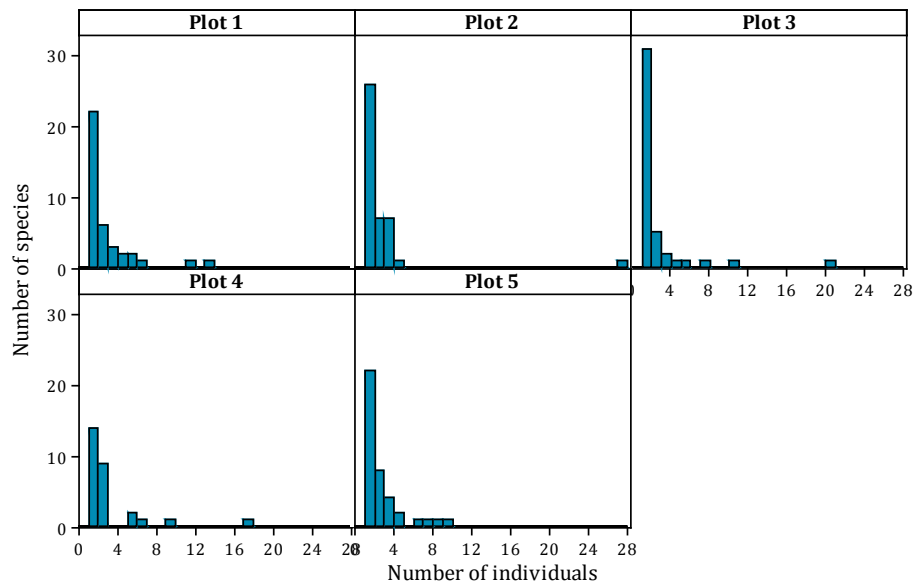| Species	1		2		3		4		5	
	Fr%	BA%	Fr%	BA%	Fr%	BA%	Fr%	BA%	Fr%	BA%
Alangium javanicum	**14.3**	12.8	3.2	3.6	**10.8**	9.8	**12.2**	7.1	**10.2**	8.6
Anthocephalus macrophyllus	0.0	0.0	0.0	0.0	0.0	0.0	2.7	**26.9**	0.0	0.0
Canarium indicum	1.1	2.0	0.0	0.0	2.2	3.3	2.7	0.3	1.1	**12.9**
Endospermum moluccanum	0.0	0.0	1.1	**13.4**	0.0	0.0	0.0	0.0	0.0	0.0
Gymnacranthera paniculata	12.1	4.2	**29.3**	**12.2**	**21.5**	**10.4**	6.8	2.6	**9.1**	6.8
Mallotus penangensis	0.0	0.0	0.0	0.0	1.1	0.2	8.1	**24.3**	4.5	4.0
Microcos ceremensis	1.1	0.1	**4.5**	1.5	1.1	0.4	0.0	0.0	1.1	0.2
Palaquium amboinense	6.6	9.8	3.3	1.8	5.4	**16.5**	2.7	8.4	0.0	0.0
Pometia pinnata	5.5	**20.2**	0.0	0.0	1.1	4.2	0.0	0.0	0.0	0.0
Terminalia supitiana	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	**16.7**
Toxotrophis iliciolia	0.0	0.0	0.0	0.0	0.0	0.0	**23.0**	3.9	8.0	2.5

Figure 11. Species abundance graphs for 0.2 ha plots at the Mawalai site, Central Seram, Indonesia. The frequency of species for each frequency of trees.
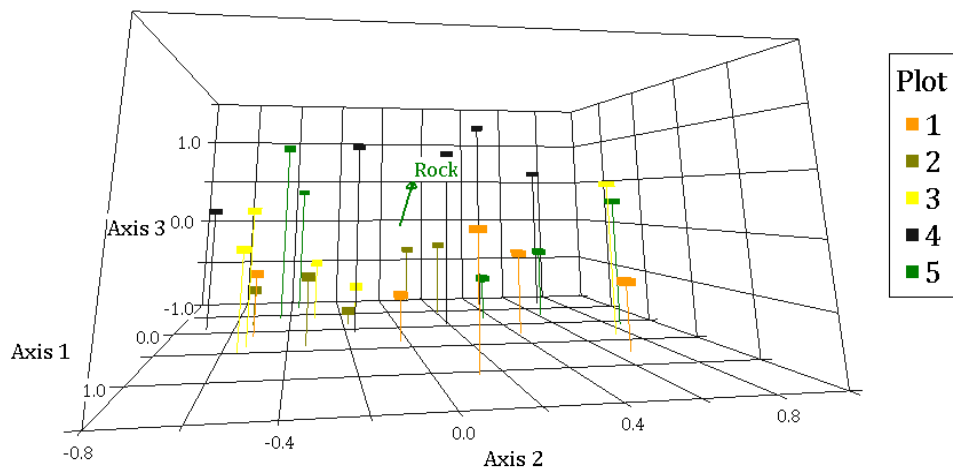

Figure 12. NMS graph showing similarities of species composition for 0.04 ha subplots at the Mawalai site, Central Seram, Indonesia. The species data has been overlaid by environmental data as well as data on other life forms. A cutoff value for $r^2 = 0.350$ shows only rock coverage as a possible explanatory variable. At the cutoff value $r^2 = 0.300$ also a variable of North-South geographical distance was shown on the graph at a similar angle in three-dimensional space as the rock coverage. R^2 is a combination of correlation between all three axes of the solution and a variable, here amount of surface rock. The subplots are on sticks to place them in 3D-space. Rocky subplots from plot 4 diverge from the rest.

30

Table 8.   Pairwise comparisons of species composition for 0.2 ha plots at the Mawalai site, Central Seram, Indonesia. Only comparisons where p-value < 0.05 (not corrected for multiple comparisons) are included. T represents the difference between groups and A is the agreement within groups and has been chance-corrected. Overall A = 0.22 and p < 0.001.

Plots compared	T	A	p
1 vs. 2	-2.2	0.15	< 0.05
1 vs. 4	-4.2	0.33	< 0.01*
1 vs. 5	-2.2	0.15	< 0.05
2 vs. 4	-3.8	0.32	< 0.01*
3 vs. 4	-2.8	0.21	< 0.05

*Significantly different also when adjusted for multiple comparisons.

Averages distances between 0.04 ha subplots within plot grouping were: plot 1 = 0.33, plot 2 = 0.28, plot 3 = 0.43, plot 4 = 0.34 and plot 5 = 0.58.

Final stress was 19 (500 iterations) for a three-dimensional solution in the ordination shown in Figure 12. The resulting stress is on the outer margins of what could have occurred by chance (Monte Carlo test, $p > 0.05$). 0.04 ha subplots are scattered in species space with no tight clustering for subplots from the same 0.2 ha plot, except possibly for plot 4. From the data set of environmental and other life form variables the amount of surface rock was the strongest explanatory variable for species composition of subplots. Geographical distance was almost as strong and since the two correlated they cannot be distinguished from each other.

Plot 4 is most strongly different from the other plots in the pairwise comparisons, with significant differences when compared to three out of four other plots (Table 8). It is the rockiest plot, situated between plot 3 and 5 on the hillside. Also in Figure 12 plot 4 subplots are farther from the rest. The one 0.04 subplot in plot 4 that is not grouped together with the others (Figure 12) is the only one with no surface rock, but also the subplot geographically closest to plot 3.

3.3.2 Lok Wae Utu, Mawalai and Wai Onye – between sites comparisons

There is a gradient in species turnover from Mawalai to Lok Wae Utu to Wai Onye in the same order as the sites are located in the landscape. Mawalai and Lok Wae Utu are close to each other and their species abundances show the same patterns of many rare species and few more abundant ones (Figure 13). Wai Onye diverge more with fewer rare species and some very abundant species. In terms of species composition all three sites differ from each other (Figure 14, Figure 15). This can also be seen in the indicator species (Appendix 5), where some species are much more frequent and abundant at one site compare to the others.

Table 9. Most frequent or most dominant species, at one of three sites or all together, Central Seram, Indonesia. Fr = % of total number of individuals for category. BA = Dominance as percent of total basal area for category. Numbers in bold are the five most abundant or dominant species per category: in each site or for all.

Species	Lok Wae Utu		Mawalai		Wai Onye		All	
	Fr%	BA%	Fr%	BA%	Fr%	BA%	Fr%	BA%
Alstonia scholaris	0.2	0.3	0.0	0.0	1.2	**6.3**	0.5	1.8
Aglaia sapindina	**5.8**	0.1	0.0	0.0	**19.6**	6.9	**9.7**	1.8
Anthocephalus macrophyllus	0.0	0.0	0.5	**6.9**	0.0	0.0	0.1	2.3
Alangium javanicum	**12.4**	**12.7**	**10.0**	**8.3**	0.9	1.7	**7.3**	**7.2**
Celtis philippinensis	**12.3**	**13.1**	3.4	4.2	0.0	0.0	**5.1**	**5.5**
Dendrocnide microstigma	**4.7**	3.2	0.0	0.0	2.9	2.4	2.7	1.6
Elaeocarpus spaericus	0.2	0.2	0.0	0.0	**8.3**	**15.9**	3.4	**4.3**
Ficus virens	0.4	**10.8**	0.0	0.0	0.0	0.0	0.1	3.4
Gymnacranthera paniculata	0.9	0.3	**16.2**	**7.0**	0.0	0.0	4.6	2.4
Knema cinerea	0.7	0.2	**4.1**	1.2	0.0	0.0	1.3	0.5
Leptonychia glabra	2.0	0.9	0.2	0.0	**15.0**	5.9	**6.6**	1.8
Mallotus penangensis	4.3	1.2	2.5	**6.9**	6.6	4.6	4.8	3.9
Myristica lancifolia	**5.4**	1.4	1.6	0.6	**13.1**	5.3	**7.4**	2.0
Octomeles sumatrana	0.2	**6.1**	0.2	0.1	0.2	**9.8**	0.2	**4.5**
Palaquium amboinense	1.8	3.9	**3.7**	**7.8**	0.0	0.0	1.6	3.8
Pertusadina eurhyncha	1.1	**5.2**	1.6	1.8	0.2	1.1	0.9	2.5
Pouteria duclitan	3.2	4.2	0.5	0.6	3.1	**12.2**	2.4	**4.7**
Toxotrophis ilicifolia	0.0	0.0	**5.5**	1.4	0.2	0.1	1.5	0.5

Table 10. Pairwise comparisons of species composition for 3 sites, Central Seram, Indonesia. T represents the difference between groups and A is the agreement within groups and has been chance-corrected. Overall A = 0.48 and p < 0.001.

Sites compared	T	A	p
Lok Wae Utu vs. Mawalai	-20.3	0.28	< 0.001
Lok Wae Utu vs. Wai Onye	-25.5	0.37	< 0.001
Mawalai vs. Wai Onye	-29.4	0.45	< 0.001

Average distances in species space between 0.04 ha subplots within the three sites were: Lok Wae Utu = 0.25, Mawalai = 0.41 and Wai Onye = 0.12.
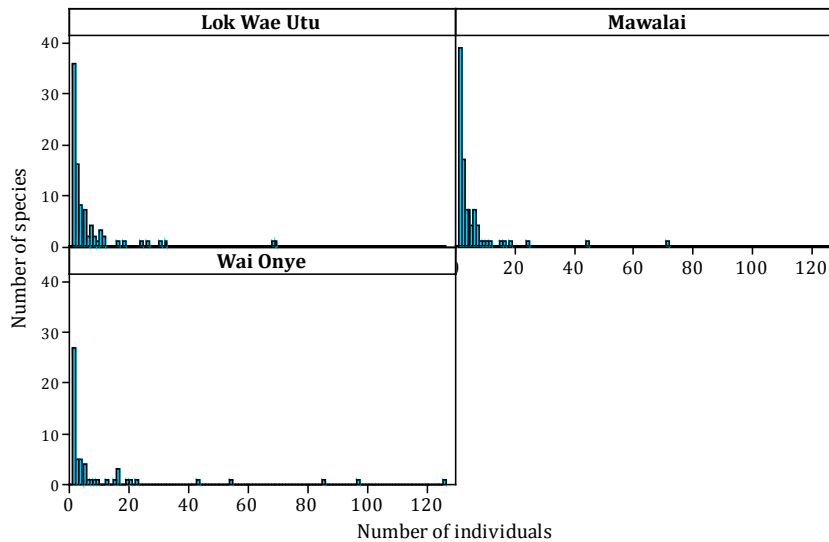
Figure 13. Species-abundance graphs for trees (≥ 10 cm drh) at three sites of one sampled hectare each in lowland limestone forest, Central Seram, Indonesia. The frequency of species for each frequency of trees.

The ordination shown in Figure 14 had a final stress of 13 (118 iterations), significantly lower than for randomized data in a Monte Carlo test (250 iterations, $p < 0.01$). PC-ORD recommended a two-dimensional solution. Plots are clearly grouped per site and possible explanatory variables are geographical distance and amount of surface rock.

Final stress for the ordination in Figure 15 was 16 (500 iterations) and significantly different from a randomized run (Monte Carlo test, $p < 0.01$). Hence any patterns found, when data are described at the recommended numbers of dimensions (here three dimensions), cannot be explained by chance. There are distinct groupings of 0.04 ha subplots for site. The 0.04 ha subplots at the Mawalai site are further from each other in species space than subplots at the other sites (Figure 15; Table 10). The 0.04 ha subplots at the Wai Onye site stand out through their closer proximity to each other in species space when compared with subplots at Lok Wae Utu with the same sampling design.

The indicator species for a site has an indicator value, a combination of relative abundance and relative frequency, which is higher for that certain site than would have been expected by chance. The species in Appendix 5 can therefore be seen as characteristic for their respective sites, though the underlying reasons for that cannot be evaluated based solely on this analysis.
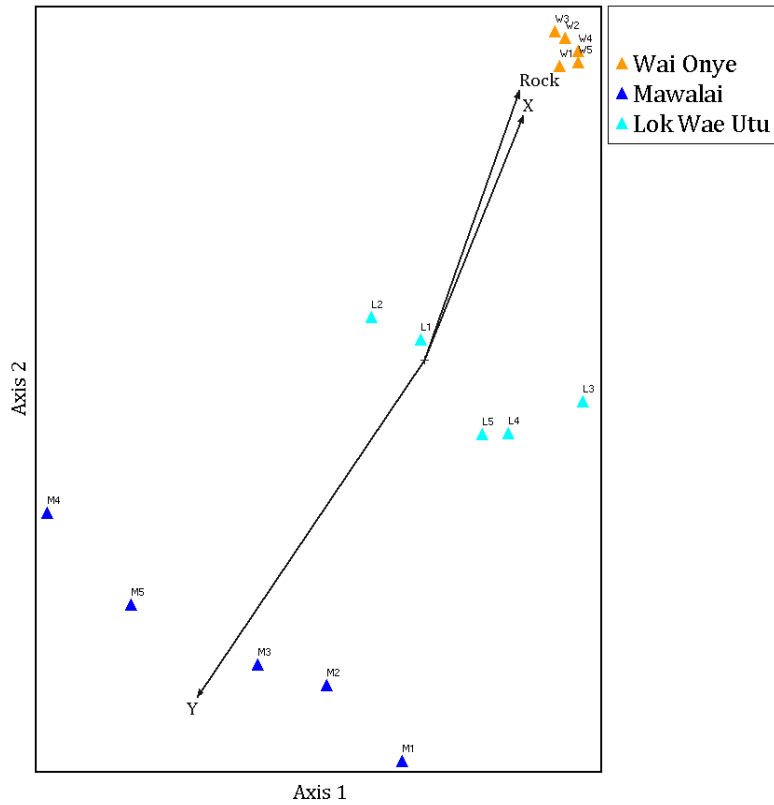
Figure 14. NMS graph showing similarities in species composition for 0.2 ha plots in lowland limes-
tone forest, Central Seram, Indonesia. The plots are from three sites: Lok Wae Utu, Mawalai and Wai
Onye. Cutoff value is set to $r^2 = 0.5$. X = geographical distance (East-West), Y = geographical dis-
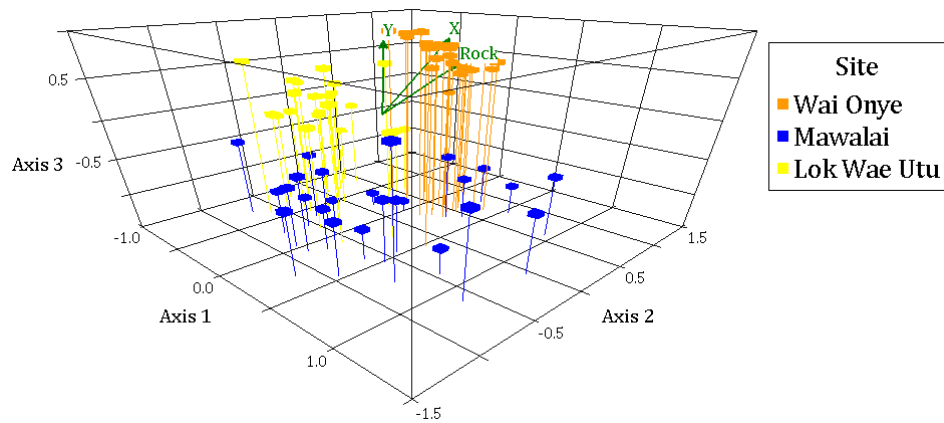tance (North-South) and Rock = average amount of surface rock per plot.

Figure 15. NMS graph showing 0.04 ha subplot similarities in species composition, 3 sites in lowland
limestone forest, Central Seram, Indonesia. The subplots are color-coded according to the site they
belong to: Wai Onye, Mawalai or Lok Wae Utu. The cutoff value for $r^2 = 0.6$. X = geographical dis-
tance (East-West), Y = geographical distance (North-South) and Rock = average amount of surface
rock. The subplots are on sticks to place them in 3D-space.

4 Discussion

Lowland forest over limestone varies here in respect to forest structure, species richness as well as species composition; this is in line with the high diversity known from other types of rain forest (Whitmore, 1984). There can be significant differences in forest structure between plots in the same forest type just a few kilometers apart, and major differences in tree species composition between pre-stratified plots only a few hundred meters from each other. Whether variation at a larger spatial scale is due to distance between sites, environmental variables that differ between sites, or a mixture of both cannot be distinguished in this study. In the multivariate analyses performed there is correlation between the amount of rock and differences in species composition. This can be seen at a smaller scale, for the within site comparison, and can be speculated to influence the distinct grouping of the rocky Wai Onye site in comparison to the other two sites.

The three sites belong to the same forest type, but there is abiotic variation among them. The Wai Onye site stands out in several respects when it comes to abiotic aspects of the site. Most notable, it has a much higher percentage of surface rock, and it is situated in a generally flat area, relatively close to a larger river and at lower altitude (100 masl). The other two sites, Lok wae Utu and Mawalai, are more similar in amount of surface rock, and both sites are located in slopes and at similar altitudes (200-300 masl and 300 masl). All three sites are considered to have had limited anthropogenic disturbance. The Lok Wae Utu site is on the boarder to the national park, and lies close to the park service office. It is, therefore, unlikely that it will experience future disturbance. It is also close to the road so there might have been some selective logging, in the general area, by local people. The Wai Onye site is in an area a short walk from gardens, but the rockiness of the site makes it unfit for cultivation. It is farther from the main road, which also makes previous logging improbable. The Mawalai site lies in between

the Masihulan village and the main road; there is some selective logging, though no tree stumps were found within plots, and new gardens are made in the vicinity.

There have been only a few studies of Malesian limestone areas, and they differ methodologically and topographically from mine, undermining comparisons between them. When limestone areas have been described in other studies they seem to be rocky, though there is not always a measure of how much surface rock there is. In any case, limestone areas provide a wide range of different habitats from hill summits to cliffs, different degree slopes and flat land (Whitmore, 1984). Terrain is often rugged, but two of the Seram study sites were located further down the hill side in gentle slopes (Mawalai and Lok Wae Utu) and the tree vegetation was higher and fairly open. The third plot (Wai Onye) was located in a low and flat area, and it had a higher tree density.

I have found published articles from three studies of limestone primary forest in Malesia. A limestone area in Sarawak, Malaysian part of Borneo, has been described as "rugged" with an average soil depth of 11cm (Proctor et al., 1983, Newbery and Proctor, 1984). The plot was located in a 25 to 30 degree slope. In Bird's Head, Indonesian part of New Guinea, the studied area was described as "limestone hills with accumulated humus over rocks or clay" (Polak, 2000). In mainland Malaysia, the surface rock cover was measured (varying from about 10 to 90%), as well as soil depth and several soil properties (Crowther, 1982). Both soil cover (opposite of rock cover) and soil depth influenced basal area in the mainland Malaysia study and both correlated with topographic position (Crowther, 1982). Although these studies have many differences, they allow for some comparisons and a slightly broader perspective.

4.1   Forest structure

The nature of variation of lowland limestone forest structure on Seram depends on scale. There are large differences between both stem density and stem diameter between the three sites. Basal areas, calculated based on the two measured variables density and diameter, differ also between plots of the same site. The only measured variable that differed between plots at Mawalai site was rattan.

A few large trees influence the basal area of plots much more than many small trees. Plot 4 compared to the other plots at the Mawalai site, and the Mawalai site compared to the other two sites have fewer trees, but more very big trees and therefore larger total basal area. A larger total basal area indicates more tree biomass so there is probably considerably more biomass at the Mawalai site than at

the Wai Onye site which has the highest numbers of trees but the lowest basal area. There is more variation in basal area within the Mawalai site (23.3-43.3 m^2ha^{-1} extrapolated) than between sites (26.5-33.5 m^2ha^{-1}); maybe because small scale patchiness is smoothed out when larger areas are compared.

Overall, variation of forest structure variables such as stem density and diameter can be large within limestone forest. Still, lowland limestone forest structure on Seram Island is comparable to other lowland primary forests in Indonesia. The Seram tree stem densities (438-657 ha^{-1}) fit well within the overall picture for lowland primary forest in the region. In Kartawinata's review of vegetation studies (1990) stem densities lie between 300 and 800 trees per hectare for lowland primary forest (excluding peat swamp forest). At Bird's Head much higher stem densities were found (960-1390 ha^{-1}) for limestone forest in New Guinea (Polak, 2000). Basal area was lowest in the secondary forest (19.0 m^2ha^{-1}), slightly higher in limestone forest (22.8 m^2ha^{-1}) and highest in mixed primary forest (35.8 m^2ha^{-1}). The three sites in my study (basal area 26.5-33.5 m^2ha^{-1}) all fall between the basal area of limestone forest and mixed primary forest at Bird's Head. Stem density in the limestone plot in Sarawak was similar to that of the Wai Onye site (644 vs. 657) but with a higher basal area (37 m^2ha^{-1}) and a lower mean height (18.8 m vs. 20.9-24.8 m) than at Mawalai (Proctor et al., 1983). The study in mainland Malaysia on limestone forest encompasses more variation with a stem density range of 200 to 1200 trees per hectare and basal areas from only a few m^2 to over 70 m^2 per hectare, though it included trees down to 15 cm girth (Crowther, 1982). The basal areas of my study are higher than that of limestone forest in one study (Polak, 2000), lower than that of one study (Proctor et al., 1983) and somewhere in the middle of the great variation of the mainland Malaysia study (Crowther, 1982). Similarly, stem densities in my study are much lower than at Bird's Head, similar to Sarawak, while the mainland Malaysia study covers all that variation and more.

4.2   Species richness

In terms of species richness, one site (Wai Onye) stood out as significantly less species rich as well as less species dense than the other two sites. The within site comparison showed no differences in species richness. It is a well known feature of the tropical rain forest to have many rare species (e.g., Whitmore, 1984). This was also the case for the three sites in this study and rarefaction curves were steep, especially for the 0.2 ha plots in the within site comparison, indicating that sample sizes were not sufficient.

Each 0.2 ha plot at Mawalai can also be compared with the rarefaction curve of the less species rich Wai Onye site. In such a comparison at least the 0.2 ha plot with lowest species richness at Mawalai would have overlapping confidence intervals with data from Wai Onye. Had the sizes of sample units been larger within the Mawalai site, within-site differences might also have been detected.

Interpretation of the rarefaction curves should be made bearing in mind the different sample methods used: 5 smaller plots of 0.2 ha were laid out over a 10 ha area at the Mawalai site while continuous 1 ha plots were studied at the Lok Wae Utu and Wai Onye sites. Larger areas cover more spatial and environmental heterogeneity, which can cause a bias when comparing with smaller areas (Collins and Simberloff, 2009). The sampled area is 1 ha for all three sites, but since the Mawalai sampled hectare is spread out and species usually have a non-uniform distribution (Scheiner, 2003) this affects how the species curves can be compared.

Tree species richness of tropical limestone forest is expected to be lower than in non-limestone areas (Monk et al., 1997). Lower, though, in relation to the world's most species rich vegetation type, the lowland tropical evergreen rain forest (Whitmore, 1984). In the review of Kartawinata (1990), 1 ha plots had 60 to 120 tree species for lowland primary forest. The Wai Onye site is on the lower end of that with its 59 species, while the other two sites (95 and 96 species) are at the middle. Some of the species-area curves in the same review show considerably higher numbers of species at 1 ha. Compared to other studies on limestone the species richness of the Seram sites is similar to, or on the higher end of, that of Sarawak (one 1 ha plot, about 75 species) on Borneo (Proctor et al., 1983) and Bird's Head, New Guinea (five 0.1 ha plots, 75 species) (Polak, 2000). Since species richness would have been expected to be lower on Seram compared to the much larger islands of Borneo and New Guinea (Roos et al., 2004) this result is surprisingly high.

4.3   Species composition

There are large differences in species composition between sites and also, though more subtle, within a site on Seram. All three ordinations indicate that the amount of surface rock might play a role in determining species composition. Unfortunately there is not a clear gradient of amount of surface rock in the data set, and it is difficult to distinguish the importance of this abiotic variable to that of spatial distance. The three sites had very different amounts of rock: Wai Onye was very rocky while the other two were not. For the within site comparison the gradient is

more continuous but the ordination was weak (with high stress) making it less reliable to draw conclusions from.

Results depend on scale, where a larger plot can include more site specific species data, but environmental data is averaged out over a larger area. Therefore I compared species composition between sites in a wide variety of ways, among them two NMS ordinations (Figure 14 and Figure 15). The data sets for the ordinations differed regarding plot size (0.2 ha and 0.04 ha, respectively) and the number of tree species (99 and 103). A larger sized plot encompass more individuals and hence more species than a smaller plot. With more species there is an increasing amount of possible species combinations and therefore a higher probability of larger distances between plots in species space. This is the case in Figure 14 where distances between sites are much greater than in Figure 15. The 0.2 ha plots contain more information on the species composition of their sites, but 0.04 ha plots can also give enough information to reveal differences between sites (see also 4.5 Reflections on sampling method). When including environmental data in ordinations there are also assumptions about at which scale they might influence species composition. That was another reason to trying different scales, and for the two I tried both showed differences in species composition that correlated to differences in spatial distance and surface rock.

Forest at the three sites differs both with respect to tree species composition and regarding spatial variation in composition within sites. There are distinct groupings of 0.2 ha plots and, though not as clearly, of 0.04 ha subplots, per site (Figure 14; Figure 15). In the MRPP for comparisons between sites there are clearly also big differences in average distances of subplots within sites (0.12-0.41). MRPP does not distinguish between differences in mean and differences in distance within groups. When, however, the NMS based on the same data set is considered, giving a visual representation of the data, there seem to be differences both in distances in between groups and differences in means of species composition.

The much greater average distance in species space between subplots (greater dissimilarity in species composition) at the Mawalai site might be due to the different sampling procedure used there. With sampling spread out instead of in one continuous plot, the larger spatial distance, or increased variation of environmental variables, can increase variation in species composition. Similarly the Wai Onye subplots have relatively small average distance in species space (similar species compostition) compared to Lok Wae Utu with the same sampling method (Table 10, Figure 15). This could reflect the lower species richness of the Wai Onye site.

Fewer species with more individuals ought to decrease distance between subplots in species space compared to many species with few individuals.

Tree species turnover, the spatial variation of tree species, can be very high in tropical rain forest. In the study at Bird's Head, Indonesian New Guinea, only 4 out of 415 tree species were present in all the forest types studied: primary rain forest (twelve 0.1 ha plots), forest over limestone (five 0.1 ha plots) and secondary forest (five 0.1 ha plots) (Polak, 2000). In total for the 3 ha studied on Seram there were 149 tree species of which 30 were found on all three sites. The Seram sites were within the same forest so less species turnover could be expected.

4.4   Biogeography

As is often the case in studies on tree species in tropical Southeast Asia, there are uncertainties in species determination. As mentioned earlier, there is not a flora that covers all of the tree species found in this study. The most comprehensive flora is the Flora Malesiana where many volumes have been published though it is still far from covering all families. Nevertheless, assuming that most identifications in this study are correct, comparisons can be made within a larger geographical context. As expected (Whitmore, 1984) tree species on Seram, being a part of Maluku, have varied total distributions. Some species, like the two most abundant species in the study *Aglaia sapindina* and *Myristica lancifolia*, have an Eastern distribution and occur in Australia and New Guinea as well as Maluku (Mabberley et al., 1995, de Wilde, 2000). Many occur only in Malesia such as the third most abundant species – *Alangium javanicum* (World Conservation Monitoring Centre, 1998) and the sixth most abundant species *Gymnacranthera paniculata* (de Wilde, 2000). Another abundant species, *Celtis philippinensis*, has a much wider distribution including tropical Africa, South and Southeast Asia as well as Northern Australia (Steenis, 1977). Also *Chisocheton ceramicus* is widely distributed in Southeast Asia (Mabberley et al., 1995). While some species, such as *Prunus wallaceaena*, have a more narrow distribution; it is confined to Sulawesi, the Lesser Sunda Islands and Maluku in Eastern Malesia (Kalkman, 1993).

It would be interesting to further look at the biogeography of the tree species of Seram, since there might still be much to discover in terms of their distribution. For example a recent volume of Flora Malesiana covers the Moraceae family and includes the species *Trophis philippinensis* with an Eastern Malesian distribution. In this study on Seram it was found at two of three sites, but in Flora Malesiana it is listed as found only on Halmahera for the Moluccas (Berg et al., 2006). Another

example is *Myristica iners* that in Flora Malesiana is described as having a Western distribution in Malesia, not stretching further East than Java or Borneo, and also found in Cambodia and Thailand (de Wilde, 2000). In Flora Malesiana there is a discussion about a possible occurrence in the Phillipines and in this study the preliminary identification suggests that *Myristica iners* occurs in one of three lowland sites on Seram. *Antiaris toxicaria* has a wide distribution but is divided into two subspecies in Asia, one with a Western distribution and one with an Eastern distribution (Berg et al., 2006). The Flora Malesiana accounts for finds of the subspecies with Eastern distribution on Halmahera but it is unclear in the flora which subspecies occur on Seram.

4.5 Reflections on sampling methodology

It can be difficult to study tropical forest in remote areas. Tree diversity is high and floras insufficient. It takes time to travel there and to organize the field work. Taking this into account, improvements are still possible of the sampling methodology applied in my study. First of all sampling has been done using two different methods. The one hectare continuous plots were already there and their tree data were collected by others. I am grateful for the opportunity I was given to analyze also these two data sets, but it causes some difficulties in interpreting data comparisons. The species identifications are preliminary since species or trees for which question marks exist have not been rechecked in the field. Also, it was not possible to collect fruits and flowers for most of the species. The results here are probably on the lower end for number of species. There is additional uncertainty in the abundance of each species since some trees were difficult to climb and time was limited.

The set up that was chosen for the Mawalai site, with 5 plots of 0.2 ha each, is a compromise between time and number of sample units. In my case I wanted to compare the tree vegetation to two other sites but I also aimed at studying the variation within a smaller area. Thus plots at the Malawai site were spread out over 10 ha. My original thought was to have a larger study site, but local topography, thick rattan and forest gardens limited the area at my disposal. According to McCune and Grace (2002), the relation of standard error of mean (SE) to the mean has been considered an evaluation of sample adequacy, where the limit for SE can be set to for example 5, 10 or 20% of mean. In Table 4 the forest structure variables all fall below the 10% limit, except for diameter at reference height for plot 4 for which SE is near 12%. In this respect a sample size of 20 0.01 ha units might therefore be

considered adequate to describe forest structure at Mawalai. Since variance is probably lower with the pseudoreplicated design of adjacent sample units, this should be considered with some caution. As expected, when considering the sample adequacy in respect to tree species a total sample size of 20 0.01 ha units cannot be deemed enough. For species, a flattening species-area curve has been thought an indication of adequate sample size (e.g., Mueller-Dombois and Ellenberg, 2002). As can be seen in the rarefaction curves for the Mawalai plots 1-5 (Figure 9) they are not yet flattening out at the number of trees corresponding to an area of 0.2 ha and at 1 ha (Figure 10) they are still increasing.

I have deliberately used pseudoreplication to enable comparative data analyses. This means that I have used adjacent, dependent subplots as independent sample units, thus violating important statistical assumptions. It is essential to bear that in mind while looking at the results and it limits the possibilities of extrapolation. It does however allow comparisons between plots and the variation within them that would not have been possible otherwise. It was also not possible to do ordinations with fewer sample units. Due to pseudoreplication, autocorrelation of sample units can be expected, though even in a spread out random sampling of smaller units there can be expected to be autocorrelation with spatial distance for ecological data (Bellehumeur et al., 1997).

The smallest area suitable for sampling can be discussed. For the NMS ordination I used two different types of data sets for comparisons between sites with the first ordination based on 0.2 ha plots and the second on 0.04 ha subplots. The distance between species composition at the three sites is greater with the larger plots, but the spatial patterning in ordination space are basically the same. It might be that in this respect sample units of 0.04 ha would be big enough to compare species composition, though there is less stress and a more readily interpreted two-dimensional solution for the ordination of larger sample units.

4.6   Conclusions

There is considerable variation within lowland limestone forest on Seram, and this needs to be acknowledged in sampling designs of vegetation studies. For instance, to adequately sample the forest for a vegetation map, samples need to be geographically widespread. It is popular to make comparisons of forests at different altitudes (e.g., Culmsee et al., 2011, Edwards et al., 1990) or for different forest types (e.g., Polak, 2000, Proctor et al., 1983). Also for such comparisons it is important to base sampling methods on some kind of knowledge on the spatial varia-

tion within every forest type. In addition, potential REDD+ funding in the area would need to consider the variation of carbon stored in trees within the same forest type, indicated by differences in basal area between sites. Similarly, the spatial differences in species richness and composition could be considered for conservation planning purposes, for example when looking for more area-efficient resource use while at the same time aiming to encompass as many species as possible. Overall there is a need of further ecological and taxonomical studies in the area.

4.7 The future

It will be interesting to see how species composition differs between primary forest over limestone and primary forest over other kinds of rock in the continuation of the COLUPSIA project. It would also be interesting to study tree species turnover for a surface rock gradient, since some results in this study suggest that the amount of surface rock might play a role in determining tree species composition. Generally there is inadequate knowledge on the tolerance of plants towards calcium-rich soils (Monk et al., 1997). Similar analyses of tree species composition and comparisons later on with data from non-limestone areas on Seram could help identify limestone indicators.

The soil in the Mawalai area is considered very good for gardens by local people. There is a constant need for new areas to turn into gardens and my plots at Mawalai are within comfortable walking distance to the village. Thus, according to some of the local people, it is likely that gardens will expand into my study area or the slope to the area already the next few to ten years. Overall deforestation on Seram has been less extensive than in many other parts of Indonesia. The large national park and previous campaigns on nature conservation have also raised awareness on the problems of environmental degradation. At the same time improved infrastructure facilitates more profit in large-scale logging. Areas of lowland forest that are neither logged nor protected, like those studied here, are becoming increasingly rare. Primary forests outside the national park are areas available for local people to hunt and pick fruits, for example, while they can also harbor many forest species. The high species turnover in tropical rain forests, including the lowland primary limestone forest on Seram, and peoples' dependency on that forest, makes it important to look for sustainable solutions over large areas.
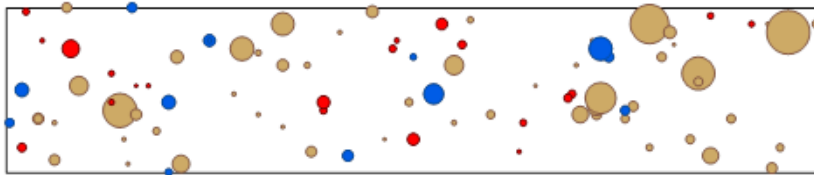
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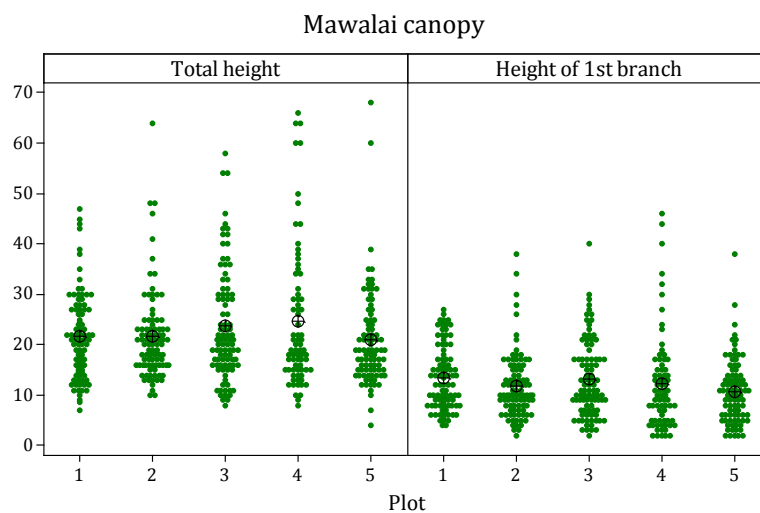
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Appendices

Appendix 1. Example of tree distribution: plot 1 at the Mawalai site, northern Seram. Circle size is relative to tree basal area. Red circles represent trees in the Myristicaceae family and blue circles represent Alangium javanicum trees in the Alangiaceae family, the most abundant families in plot 1. Brown circles represent trees of other families.

Appendix 2. Height distribution for trees (≥10cm drh) in Mawalai plots, Central Seram. The first panel shows the total height of each tree and the second panel presents the height of first branch for the same trees. Every point represents the height value (in meters) for a tree in that plot. For each plot the mean height is marked.

Appendix 3. Life forms other than trees (Φ > 10 cm) for plots 1-5 at the Mawalai site. Mean values with SE for each 0.2 ha plot and for all together. Means are per 50 m² and of counts or, for rattan, length in meters.

Life form	1	2	3	4	5	All
Pole trees	3.5 ± 0.6	4.6 ± 1.0	3.9 ± 1.2	3.6 ± 0.8	2.7 ± 0.5	3.7 ± 0.4
Saplings	21.9 ± 3.6	25.6 ± 3.3	17.9 ± 3.8	18.1 ± 2.9	23.6 ± 4.0	21.4 ± 1.6
Shrubs	0.5 ± 0.3	1 ± 0.4	0.8 ± 0.4	0.8 ± 0.6	0.9 ± 0.4	0.8 ± 0.2
Palms	11.3 ± 3.1	16.3 ± 3.2	9.5 ± 3.1	14.9 ± 2.4	13.0 ± 3.1	13.0 ± 1.3
Pandan	0.9 ± 0.3	0.4 ± 0.3	0.3 ± 0.2	0.8 ± 0.3	1.6 ± 0.4	0.8 ± 0.2
Ferns	0.6 ± 0.3	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.1	0.5 ± 0.3	0.3 ± 0.1
Rattan	9.8 ± 1.9	14 ± 1.8	9.7 ± 3.1	6.1 ± 1.9	7.3 ± 2.6	9.4 ± 1.1
Woody climbers	2.2 ± 0.7	3.9 ± 1.4	5.5 ± 1.7	0.4 ± 0.3	3.3 ± 1.6	3.1 ± 0.6
Vascular epiphytes	0.4 ± 0.3	0.5 ± 0.4	0.3 ± 0.2	1.1 ± 0.5	2.7 ± 1.4	1.0 ± 0.3

Appendix 4. Emergent trees Mawalai, Central Seram, Indonesia. The number of trees ≥ 40 m high for each species (per species: (no. emergent trees/total no. of individuals)×100) in 5 0.2 ha plots.

Species	No. trees (% of total)
Palaquium amboinense	5 (31)
Neonauclea moluccana	3 (38)
Pometia pinnata	3 (50)
Canarium indicum	2 (33)
Anthocephalus macrophyllus	2 (100)
Pangium edule	2 (40)
Celtis philippinensis	2 (13)
Terminalia supitiana	1 (100)
Maranthes corymbosa	1 (25)
Endospermum moluccanum	1 (100)
Mallotus penangensis	1 (9)
Xanthophyllum papuanum	1 (100)
Ficus sp.2	1 (33)
Terminalia copelandii	1 (100)
Canarium sp.1	1 (100)
Litsea elliptica	1 (100)
Dendrocnide stimulans	1 (25)
Homalium foetidum	1 (17)
Pouteria duclitan	1 (50)
Sterculia insularis	1 (33)

Appendix 5. Indicator species for each site. Species shown are those that showed a statistically significant indicator value (IV), p<0.05.

Site, IV rank	Species Code	IV	Mean	St. dev.	p
Lok Wae Utu					
1	*Celtis philippinensis*	73.9	20.9	4.18	0.0002
2	*Alangium javanicum*	51	26.9	3.8	0.0004
3	*Dendrocnide microstigma*	27.3	18.1	4.27	0.0442
4	*Syzygium* sp1	25.7	11.4	3.84	0.011
5	*Dysoxylum densiflorum*	21.8	8	3.43	0.01
6	*Alangium griffithii*	20	6.7	3.25	0.0098
7	*Pterocarpus indicum*	16	5.8	2.89	0.0312
Mawalai					
1	*Gymnacranthera paniculata*	75.6	17.2	4.18	0.0002
2	*Knema cinerea*	42.1	13.5	4.02	0.0002
3	*Toxotrophis ilicifolia*	26.2	8.5	3.46	0.0012
4	*Palaquium amboinense*	24.9	13.6	4.04	0.0172
5	*Canarium indicum*	24	7.1	3.2	0.0016
6	*Gulubia constata*	24	7.3	3.29	0.0024
7	*Neonauclea moluccana*	22.4	9.1	3.47	0.013
8	*Horsfieldia bivalvis*	22.2	10.8	3.7	0.022
9	*Microcos ceramensis*	19.6	9.5	3.5	0.0396
10	*Aglaia elliptica*	16	6	2.87	0.0288
11	*Mastixiodendron pachyclados*	16	5.8	2.88	0.031
Wai Onye					
1	*Leptonychia glabra*	80.2	22.3	4.21	0.0002
2	*Elaeocarpus sphaericus*	70.1	14.8	4.21	0.0002
3	*Aglaia sapindina*	65.3	24.3	3.97	0.0002
4	*Myristica lancifolia*	52.2	28.2	3.89	0.0002
5	*Voacanga grandifolia*	48	11	3.83	0.0002
6	*Mallotus penangensis*	45.9	20.5	4.21	0.0002
7	*Gonocaryum litorale*	33.8	10.9	3.77	0.0006
8	*Pouteria duclitan*	28.2	17.6	4.13	0.0268
9	*Diospyrus pilosanthera*	26.4	13.9	3.85	0.0108
10	*Syzygium stipulare*	25.6	10.1	3.65	0.0036

Appendix 6. Environmental data for three sites, Central Seram, Indonesia. Range are the lowest and highest value of a 0.01 ha subplot within the plot or site. Averages are of all 0.01 ha subplots within the plot or site. At the Mawalai site data was collected from all 0.01 ha subplots, at the Lok Wae Utu and Wai Onye sites data was collected from half of the 0.01 ha subplots.

Site	Plot	Rock cover average (%)	Rock cover range (%)	Slope average (degrees)	Slope range (degrees)	Soil depth average (cm)	Soil depth range (cm)
Mawalai	1	1	0 – 4	15	5 – 26	50	20 – > 100
Mawalai	2	2	0 – 17	10	1 – 22	44	24 – > 100
Mawalai	3	0.3	0 – 4	8	2 – 19	30	10 – 73
Mawalai	4	22	0 – 80	15	2 – 24	48	10 – > 100
Mawalai	5	8	0 – 23	17	7 – 27	44	10 – > 100
Mawalai	All	7	0 – 80	13	1 – 27	43	10 – > 100
Lok Wae Utu	All	2	0 – 7	13	5 – 26	–	–
Wai Onye	All	69	3 – 90	9	0 – 20	–	–

Appendix 7. Preliminary species list for three sites (Lok Wae Utu, Mawalai and Wai Onye), Central Seram, Indonesia. Includes the taxonomic level that the preliminary species identification has reached.

Alangiaceae	*Alangium griffithii* Harms, *Alangium javanicum* (Blume) Wangerin
Anacardiaceae	*Buchanania amboinensis* Miq. Volk., *Buchanania macrocarpa* Lauterb., *Campnosperma brevipetiolata* Volk., *Mangifera laurina* Blume
Annonaceae	*Alphonsea* sp., *Mitrephora* sp., *Polyalthia glauca* Boerl., *Polyalthia lateriflora* King, *Popowia schefferiana* Diels, *Pseuduvaria reticulata* Miq., *Xylopia peekelii* Diels
Apocynaceae	*Alstonia scholaris* (L.) R. Br., *Voacanga grandifolia* (Miq.) Rolfe
Arecaceae	*Caryota rumphiana* Mart., *Gulubia costata* Becc.
Bombacaceae	*Neesia altissima* (Blume) Blume
Burseraceae	Canarium *acutifolium* (DC.) Merr., *Canarium cf. oleosum* (Lam) Engl., *Canarium indicum* Will., *Canarium* sp.1, *Canarium vrieseanum* Engl., *Haplolobus floribundus* (K. Sch.) H.J. Lam var. *moluccanum, Haplolobus floribundus* (K. Schum.) H.J. Lam
Chrysobalanaceae	*Maranthes corymbosa* Blume, *Siphonodon celastrineus* Griff.
Clusiaceae	*Calophyllum soulatri* Burm.f. ex F. Mull., *Calophyllum* sp., *Garcinia tetrandra* Pierre, *Garcinia torensis* Lauterb.
Combretaceae	*Terminalia copelandii* Elmer, *Terminalia microcarpa* Decne, *Terminalia supitiana* Koord.
Datiscaceae	*Octomeles sumatrana* Miq.
Ebenaceae	*Diospyros cauliflora* Blume, *Diospyros korthalsiana* Hiern., *Diospyros pilo-*

	santhera Blanco, *Diospyros rostrata* (Merr.) Bakh.
Elaeocarpaceae	*Elaeocarpus multiflorus* Villar, *Elaeocarpus sphaericus* (Gaertn.) Schumann
Euphorbiaceae	*Pimelodendron amboinicum* Hassk., *Antidesma excavatum* Miq., *Baccaurea* sp, *Blumeodendron tokbrai* J.J.Smith., *Drypetes longifolia* Pax. & K. Hoffm., *Endospermum moluccanum* Becc., *Glochidion perakense* Hook.f., *Mallotus floribundus* Muell. Arg., *Mallotus penangensis* Muell. Arg.
Fabaceae	*Albizia saponaria* (Lour.) Bl. ex Miq., *Inocarpus fagiferus* (Parkinson) Fosberg., *Ormosia calavensis* Azaola, *Pterocarpus indicus* Willd.
Flacourtiaceae	*Casearia glabra* Roxb., *Casearia grewiaefolia* Vent., *Homalium foetidum* Benth., *Pangium edule* Reinw.
Icacinaceae	*Gomphandra mappioides* Valeton, *Gonocaryum litorale* (Blume) Sleum.
Lauraceae	*Actinodaphne procera* Nees, *Beilschmiedia madang* Blume, *Cryptocarya ceramica* A.J.G.H.Kosterm., *Cryptocarya cf. affinis* Merr., *Cryptocarya* sp, *Litsea cf. ferruginea* Blume, *Litsea elliptica* Blume, *Litsea forstenii* Boerl., *Litsea glutinosa* (Lour.) C.B.Rob., *Nothaphoebe umbelliflora* Blume
Leeaceae	*Leea indica* Merr.
Loganiaceae	*Fagraea racemosa* Jack, *Neuburgia moluccana* (Scheff.ex Boerl.) Leenh.
Meliaceae	*Aglaia elliptica* Blume, *Aglaia sapindina* Harms., *Aphanamixis polystachya* (Wall.) R.N.Parker, *Chisocheton ceramicus* (Miq.) C.DC., *Chisocheton microcarpus* Koord. & Valet., *Chisocheton patens* Blume, *Chisocheton warburgii* Harms., *Dysoxylum alliaceum* Blume, Dysoxylum *densiflorum* Miq., *Dysoxylum parasiticum* (Osbeck) Kosterm., *Vavaea amicorum* Benth.
Moraceae	*Antiaris toxicaria* Leschenault, *Artocarpus altilis* (Parkinson) Fosberg, *Artocarpus dasyphylla* Miq., *Ficus* spp., *Ficus variegata* Blume, Ficus *virens* Ait., *Toxotrophis ilicifolia* Vidal, *Trophis philippinensis* (Bur.) Corner
Myristicaceae	*Gymnacranthera paniculata* Warb., *Horsfieldia bivalvis* Merr., *Horsfieldia sylvestris* Warb., *Knema cinerea* (Poir.) Warb., *Knema* sp., *Myristica fatua* Blume, *Myristica fatua* Blume var. papuana, *Myristica iners* Blume, *Myristica lancifolia* Poir., *Myristica* sp.
Myrsinaceae	*Ardisia lanceolata* Gaertn.f.
Myrtaceae	*Decaspermum bracteatum* (Roxb.) A.J. Scott, *Syzygium acuminatissimum* (Bl.) Merr.& Perry, *Syzygium aphamyrtus* Miq., *Syzygium boerlagei* Merr., *Syzygium cf. acuteangulatum*, *Syzygium cf. claviflorum* Wall., *Syzygium lineatum* (DC.) Merrill & Perry, *Syzygium malaccense* (L.) Merrill & Perry, Syzygium sp., *Syzygium stipulare* (Blume) Miq.
Nyctaginaceae	*Pisonia grandis* R. Br.
Opiliaceae	*Chaempereia manilana* (Blume) Merr.
Pandanaceae	*Pandanus* sp.
Polygalaceae	*Xanthophyllum papuanum* Whitmore ex van der Meijden
Rosaceae	*Prunus wallaceana* Kalkm.
Rubiaceae	*Anthocephalus macrophyllus* Havil., *Mastixiodendron pachyclados* (K. Schum.) Melch., *Neonauclea moluccana* Merrill, *Pertusadina eurhyncha* (Miq.) C.E. Ridsdale, *Timonius anodon* Boerl.
Sabiaceae	Meliosma *pinnata* (Roxb.) Walp.
Sapindaceae	*Ellatostachys* sp., *Euphorianthus obtusstus* Radlk., *Mischocarpus sundaicus* Blume, *Pometia pinnata* J.R. & G. Forst.

Sapotaceae	*Chrysophyllum lanceolatum* A.DC., *Palaquium amboinense* Burck, *Palaquium lobbianum* Burck, *Palaquium obtusifolium* Burck., *Pouteria duclitan* (Blanco) Bakh.f.
Sterculiaceae	*Heritiera littoralis* Dryand., *Heritiera trifoliolata* (F. Muell.) Kosterm., *Kleinhovia hospital* Linn., *Leptonychia glabra* Turcz., *Sterculia insularis* R. Br.
Thymelaeaceae	*Phaleria capitata* Jack
Tiliaceae	*Microcos ceramensis* Burret
Ulmaceae	*Celtis philippinensis* Blanco, *Celtis rigescens* (Miq.) Planch.
Urticaceae	*Dendrocnide microstigma* (Gaudich. ex Wedd.) Chew, *Dendrocnide stimulans* (L.f.) Chew.
Verbenaceae	*Clerodendron laevifolium* Blume, *Teijsmanniodendron bogoriense* Koord., *Vitex cofassus* Reinw. ex Blume