

The Vegetation of Lambusango Forest, Buton, Indonesia

by Powling, A., Phillips, A., Pritchett, R., Segar, S.T., Wheeler, R. and Mardiasuti, A.

Copyright, publisher and additional information: Publishers' version distributed under the terms of the Creative Commons Attribution License: [Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License](https://creativecommons.org/licenses/by-nc-sa/4.0/)

DOI: [10.14203/reinwardtia.v14i2.1671](https://doi.org/10.14203/reinwardtia.v14i2.1671)



THE VEGETATION OF LAMBUSANGO FOREST, BUTON, INDONESIA

Received April 03, 2015; accepted June 27, 2015

ANDREW POWLING

School of Biological Sciences, University of Portsmouth, Portsmouth, UK. E-mail: andrew.powling@port.ac.uk.

AURORA PHILLIPS

School of Biological Sciences, University of Brighton, Brighton, UK.

ROSIE PRITCHETT

Centre for Biological Sciences, University of Southampton, Highfield Campus, Southampton, UK.

SIMON T. SEGAR

School of Biological Sciences, University of Reading, Reading, UK.

REBECCA WHEELER

School of Biological Sciences, University of Portsmouth, Portsmouth, UK.

ANI MARDIASTUTI

Faculty of Forestry, Bogor Agricultural University, Bogor, Indonesia.

ABSTRACT

POWLING, A., PHILLIPS, A., PRITCHETT, R., SEGAR, S. T., WHEELER, R. & MARDIASTUTI, A. 2015. The vegetation of Lambusango Forest, Buton, Indonesia. *Reinwardtia* 14(2): 265 – 286. — Lambusango Forest is a tropical rainforest on the island of Buton, which lies close to south east Sulawesi. The forest covers an area of about 95.000 ha, with different parts of the forest having different levels of conservation protection. It lies on rocks of both calcareous (limestone) and non-calcareous (sandstone, conglomerate, peridotite and chert) nature, which give rise to soils with varying pH values, nutrient levels and water-holding capacities. The climate is seasonal, with a dry season of three months and considerable year-to-year variability due to El Niño and La Niña events. The vegetation on the different soils and in different habitats has been studied. Over 300 species of vascular plants found in the forest and surrounding areas are listed, including trees and shrubs, herbs, climbers, epiphytes, ferns and club-mosses. Two genera, *Calamus* with 18 species and *Ficus* with 29 species, are particularly species-rich, apparently due to their ability to occupy numerous edaphic and ecological niches. Species of these two genera are also good colonists and so better able to reach Buton in the recent past than other species. The plants of the forest indicate that Buton is floristically very similar to Sulawesi, with at least 83% of the species found in the forest also being known from Sulawesi. Most of the plant families and genera present on Buton are common in SE Asia, indicating colonisation primarily from that continent. Many fewer families and genera have colonised from the Australasian continent. The conservation of plant diversity is necessary for the forest to continue as a functioning ecosystem, to the benefit of the animals of the forest and also the local people.

Key words: Buton, *Calamus*, climate, *Ficus*, floristics, Lambusango, soils, Sulawesi.

ABSTRAK

POWLING, A., PHILLIPS, A., PRITCHETT, R., SEGAR, S. T., WHEELER, R. & MARDIASTUTI, A. 2015. Vegetasi hutan Lambusango, Buton, Indonesia. *Reinwardtia* 14(2): 265 – 286. — Hutan Lambusango adalah hutan hujan tropik di Pulau Buton yang terletak dekat dengan Sulawesi Tenggara. Luas hutan ini adalah 95.000 ha dengan beberapa bagian hutan yang mempunyai tingkat perlindungan konservasi yang berbeda. Hutan ini berkembang pada tanah berkapur (*limestone*) dan non-berkapur (batupasir, konglomerat, peridotit dan rijang) sehingga tanahnya memiliki berbagai nilai pH, kadar hara dan kapasitas penahan air. Daerahnya beriklim musiman, dengan musim kemarau tiga bulan dan bervariasi tinggi dari tahun ke tahun karena pengaruh El Niño dan La Niña. Vegetasi pada tanah yang berbeda dan dalam habitat yang berbeda telah dipelajari. Lebih dari 300 jenis tumbuhan yang ditemukan di hutan dan daerah sekitarnya, termasuk pohon-pohon dan semak-semak, herba, liana, epifit, tumbuhan paku dan kerabatnya. Dua marga, *Calamus* dengan 18 jenis dan *Ficus* dengan 29 jenis, termasuk jenis yang berlimpah, tampaknya karena kemampuan mereka untuk menempati berbagai relung ekologis dan edafis. Jenis dari dua marga ini juga merupakan penjelajah yang baik dan lebih mampu untuk mencapai Buton pada masa lalu dibandingkan jenis lainnya. Tumbuhan di hutan menunjukkan bahwa Buton secara floristik sangat mirip dengan Sulawesi, setidaknya 83% dari jenis yang ditemukan di daerah ini juga terdapat di Sulawesi. Sebagian besar tumbuhan di Buton merupakan jenis umum di Asia Tenggara, sehingga menunjukkan kolonisasi terutama dari benua tersebut. Hanya sedikit suku dan marga yang berasal dari benua Australasia. Konservasi keanekaragaman tumbuhan diperlukan bagi hutan untuk melanjutkan fungsi ekosistem, serta untuk kepentingan binatang dan juga masyarakat setempat.

Kata kunci: Buton, *Calamus*, *Ficus*, floristik, iklim, Lambusango, Sulawesi, tanah.

INTRODUCTION

The biogeographic region known as Wallacea includes Sulawesi and its neighbouring islands, the Moluccas and the Lesser Sunda Islands. The region has always been separated by deep seawater from the continental masses of both Asia and Australasia, so is occupied by organisms which colonised from one or other of the continents and also by species that evolved in the region. As a result the forests of Wallacea are in some ways different from those known in Asia and Australasia, with different communities of plants and animals (Primack & Corlett, 2005). Wallace's Line marks the western edge of Wallacea and the westernmost limit of organisms which originated on the Australasian continent.

Buton is an island lying close to South-East Sulawesi, the biggest island in Wallacea (Fig. 1). Lambusango Forest is situated in the southern half of the island (Fig. 2) between 5°S, 122.68°E and 5.5°S, 123.22°E (Widayati & Carlisle, 2012). The altitude of the forest ranges from sea level to about

700 m above sea level (asl), so all the area can be classified as lowland forest. The forest is seasonal evergreen rain forest with almost continuous canopy cover. It consists of many different sub-types due to the varied geology and topology of the area. Some parts of the forest have steep slopes with thin soils due to Karst limestone; other parts are flatter with deeper soils produced from sandstone and ultrabasic bedrock. Chert ridges and volcanic rocks are very exposed, with poor and drought-prone soils. Valleys and their alluvial soils are a major habitat type, formed by the rivers that flow outwards from the high ground in the centre of the forest. The forest covers 95,000 ha, of which 27,000 ha in the west of the forest is the Lambusango Wildlife Sanctuary, an area in which no logging, rattan harvesting or hunting is officially permitted. The remaining 68,000 ha is production forest or limited production forest with less stringent conservation regulations (Widayati & Carlisle, 2012). The officially separate Kakenauwe Nature Reserve, a small (810 ha) spur of forest immediately adjoining to the north, is here treated as part of the Lambusango Forest. Surrounding the forested areas to a width of a few kilometres is a 'non-forest zone' which has been mostly cleared and used for settlements and agriculture, although some small areas of forest still exist (Widayati & Carlisle, 2012).

Lambusango Forest is the subject of an ongoing research effort led by Operation Wallacea and it was investigated as part of a programme financed by the World Bank's Global Environment Fund (Purwanto, 2008). The programme ran from 2005 to 2008. It involved the study of biodiversity in Lambusango Forest by Indonesian and British scientists, together with conservation agreements with local villagers whereby they agreed to forest conservation measures in exchange for investment in educational and business development, including ecotourism. Little has been published on the vegetation of Buton and this paper, part of the Operation Wallacea research programme, is the first general description of the vegetation of Lambusango Forest.

Research Site

General

Buton is separated from South-East Sulawesi by a strait 10 km wide with depth less than 100 m. It has thus been connected by land to Sulawesi at times of lower sea level during the repeated ice ages of the Pleistocene Epoch (Voris, 2000). There are reasons to think that the climate of Sulawesi was cooler and dryer during the ice ages (De Deckker *et al.*, 2003; Whitten *et al.*, 2002). Such a climate



Fig. 1. Map of Buton and SE Sulawesi; Lambusango Forest is shown by the dashed line.

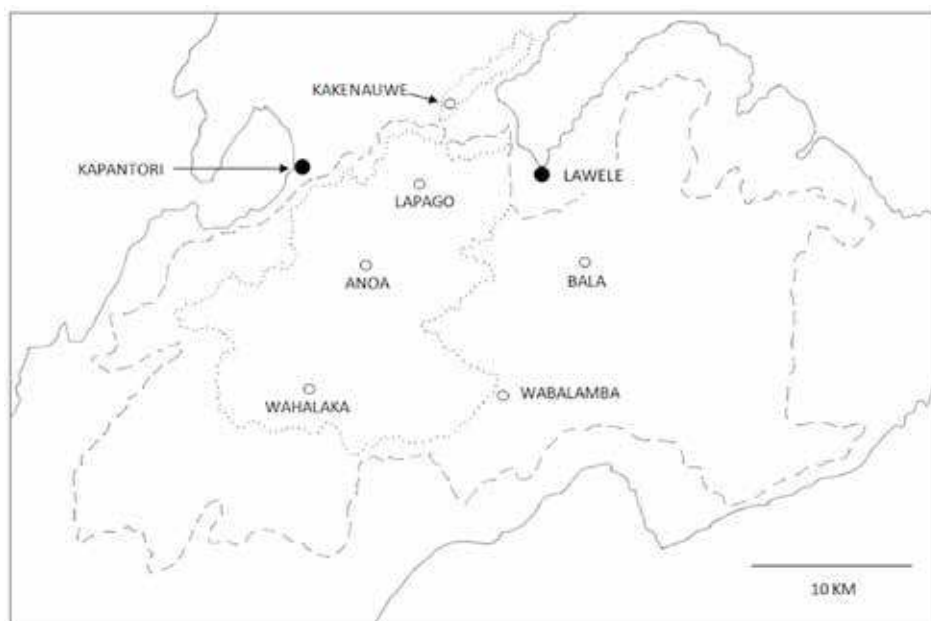


Fig. 2. South-central Buton showing Lambusango Forest. Dashed line = Production forest; dotted line = Conservation forest (information from Widayati & Carlisle, 2012); open circles = sites from which the forest was surveyed.

might well have affected the nature and extent of forest on Sulawesi and Buton.

Following the declaration of conservation zones in the early 1980s, villages were moved to the periphery of the forest. Areas formerly inhabited or cultivated are regenerating but clearly show evidence of their previous usage. People still exert an influence on the forest by legal and illegal logging, legal rattan harvest and hunting. Some encroachment into the forest has occurred due to land being taken for settlement and conversion to agriculture (Purwanto, 2008).

Geology and Soils

Buton is a fragment of the Australasian continent that separated from Australia in the late Triassic or early Jurassic and accreted onto the Eurasian plate in the early or middle Miocene (Milsom, 2000). Rocks formed since the Triassic consist of a variety of marine sedimentary strata, some calcareous and some non-calcareous in nature. After the middle Miocene the geological history of Buton is similar to that of eastern Sulawesi and includes the emplacement of ophiolite during the mid to late Miocene. Chalks, marls and reef carbonates were deposited during the last five million years as Buton subsided to bathyal depths and later rose again (Milsom, 2000).

As a result of this history Buton has a wide variety of rock types which give rise to a range of soils. The main types of rocks are: i. Limestones and other calcareous rocks of various ages from late Triassic to very recent times; ii. Late Cenozoic

sandstones and conglomerates; iii. Mesozoic chert sediments that now form steep ridges; iv. Ultrabasic (ultramafic) rocks of the ophiolite body including peridotites (J. Milsom, *pers. comm.*) Ultrabasic rocks have low percentages of silicates and frequently high levels of minerals that are toxic to plants. The limestones give rise to calcareous, basic soils which are often thin and free-draining, although sometimes containing appreciable clay and organic components. The sandstones and conglomerates produce acidic soils which are generally nutrient poor, whilst the ultrabasic rocks produce soils, often called ultramafic soils, with a distinctive vegetation of noticeably small stature. A minor component of the geology is chert, which forms very acidic soils with distinctive vegetation. River valleys contain alluvial deposits that can be very variable in composition, depending on which sediments are being washed into the valleys by side streams. Because of the variety of soils in close proximity to each other, Lambusango Forest is expected to have diverse vegetation.

Climate

Buton has a seasonal climate with a dry season lasting normally from August to October, due to south easterly winds blowing from the dry continent of Australia (Whitten *et al.*, 2002). Annual rainfall has been measured at the coastal town of KapanTORI, on the north east edge of Lambusango Forest, for the five years from 1997 to 2001. The average figure was 1967 mm, with a highest figure of 2488 mm in 1999 and a lowest of 941 mm in 1997. The

year 1997 was very dry due to a developing El Niño event, with no rainfall during the months of August, September and October. The higher parts of Lambusango Forest almost certainly receive more rainfall than Kapantori, but no measurements have been made. The temperatures measured at Kapantori give a mean daily maximum figure of 26.8°C, with a yearly range from 25.7°C in June to 27.7°C in October and December (Ministry of Agriculture, Bau Bau, South-East Sulawesi, *pers. comm.*).

Two series of annual rainfall measurements exist for the island of Toba Besar, which lies close to the north west coast of Buton, together making a total of 15 years (1954-1960 and 1975-1982). These measurements give an average of 1678 mm and the site normally has its driest month in September or October (Whitten *et al.*, 2002). Yearly totals for Toba Besar (read from the bar chart on page 27 in Whitten *et al.*, 2002) have been compared with the yearly cumulative totals of the Oceanic Niño Index (ONI) produced by the National Oceanic and Atmospheric Administration, USA, (NOAA, 2014). The cumulative totals of the ONI give positive values for El Niño years and negative values for La Niña years. A significant inverse relationship between the ONI and yearly rainfall totals was found ($r = -0.641$, $p=0.010$).

Since El Niño and La Niña conditions normally develop during the second half of the year, the cumulative ONI values for just the second half were also tested for correlation with observed rainfall measurements and a closer correlation was found ($r = -0.729$, $p = 0.002$). This confirms that in El Niño years there is below average rainfall in the region and in La Niña years there is above average rainfall. As noted above, 1997 was an El Niño year, while heavy rainfall was experienced on Buton in the Augusts of 2007 and 2010, both years in which La Niña conditions developed. Therefore the vegetation of Lambusango must be able to cope with very irregular rainfall amounts both during a year and from year to year.

A yearly average rainfall of approximately 2000 mm or higher with a dry season of about three months means that Lambusango Forest can be classified as a seasonal rain forest. It is thus distinguished from ever-wet forests with no dry season and monsoon forests with a longer dry season (Primack & Corlett, 2005).

MATERIALS AND METHODS

Investigation of the soils and the forest was undertaken during the months of July and August in the years 2001 to 2012. Soils were tested to

determine their pH values and also their conductivities, low values of which indicate low levels of soluble mineral nutrients. Soil samples were taken from the top 10 cm of soil, usually from near paths or transect lines running through the forest. Two to five sites were sampled for each underlying rock type, with at least six samples from each site. The spacing of samples within a site varied between 30-60 m. A volume of 20 ml of loose soil was mixed with an equal volume of deionised water. A Hanna Combo pH and EC meter was used to make pH and conductivity measurements. Analysis of Variance, with Tukey's HSD comparisons, was used to determine significant differences between the means of the measurements. Analysis of Variance was performed using the computer program Minitab. Chi-square tests were done manually.

The forest was explored from sites and camps within the forest, as shown in Figure 2: Kakenauwe (limestones), Lapago (limestones, sandstones, alluvial), Anoa (sandstones, ultrabasic), Bala (chert, conglomerates, alluvial), Wahalaka (limestones) and Wabalamba (limestones, alluvial). Exploration was conducted mostly by following pre-existing paths or transect lines. The transect lines, which had different orientations in different sites, were 3 km long and ran straight through the forest, so crossed many different geological features and habitat types. Specimens of canopy trees and their epiphytes were obtained by tree climbers. Plant parts, mainly leaves, were either: (i) collected and pressed as herbarium specimens and then sent to Herbarium Bogoriense for confirmation of identification, or (ii) photographed and the photographs compared with specimens in the Royal Botanic Gardens' Herbarium at Kew, London, for identification to species with the expert assistance of Herbarium staff.

Information on the identities of many forest trees was obtained from the listing of Lambusango trees published on the internet by Widayati *et al.* (2008). These authors also collected specimens which were identified and stored at Herbarium Bogoriense, Bogor. For the present work nearly all information on plant species obtained from the various sources was checked by comparison of photographs with identified specimens in Kew Herbarium.

RESULTS AND DISCUSSION

Soils

The results of the soil tests are summarised in Table 1. It was found that soils derived from calcareous rocks gave relatively high pH values (mean pH = 6.54), with high values for

Table 1. pH and conductivity measurements for soils derived from different rock types found at or near the forest sites

Rock Type	Sites	Samples	pH		Conductivity (μ S)	
	N	N	Mean	SD	Mean	SD
Calcareous*	5	66	6.54 ^a	0.61	116.2 ^a	46.8
Alluvial	2	21	6.43 ^a	0.88	117.1 ^a	50.3
Non-calcareous*	5	40	5.08 ^b	0.63	51.5 ^b	24.8
Chert	2	15	4.28 ^b	0.71	56.7 ^b	30.4
Ultrabasic	2	19	5.03 ^b	0.37	34.0 ^c	11.9

*= limestones; **= sandstones, conglomerates; μ S = micro Siemens ; SD = standard deviation.

^a, ^b, ^c, indicate distinct statistical populations, as determined by Analysis of Variance using Tukey's HSD comparison with a family error rate of $p = 0.01$.

conductivities also. This suggests that these soils contain comparatively high levels of mineral nutrients necessary for plant growth, as might be expected from the active erosion of surface rocks creating new soil. Soils in river valleys were mostly similar to calcareous soils in their pH and conductivity values, despite the mixed origins of the sediments forming them. Waters from many rivers originate from or flow through areas with calcareous rocks, so it is to be expected that alluvial soils in the river valleys have some characteristics of calcareous soils.

The other soils tested were derived from: non-calcareous sandstones, siltstones and conglomerates (soil mean pH = 5.08); chert (soil mean pH = 4.28); and ultrabasic rocks such as peridotites (soil mean pH = 5.03). All these soils gave pH and conductivity measurements lower than the calcareous and alluvial soils. This indicates that these soils are strongly leached and have low levels of mineral nutrients necessary for plant growth.

Analysis of variance using Tukey's HSD comparisons showed that the latter three soil types are all significantly different, at the 1% level, from the calcareous and alluvial soils (Table 1). It should be noted that, although the soils derived from the ultrabasic rocks have low conductivities, they may contain levels of certain mineral ions that are toxic to many plants. Nickel, chromium and manganese are present at high levels in ultrabasic soils in Sulawesi (Whitten *et al.*, 2002) and nickel is produced commercially on Buton.

Vegetation of the Forest

Forest types are divided according to the rock and soils on which they grow. Two general categories of calcareous and non-calcareous (acidic) soils are discussed, but two subcategories of acidic soils, soils derived from chert and ultrabasic rocks, are

sufficiently different to be described separately. Other types of forest, namely riverine, coastal and regenerating secondary, are also described. Two very species-rich genera, *Calamus* and *Ficus* are described separately.

Over 300 species, consisting of approximately 150 trees, 20 shrubs, over 50 climbing plants and epiphytes, 40 herbs, 40 ferns and three club mosses were found growing *in the wild* in Lambusango Forest, including areas used for human settlements and agriculture (Table 2). Species planted by people for food, medicine or decoration are not included. The list is not complete; many species were seen but not identified and many more must have remained unseen. Soil preferences for some of the commoner tree species are shown in Table 3.

Forest on calcareous rocks

Considerable areas of the forest have calcareous soils formed from limestone. The soils vary from new, formed recently from the protruding limestone; to older, with high organic content and in places regularly waterlogged at times of heavy rain. Some areas have much limestone rock protruding at the surface with thin pockets of soil; this soil is clearly very dry during the dry season, due to the rapid loss of water through the underlying limestone. Tree species, considered to be common based on frequency of encounter, include *Buchanania arborescens* and *B. sessilifolia*, *Canarium asperum*, *Dillenia serrata*, *Elaeocarpus angustifolius*, *Heritiera trifoliata*, *Planchonia valida*, *Pometia pinnata*, *Pterocymbium javanicum*, *Pterospermum celebicum* and *P. diversifolium* (Table 2). Many species of figs (genus *Ficus*) are present, although most are rare. Among the tallest trees are *Bombax ceiba*, *Tetrameles nudiflora* and some strangling figs, for example *F. glandifera* which can be over 60 m in height.

Table 2. Vascular plant species recorded in Lambusango Forest and the surrounding area. Families are grouped alphabetically within the Classes listed by Mabberley (2008), Appendix.

No.	Class/ Family	Species
	Class Lycopodiopsida	
1	Lycopodiaceae	<i>Lycopodiella cernua</i> (L.) Pic.Serm <i>Huperzia phlegmaria</i> (L.) Rothm.
2	Selaginaceae	<i>Selaginella plana</i> (Desv. ex Poir.) Hieron.
	Class Psilotopsida	
3	Ophioglossaceae	<i>Ophioglossum pendulum</i> L.
	Class Marattiopsida	
4	Marattiaceae	<i>Angiopteris evecta</i> (G. Forst.) Hoffm.
	Class Polypodiopsida	
5	Aspleniaceae	<i>Asplenium longissimum</i> Blume <i>Asplenium macrophyllum</i> Sw. <i>Asplenium nidus</i> L.
6	Blechnaceae	<i>Stenochlaena palustris</i> (Burm.) Bedd.
7	Cyatheaceae	<i>Cyathea</i> cf. <i>roroka</i> Hovenkamp <i>Cyathea</i> cf. <i>elmeri</i> Copel. <i>Cyathea contaminans</i> Copel. <i>Cyathea moluccana</i> R. Br. ex Desv.
8	Davalliaceae	<i>Davallia denticulata</i> (Burm.) Mett. ex Kuhn
9	Dennstaedtiaceae	<i>Pteridium aquilinum sensu lato</i> (L.) Kuhn
10	Dryopteridiaceae	<i>Teratophyllum aculeatum</i> (Blume) Mett. <i>Dicranopteris linearis</i> (Burm. f.) Underw.
11	Gleicheniaceae	<i>Sticherus truncatus</i> (Willd.) Nakai
12	Lindsaeaceae	<i>Lindsaea lucida</i> Blume
13	Lomariopsidaceae	<i>Nephrolepis biserrata</i> (Sw.) Schott <i>Nephrolepis hirsutula</i> (G. Forst.) C.Presl.
14	Lygodiaceae	<i>Lygodium circinnatum</i> (Burm) Sw.
15	Polypodiaceae	<i>Drynaria quercifolia</i> (L.) J. Sm. <i>Drynaria sparsisora</i> (Desv.) T. Moore <i>Microsorium membranifolium</i> (R. Br.) Ching <i>Microsorium punctatum</i> (L.) Copel. <i>Phymatosorus scolopendria</i> (Burm. f.) Pic.Serm. <i>Pyrrosia longifolia</i> (Burm. f.) C.V.Morton <i>Pyrrosia piloselloides</i> (L.) M. G. Price
16	Pteridaceae	<i>Acrostichum aureum</i> L. <i>Adiantum malesianum</i> J. Ghatak <i>Pteris ensiformis</i> Burm. <i>Pteris moluccana</i> Blume <i>Pteris tripartita</i> Sw. <i>Pteris vittata</i> L.
17	Schizaceae	<i>Schizaea dichotoma</i> (L.) Sm. <i>Schizaea digitata</i> (L.) Sw.
18	Tectariaceae	<i>Pleocnemia irregularis</i> (C. Presl.) Holttum <i>Pteridrys sylvatica</i> (Willd.) C. Chr. & Ching

Table 2. Vascular plant species recorded in Lambusango Forest and the surrounding area (continued)

No.	Class/ Family	Species
		<i>Stenosemia aurita</i> (Sw.) C. Presl.
		<i>Tectaria crenata</i> Cav
19	Thelypteridaceae	<i>Cyclosorus callosus</i> (Blume) Ching
		<i>Cyclosorus heterocarpus</i> (Blume) Ching
		<i>Cyclosorus subpubescens</i> (Blume) Ching
20	Woodsiaceae	<i>Diplazium</i> sp.
	Class Cycadopsida	
21	Cycadaceae	<i>Cycas rumphii</i> Miq.
	Class Pinopsida	
22	Araucariaceae	<i>Agathis dammara</i> (Lamb.) Rich.
23	Gnetaceae	<i>Gnetum gnemon</i> L.
	Class Magnoliopsida	
	Basal Angiosperms	
24	Annonaceae	<i>Cananga odorata</i> (Lam.) Hook. f. & Thomson
		<i>Polyalthia lateriflora</i> Kurz
25	Hernandiaceae	<i>Hernandia ovigera</i> L.
26	Lauraceae	<i>Alseodaphne borneensis</i> Gamble
		<i>Cinnamomum celebicum</i> Miq.
		<i>Litsea cordata</i> Hook.f.
27	Myristicaceae	<i>Myristica koordersii</i> Warb.
		<i>Myristica malaccensis</i> Hook. f.
28	Piperaceae	<i>Piper abbreviatum</i> Opiz
		<i>Piper amboinense</i> C. DC.
		<i>Piper betle</i> L.
		<i>Piper caninum</i> Blume
		<i>Piper cf. bantamense</i> Blume
		<i>Piper fragile</i> Benth.
	Monocotyledons	
29	Amaryllidaceae	<i>Crinum asiaticum</i> L.
30	Araceae	<i>Alocasia cf. balgooyi</i> A. Hay
		<i>Amorphophallus</i> sp.
		<i>Pothos cylindricus</i> C. Presl.
		<i>Pothos scandens</i> L.
		<i>Rhaphidophora cf. koordersii</i> Engl.
		<i>Rhaphidophora korthalsii</i> Schott
31	Asparagaceae	<i>Dracaena angustifolia</i> (Medik.) Roxb.
32	Cyperaceae	<i>Cyperus kyllingia</i> Endl.
33	Commelinaceae	<i>Commelina diffusa</i> Burm. f.
34	Dioscoreaceae	<i>Dioscorea cf. pyrifolia</i> Kunth
		<i>Dioscorea hispida</i> Dennst.
35	Flagellariaceae	<i>Flagellaria indica</i> L.
36	Graminae	<i>Apluda mutica</i> L.
		<i>Cenchrus brownii</i> Roem. & Schult.

Table 2. Vascular plant species recorded in Lambusango Forest and the surrounding area (continued)

No.	Class/ Family	Species
		<i>Coix lacryma-jobi</i> L.
		<i>Cynodon dactylon</i> (L.) Pers.
		<i>Dactyloctenium aegyptium</i> (L.) Willd.
		<i>Digitaria ciliaris</i> (Retz.) Koeler
		<i>Eleusine indica</i> (L.) Gaertn.
		<i>Eragrostis tenella</i> Roem. & Schult.
		<i>Imperata cylindrica</i> (L.) P. Beauv.
		<i>Oplismenus compositus</i> (L.) P. Beauv.
		<i>Polytrias amauroa</i> Kuntze
		<i>Saccharum spontaneum</i> L.
		<i>Setaria palmifolia</i> Stapf
		<i>Sorghum propinquum</i> (Kunth) Hitchc.
37	Marantaceae	<i>Donax canniformis</i> K. Schum.
38	Orchidaceae	<i>Bulbophyllum flabellum-veneris</i> (J. Koenig) Aver.
		<i>Calanthe millikenii</i> P. J. Cribb
		<i>Trichoglottis geminata</i> J. J. Sm.
39	Palmae*	<i>Areca catechu</i> L.
		<i>Arenga pinnata</i> (Wurmb) Merr.
		<i>Areca vestiaria</i> Giseke
		<i>Calamus koordersianus</i> Becc.
		<i>Calamus leiocaulis</i> Becc. ex K. Heyne
		<i>Calamus leptostachys</i> Becc. ex K. Heyne
		<i>Calamus macrosphaerion</i> Becc.
		<i>Calamus minahassae</i> Warb. ex Becc.
		<i>Calamus mindorensis</i> Becc.
		<i>Calamus ornatus</i> Blume var. <i>ornatus</i>
		<i>Calamus pachystachys</i> Warb. ex Becc.
		<i>Calamus paucijugus</i> Becc. ex K. Heyne
		<i>Calamus pedicellatus</i> Becc. ex K. Heyne
		<i>Calamus robinsonianus</i> Becc.
		<i>Calamus siphonopathus</i> Mart. var. <i>dransfieldii</i> Baja-Lapis
		<i>Calamus suaveolens</i> W.J.Baker & J. Dransf.
		<i>Calamus subinermis</i> H.Wendl. ex Becc.
		<i>Calamus symphysipus</i> Mart.
		<i>Calamus zollingeri</i> Becc.
		<i>Calamus</i> L. spp.
		<i>Caryota mitis</i> Lour.
		<i>Corypha utan</i> Lam.
		<i>Daemonorops robusta</i> Warb. ex Becc.
		<i>Hydriastele selebica</i> (Becc.) W. J. Baker & Loo
		<i>Licuala celebica</i> Miq.
		<i>Nypa fruticans</i> Wurmb
		<i>Oncosperma horridum</i> (Griff.) Scheff.

Table 2. Vascular plant species recorded in Lambusango Forest and the surrounding area (continued)

No.	Class/ Family	Species
		<i>Pinanga rumphiana</i> (Mart.) J. Dransf. & Govaerts
		<i>Saribus rotundifolius</i> (Lam.) Blume
40	Pandanaceae	<i>Freycinetia</i> cf. <i>devriesi</i> Solms
		<i>Freycinetia</i> cf. <i>funicularis</i> Merr.
		<i>Pandanus</i> cf. <i>borneensis</i> Warb.
	Eudicotyledons	
41	Acanthaceae	<i>Acanthus ebracteatus</i> Vahl
		<i>Andrographis paniculata</i> Nees
42	Achariaceae	<i>Pangium edule</i> Reinw.
43	Anacardiaceae	<i>Buchanania arborescens</i> Blume
		<i>Buchanania sessilifolia</i> Blume
		<i>Dracontomelon dao</i> (Blanco) Merr. & Rolfe
		<i>Koordersiodendron pinnatum</i> Merr.
		<i>Semecarpus</i> cf. <i>cuneiformis</i> Blanco
		<i>Spondias pinnata</i> (L. f.) Kurz
44	Apocynaceae	<i>Alstonia macrophylla</i> Wall.
		<i>Alstonia scholaris</i> (L.) R. Br. var. <i>velutina</i>
		<i>Dischidia nummularia</i> R. Br.
		<i>Hoya diversifolia</i> Blume
		<i>Tabernaemontana macrocarpa</i> Jack
45	Araliaceae	<i>Arthrophyllum</i> sp.
46	Balanophoraceae	<i>Balanophora fungosa</i> J. R. Forst. & G. Forst.
47	Balsaminaceae	<i>Impatiens platypetala</i> Lindl.
48	Burseraceae	<i>Canarium asperum</i> Benth.
		<i>Canarium</i> cf. <i>balsamiferum</i> Willd.
49	Calophyllaceae	<i>Calophyllum inophyllum</i> L.
		<i>Calophyllum soulattri</i> Burm. ex F. Mull.
50	Capparaceae	<i>Crateva religiosa</i> G. Forst.
51	Casuarinaceae	<i>Gymnostoma sumatranum</i> (Jung. ex deVriese) L.A.S. Johnson
52	Combretaceae	<i>Terminalia copelandii</i> Elmer
53	Compositae	<i>Ageratum conyzoides</i> L.
		<i>Blumea balsamifera</i> DC.
		<i>Chromolaena odorata</i> (L.) R. M. King & Rob.
		<i>Emilia sonchifolia</i> (L.) DC.
		<i>Erechtites valerianifolius</i> (Wolf) DC.
		<i>Erigeron sumatrensis</i> Retz.
		<i>Gynura procumbens</i> Merr.
		<i>Pluchea indica</i> (L.) Less.
		<i>Synedrella nodiflora</i> Gaertn.
		<i>Tridax procumbens</i> L.
		<i>Vernonia cinerea</i> (L.) Less.
54	Convolvulaceae	<i>Ipomoea aquatica</i> Forssk.
		<i>Ipomoea hederifolia</i> L.
		<i>Ipomoea pes-caprae</i> (L.) R. Br.
		<i>Merremia peltata</i> Merr.

Table 2. Vascular plant species recorded in Lambusango Forest and the surrounding area (continued)

No.	Class/ Family	Species
55	Cucurbitaceae	<i>Gymnopetalum cochinchinense</i> Kurz <i>Indomelothria</i> W. J. de Wilde & Duyfjes sp.
56	Datisceae	<i>Tetrameles nudiflora</i> R. Br.
57	Dilleniaceae	<i>Dillenia serrata</i> Thunb.
58	Ebenaceae	<i>Diospyros</i> aff. <i>lanceifolia</i> Roxb. <i>Diospyros malabarica</i> Kostel.
59	Elaeocarpaceae	<i>Elaeocarpus angustifolius</i> Blume
60	Euphorbiaceae	<i>Cleistanthus oblongifolius</i> (Roxb.) M. A. <i>Macaranga</i> cf. <i>grandifolia</i> Merr. <i>Macaranga gigantea</i> Müll. Arg. <i>Macaranga tanarius</i> Müll. Arg. <i>Mallotus floribundus</i> Müll. Arg. <i>Phyllanthus niruri</i> L.
61	Fagaceae	<i>Castanopsis buruana</i> Miq. <i>Lithocarpus celebicus</i> Rehder
62	Goodeniaceae	<i>Scaevola sericea</i> Vahl
63	Icacinaceae	<i>Iodes cirrhosa</i> Turcz. <i>Phytocrene hirsuta</i> Blume
64	Lamiaceae	<i>Clerodendrum paniculatum</i> L. <i>Hyptis capitata</i> Jacq. <i>Lantana camara</i> L. <i>Premna serratifolia</i> L. <i>Stachytarpheta jamaicensis</i> (L.) Vahl <i>Vitex cofassus</i> Reinw. ex Blume <i>Vitex quinata</i> F.N. Williams
65	Lecythidaceae	<i>Barringtonia</i> aff. <i>pendula</i> Kurz <i>Barringtonia racemosa</i> (L.) Spreng. <i>Planchonia valida</i> Blume
66	Leguminosae	<i>Albizia lebbeck</i> (L.) Benth. <i>Clitoria ternatea</i> L. <i>Cynometra cauliflora</i> L. <i>Entada</i> Adans. spp. <i>Erythrina subumbrans</i> Merr. <i>Erythrina variegata</i> L. <i>Flemingia strobilifera</i> (L.) W.T. Aiton <i>Inocarpus fagiferus</i> (Parkinson) Fosberg <i>Intsia palembanica</i> Miq. <i>Mimosa pudica</i> L. <i>Mucuna</i> sp. <i>Mucuna pruriens</i> (L.) DC. <i>Parkia sumatrana</i> Miq. <i>Pterocarpus indicus</i> Willd. <i>Senna alata</i> (L.) Roxb. <i>Vigna marina</i> Merr.

Table 2. Vascular plant species recorded in Lambusango Forest and the surrounding area (continued)

No.	Class/ Family	Species
67	Loganiaceae	<i>Strychnos axillaris</i> Colebr.
68	Lythraceae	<i>Duabanga moluccana</i> Blume
69	Malvaceae	<i>Bombax ceiba</i> L. <i>Grewia glabra</i> Blume <i>Heritiera littoralis</i> Aiton <i>Heritiera trifoliolata</i> (F.Muell.) Kosterm. <i>Hibiscus tiliaceus</i> L. <i>Kleinhovia hospita</i> L. <i>Microcos paniculata</i> L. <i>Pterocymbium javanicum</i> R.Br. <i>Pterospermum celebicum</i> Miq. <i>Pterospermum diversifolium</i> Blume <i>Sterculia longifolia</i> Vent. <i>Sterculia macrophylla</i> Vent. <i>Urena lobata</i> L.
70	Melastomataceae	<i>Melastoma malabathricum</i> L.
71	Meliaceae	<i>Aglaia odoratissima</i> Blume <i>Chisocheton kingii</i> Harms <i>Dysoxylum arborescens</i> Miq. <i>Xylocarpus granatum</i> Koen.
72	Menispermaceae	<i>Arcangelisia flava</i> Merr. <i>Pycnarrhena tumefacta</i> Miers <i>Tinospora crispa</i> (L.) Hook.f. & Thomson
73	Moraceae	<i>Artocarpus elasticus</i> Reinw. <i>Artocarpus heterophyllus</i> Lam. <i>Ficus adenosperma</i> Miq. <i>Ficus benjamina</i> L. <i>Ficus botryocarpa</i> Miq. <i>Ficus callophylla</i> Blume <i>Ficus caulocarpa</i> (Miq.) Miq. <i>Ficus chrysolepis</i> Miq. subsp. <i>chrysolepis</i> <i>Ficus congesta</i> Roxb. var. <i>menadana</i> (Miq.) Corner <i>Ficus cordatula</i> Merr. <i>Ficus crassiramea</i> (Miq.) Miq. subsp. <i>crassiramea</i> <i>Ficus disticha</i> Blume subsp. <i>disticha</i> <i>Ficus drupacea</i> Thunb. <i>Ficus fistulosa</i> Reinw. ex Blume <i>Ficus glandifera</i> Summerh. <i>Ficus gul</i> K.Schum. & Lauterb. <i>Ficus heteropleura</i> Blume <i>Ficus hispida</i> L.f. <i>Ficus hombroniana</i> Corner var. <i>madhucifolia</i> <i>Ficus lawesii</i> King <i>Ficus lepigarpa</i> Blume <i>Ficus magnoliifolia</i> Blume

Table 2. Vascular plant species recorded in Lambusango Forest and the surrounding area (continued)

No.	Class/ Family	Species
		<i>Ficus microcarpa</i> L. f.
		<i>Ficus nervosa</i> Roth. subsp. <i>pubinervis</i> (Blume) C.C. Berg
		<i>Ficus pisifera</i> Wall. ex Voigt
		<i>Ficus prasinicarpa</i> Elmer ex C.C. Berg
		<i>Ficus racemosa</i> L.
		<i>Ficus recurva</i> Blume var. <i>urnigera</i> (Miq.) King
		<i>Ficus riedelii</i> Teijsm. ex Miq.
		<i>Ficus septica</i> Burm. f.
		<i>Ficus sumatrana</i> (Miq.) Miq.
		<i>Ficus tinctoria</i> G. Forst. subsp. <i>gibbosa</i> (Blume) Corner
		<i>Ficus variegata</i> Blume var. <i>sycomoroides</i> (Miq.) Corner
		<i>Ficus variegata</i> Blume var. <i>variegata</i>
		<i>Ficus variegata</i> Blume var. <i>viridicarpa</i> Corner
		<i>Ficus virens</i> Aiton
74	Myrtaceae	<i>Syzygium zeylanicum</i> (L.) DC.
		<i>Syzygium zollingerianum</i> (Miq.) Amshoff
		<i>Xanthostemon petiolatus</i> (Valeton) Peter G. Wilson
75	Oleaceae	<i>Chionanthus montanus</i> Blume
76	Oxalidaceae	<i>Averrhoa carambola</i> L.
77	Passifloraceae	<i>Passiflora foetida</i> L.
78	Proteaceae	<i>Macadamia hildebrandtii</i> Steenis
79	Ranunculaceae	<i>Naravelia laurifolia</i> Wall. ex Hook. f. & Thomson
80	Rhizophoraceae	<i>Bruguiera gymnorhiza</i> (L.) Lam.
		<i>Rhizophora apiculata</i> Blume
		<i>Rhizophora mucronata</i> Lam.
		<i>Sonneratia ovata</i> Backer
81	Rubiaceae	<i>Borreria laevicaulis</i> Ridl.
		<i>Hydnophytum formicarum</i> Jack
		<i>Hymenodictyon horsfieldii</i> Miq.
		<i>Ixora</i> sp.
		<i>Morinda citrifolia</i> L.
		<i>Myrmecodia tuberosa</i> Jack var. <i>bullosa</i>
		<i>Myrmeconuclea</i> cf. <i>stipulacea</i> Ridsdale
		<i>Nauclea orientalis</i> (L.) L.
		<i>Neolamarckia cadamba</i> (Roxb.) Bosser
		<i>Neolamarckia macrophylla</i> (Roxb.) Bosser
		<i>Neonauclea calycina</i> (Bartl. ex DC.) Merr.
		<i>Neonauclea</i> cf. <i>haviglandii</i> Koord. ex Ridsdale
		<i>Pavetta</i> cf. <i>montana</i> Reinw. ex Blume
82	Sabiaceae	<i>Meliosma sumatrana</i> (Jack) Walp.
83	Salicaceae	<i>Homalium foetidum</i> Benth.

Table 2. Vascular plant species recorded in Lambusango Forest and the surrounding area (continued)

No.	Class/ Family	Species
84	Sapindaceae	<i>Dimocarpus dentatus</i> Meijer ex Leenh. <i>Lepisanthes cf. rubiginosa</i> (Roxb.) Leenh. <i>Lepisanthes tetraphylla</i> Radlk. <i>Pometia pinnata</i> J. R. Forst. & G. Forst. <i>Schleichera oleosa</i> (Lour.) Oken <i>Madhuca betis</i> (Blanco) J.F. Macbr. <i>Palaquium obovatum</i> (Griff.) Engl. <i>Palaquium obtusifolium</i> Burck. <i>Planchonella duclitan</i> (Blanco) Bakh.f. <i>Planchonella obovata</i> (R.Br.) Pierre
85	Solanaceae	<i>Solanum ferox</i> L.
86	Thymelaeaceae	<i>Phaleria capitata</i> Jack
87	Ulmaceae	<i>Trema orientalis</i> Blume
88	Urticaceae	<i>Dendrocnide oblanceolata</i> (Merr.) Chew <i>Dendrocnide sinuata</i> (Blume) Chew <i>Dendrocnide stimulans</i> (L.f.) Chew <i>Poikilospermum suaveolens</i> (Blume) Merr.
89	Vitaceae	<i>Cissus</i> sp. <i>Leea aculeata</i> Blume <i>Leea angulata</i> Korth. ex Miq. <i>Tetrastigma cf. pedunculare</i> Planch. <i>Tetrastigma lanceolarium</i> Planch.

Small trees and shrubs commonly found in the understorey include *Caryota mitis*, *Cleistanthus oblongifolius*, *Dysoxylum arborescens*, *Leea aculeata* and *L. angulata*, *Phaleria capitata* and *Pinanga rumphiana*. Where water and organic matter can accumulate a characteristic plant is a species of *Pandanus*, possibly *P. borneensis*, which forms one of the tallest elements of the understorey when well grown.

Certain species of tree are valued for their timber by local people. The best timber comes from *Vitex cofassus*, *Intsia palembanica*, *Pterocarpus indicus* and *Madhuca betis*. Other species appreciated for their timber include *Dracontomelon dao*, *Homalium foetidum* and various species in family Sapotaceae including *Palaquium obovatum*, *Planchonella duclitan* and *Planchonella obovata*. A few species are valued for specialised and ornamental uses, including *Pterocarpus indicus* and at least one unidentified *Diospyros* species. *Neolamarckia macrophylla* is grown in plantations as a source of planks for fences to keep pigs out of fields. Another species appreciated for a particular use is *Tetrameles nudiflora*, which is used for dug-out canoes.

Root-climbing plants are common, among them two species of *Pothos*, *P. cylindricus* and *P. scandens*, and two species of *Freycinetia*, believed to be *F. devriesii* and *F. funicularis*. Two root-climbing figs, *Ficus disticha* subsp. *disticha* and *F. recurva* var. *urnigera*, are also found. *Rhaphidophora korthalsii* is a plant of more open situations. Species that can be grouped as climbers and lianas include *Hoya diversifolia*, *Dioscorea hispida*, *Flagellaria indica*, *Arcangelisia flava* and *Poikilospermum suaveolens*. The commonest group of climbing plants is the rattans, which have been described by Powl- ing (2009). As a group these can be dominant in places where forest is regenerating but also persist at a lower density in areas of mature forest.

Where significant light penetrates under the normally dense canopy cover various herbaceous plant species are found. The clubmoss *Selaginella plana* is widespread and common, while the fern *Lygodium circinnatum* is common in places. Colourful flowers are rare but include *Impatiens platypetala*, while *Solanum ferox* is distinctive. The root parasite *Balanophora fungosa* is relatively common on both basic and acidic soils.

Table 3. Tree species present in forest on various soils and of various types.

Tree species	Soil Type or Forest Type						
	Calcareous	Riverine	Non-Calc*	Ultrabasic	Chert	Coastal	Secondary
<i>Agathis dammara</i>			×				
<i>Barringtonia racemosa</i>	×	×					
<i>Buchanania arborescens</i>	×						
<i>Castanopsis buruana</i>			×	×	×		
<i>Dillenia serrata</i>	×	×	×				
<i>Dimocarpus dentatus</i>			×				
<i>Dracontomelum dao</i>	×	×					
<i>Duabanga moluccana</i>		×					
<i>Heritiera trifoliata</i>	×						
<i>Inocarpus fagiferus</i>						×	
<i>Lithocarpus celebicus</i>			×				
<i>Macaranga gigantea</i>		×					
<i>Mallotus floribundus</i>							×
<i>Myristica malaccensis</i>	×	×					
<i>Neolamarckia macrophylla</i>	×						×
<i>Parkia sumatrana</i>		×	×				
<i>Palaquium obovatum</i>	×	×					
<i>Planchonia valida</i>	×	×	×				
<i>Pometia pinnata</i>	×	×					
<i>Polyalthia lateriflora</i>	×						
<i>Schleichlera oleosa</i>						×	
<i>Syzygium zeylanicum</i>		×	×	×	×		
<i>Terminalia copelandii</i>		×					
<i>Tetrameles nudiflora</i>	×						
<i>Vitex cofassus</i>	×						
<i>Xanthostemon petiolatus</i>					×		
<i>Xylocarpus granatum</i>						×	

* = Non-calcareous

Grasses are all but absent from areas with substantial canopy cover, but one species found in clearings is *Oplismenus compositus*.

Some conspicuous examples of plant-ant symbioses were observed. Two epiphytic ant plants of the family Rubiaceae were found, *Hydnophytum formaricum* in the forest, and *Myrmecodia tuberosa* on trees near the coast. Another species in the genus Rubiaceae, possibly *Myrmeconuclea stipulacea*, also has a symbiosis with ants. This species has ants living in swollen and hollow sections of its twigs, entering and exiting through small holes. A common epiphytic ant plant on trees in more open areas and in plantations is *Dischidia nummularia*, while a damaged specimen of a fern in the ant-sheltering genus *Lecanopteris* was once found on the forest floor after it had fallen. These plants gain nitrogenous compounds from the excreta and dead bodies of the ants, and the ants also defend the plants against herbivores (Primack & Corlett, 2005).

Many epiphytic orchids were seen but only two were found in flower and therefore identified: *Trichoglottis geminata* and *Bulbophyllum flabellum-veneris*. Two species of fern are very common as epiphytes; *Asplenium nidus* grows in areas of forest with dense canopy cover, whilst *Drynaria sparsisora* tends to occur where the canopy is sparser, so light levels are higher and presumably the humidity lower. *Microsorium punctatum* is also a common epiphytic fern, one that superficially resembles *A. nidus*. Some epiphytic species have been observed growing from the 'bird's nests' of *A. nidus*, among them the club moss *Huperzia phlegmaria* and, once, the fern *Ophioglossum pendulum*, but this latter species appears to be rare. Stag's horn ferns (*Platynerium* Desv.) have not been observed on Buton. Common epiphytes on trunks include *Pyrrosia longifolia* and *Pyrrosia piloselloides*. Species of the forest floor that scramble up tree trunks include *Stenochlaena palustris*, *Teratophyllum aculeatum* and *Lygodium circinatum*. *Phymatosorus scolopendria* is found growing on tree trunks but is also found on rocks which are exposed and often dry. A species of open areas that can be common in forest clearings with exposed rock and sparse soil is *Pteris tripartita*.

Forest on non-calcareous, acidic, rocks

A small number of tree species are very characteristic of forests on acidic soils derived from sandstone, siltstone and conglomerate rocks. *Castanopsis buruana* is common in places and its

typical form, with many suckers encircling the main trunk, is a clear marker for sandy, acidic soils. It is found at altitudes of 350 m and above. *Lithocarpus celebicus* is found on similar soils, although at higher altitudes (500-600 m). It can be abundant in areas with sandy soil of low pH and low conductivity. Other species found frequently on acidic soils include *Dillenia serrata* and *Dimocarpus dentatus*. Some species, such as *Artocarpus elasticus* and *Barringtonia racemosa*, are like *D. serrata* in that they are able to grow on acidic soils but are also found on other soil types (Table 3). Only one species of conifer was found in the forest, *Agathis dammara* (synonym *A. celebica*). This was a single well grown individual at about 400 m asl.

An understory palm, *Licuala celebica*, is often found growing on acidic soils and in places can be very frequent. Another palm species, *Oncosperma horridum*, is less common.

In areas of acidic, nutrient-poor soils the canopy is usually lower and thinner than on limestone soils. In these places *Drynaria sparsisora* is the most common epiphytic fern, although *Asplenium nidus* is still found in darker and damper places, such as river valleys. A characteristic fern of tree trunks is *Davallia denticulata*. The forest floor in clearings caused by human activities and in other areas of high light intensity can be dominated by *Dicranopteris linearis*, in combination with *Pteridium aquilinum* (*sensu lato*) in places. Indeed, the presence of *D. linearis* serves as a good indicator that the soil is acidic. Steep slopes with unstable soil can be covered with *Sticherus truncatus*. A species of *Lindsaea*, probably *L. lucida*, occurs on ground with little cover, often in the shelter of exposed tree roots. Other forest floor species on thin acidic soils include *Lycopodiella cernua*, *Schizaea digitata* and *S. dichotoma*, whilst on deeper soils *Pleocnemia irregularis* occurs. Two species of tree fern were found at altitudes varying between 400 to 600 m asl., *Cyathea contaminans* and a species with affinities to *C. roroka*.

In the west of the forest are steep slopes of exposed igneous rock (J. Milsom, *pers. comm*) with pockets of thin soil. Vegetation is sparse on these slopes but one tree species is dominant in very exposed places, *Gymnostoma sumatrana*, where it forms apparently permanent stands. This species gives a completely different, more open, character to the forest. The palm *Hydriastele celebica* grows in more sheltered places on these slopes, while the rattan *Calamus koordersianus* grows widely, including on rocky, exposed terrain.

Forest on chert ridges

In the east of the forest are some ridges formed from chert (J. Milsom, *pers. comm.*). These can have steeply sloped or horizontal crests, but always have thin soils which are very acidic (Table 1) and must be very drought prone. They have characteristic vegetation made up of a limited number of species, in some ways analogous to heath forest in other parts of SE Asia. Very common on the higher parts of the steep ridges and on the horizontal crests are *Syzygium zeylanicum*, a small tree with small, hard leaves and characteristic red, flaking bark; and the palm *Hydriastele selebica*. Lower down on these ridges, where there is more moisture in the soils, are found two other palms, *Areca vestiaria* and *Licuala celebica*, although these two species are widespread on acidic soils and not confined to chert ridge habitats. On the crests of horizontal ridges are very large specimens of *Xanthostemon petiolatus*, which must be able to get their roots into lower levels of the rocks where there is sufficient water. These large trees produce valuable timber but their remote locations save them from felling, due to the difficulty of carrying the timber out of the forest. The small tree fern *Cyathea moluccana* is common on the very exposed crests of these ridges, where the soil is evidently thin and fast drying. *Lycopodiella cernua* and *Schizaea dichotoma* are also found on the ridges.

Forest on ultrabasic (ultramafic) soils

Forest on ultrabasic soil is made up of small trees, their growth restricted by the general lack of mineral nutrients and the presence of elements which inhibit plant growth, such as nickel. Identifying tree species in these forests presents problems, due to the stunted growth. There is also the possibility that some plants present, having evolved to grow on ultrabasic soils, might be better considered as new species.

Among the restricted range of tree species present are some also able to grow on the nutrient-poor sandstone soils, such as *Castanopsis buruana* and *Syzygium zeylanicum*. Some other species present are also found on calcareous soils, for example *Syzygium zollingerianum* and a species in the family Rubiaceae believed to be *Neonauclea calycina*. Another species present that is very widespread on different soil types is *Dillenia serrata*. The palm *Saribus rotundifolius* is found here but not restricted to such areas. A species of tree fern, probably *Cyathea elmeri*, appeared to be limited to ultrabasic soils, while *Lycopodiella*

cernua and a species of *Nephrolepis*, possibly *N. biserrata*, are common in places.

River valleys

River valleys can be divided into two general types: steep-sided valleys with densely vegetated alluvial soils which must sometimes flood; and more open valleys with larger rivers which have areas of incompletely vegetated stone and gravel deposits. These two types of valley have differing plant species and will be treated separately.

Due to the abundance of calcium carbonate containing rocks, water in rivers is often alkaline (pH > 7.0) even if the rocks in the area it is flowing through are acidic in nature. This is shown by the presence of tufa (calcium carbonate) dams on the river bed.

Steep sided river valleys contain some of the tallest trees in the forest. These include *Terminalia copelandii*, which grows with its roots in the river water, and *Parkia sumatrana*, growing on more acidic alluvial soils in regions of sandstone and conglomerate rocks. Many species are common on river alluvium, but not confined to it. These include *Barringtonia racemosa*, *Calophyllum soulattri*, *Crateva religiosa*, *Hernandia ovigera*, *Macaranga gigantea*, *Myristica malaccensis*, *Oncosperma horridum*, *Pangium edule* and *Pometia pinnata*. Valleys with dense canopy cover are also the habitat of large lianas of the genus *Entada*, and the epiphytic fern *Asplenium nidus* is common as well.

River valleys and areas of wet soil can have large patches of ground covered by *Donax canniformis*, and a species of *Alocasia*, thought to be *A. balgooyi*, also occurs in such habitats. Some flowering plants of the ground orchid *Calanthe millikenii* were seen in 2008, but not in other years. Among the many ferns found in valleys *Angiopteris evecta* occurs rarely on the sides of deep river valleys, whereas *Aspidium crenatus* occurs on flatter alluvial areas. *Tectaria crenata* grows as a rheophyte on the rocky beds of rivers, where it is frequently inundated but sometimes common.

The gravel and boulder banks of faster flowing rivers in open valleys form an unstable substrate for plant growth, so it is to be expected that many species found are pioneers in the ecological sense. Many probably need the open, disturbed habitat rather than the river water. Small trees that can establish near the river edge include *Duabanga moluccana* and *Microcos paniculata*, whilst *Terminalia copelandii* and *Macaranga gigantea* are found in more stable areas. Smaller plants include *Mucuna pruriens* and *Flemingia strobilifera*.

The grass *Saccharum spontaneum* forms large clumps and is probably one of the first species to colonise bare shingle and gravel. The fern *Pteris moluccana* is also found in this habitat. Open, stony river valleys are possibly the only natural habitat in the forest that has been colonised by non-native plants brought to Buton by people. Species of this type which are present include *Lantana camara*, *Senna alata* and *Chromolaena odorata*. These are colonising species that benefit from the high light levels and lack of established competition.

Mangroves and coastal forest

The main species of mangrove include *Bruguiera gymnorhiza*, *Rhizophora apiculata*, *R. mucronata* and *Sonneratia ovata*. Behind the mangroves and the *Nypa fruticans*, in the forest surrounding tidal creeks, tree species include *Inocarpus fagifer*, *Schleichera oleosa* and *Xylocarpus granatum*. Also present is *Heritiera littoralis*, a species which, perhaps surprisingly given the size of its fruits, occurs in nearby forest on limestone about 100-200 m asl. The fern *Acrostichum aureum* grows in brackish water and the epiphytic ant-plant *Myrmecodia tuberosa* was found in trees, both just behind beaches. Dry, sandy ground can be covered by *Ipomoea pes-caprae* and *Vigna marina*.

No clear examples of the 'Barringtonia' or the 'pes caprae' formations (Whitten *et al.*, 2002) were found. This was probably due to few coastal areas being investigated and also because those coastal areas that were accessed had been extensively altered by people. Individual species characteristic of the formations were found, however, and examples most probably exist around the Lambusango Forest. The 'pes caprae' formation is found on the nearby island of Hoga in the Wakatobi peninsula, off the south east coast of Buton.

Cleared areas and secondary forests

Around the edge of Lambusango Forest ground has been cleared at various times for plantations and arable fields. Many are still in use but some have been abandoned and are in various stages of reversion to forest. Within the continuous forest are many areas where habitations were abandoned in the late 1970s and early 1980s and which are now regenerating and can be classified as secondary forest. The road running around edge of the forest actually passes through dense forest between the north of Lambusango and the smaller Kakenauwe reserve. Various plants of secondary

forests grow on these verges, many of which have been introduced from other places in the tropics, mainly herbaceous plants ("weeds"), including many of the members of the families Graminae and Compositae listed in Table 2. *Imperata cylindrica* is a common grass of open, man-made habitats. *Ipomoea aquatica* grows in wetter areas, whilst *Ipomoea pes-caprae* can appear in more ruderal, human-dominated habitats.

Two species of fern can be common and even dominant on cleared and steep soils, particularly the sides of road cuttings: *Nephrolepis hirsutula* and *Cyclosorus callosus*. Plants of a mid stage of succession in fields include *Blumea balsamifera*, while cleared areas in full sun are often dominated by the introduced species *Lantana camara* and *Eupatorium odoratum*. These species normally cover ground densely and must retard the progress of succession back to forest. Small trees of regenerating habitats include species of *Macaranga* and *Mallotus*, with *Neolamarckia macrophylla* and other members of the family Rubiaceae soon appearing as well.

No examples of deliberate forest regeneration for nature conservation are known, but some small-scale plantations of trees, mainly *Tectona grandis*, *Gmelina arborea* and *Vitex cofassus*, have been started for timber production on abandoned farm land.

Two species-rich genera: *Calamus* and *Ficus*

Table 2 shows that more species were found in the genera *Calamus* (16 identified species, also at least two unidentified species) and *Ficus* (29 identified species) than in other genera.

Palms, including *Calamus*, have been covered in a separate publication (Powling, 2009). Nineteen species of rattan have been found in Lambusango Forest and at least two more (one being *Korthalsia celebica*) have been found in northern Buton. A reason for the co-existence of many *Calamus* species is that different species have adapted to different soil types (Table 4); so they occupy many different ecological niches, reducing the competition between them. Some are colonising species adapted to the high light levels in areas cleared and abandoned by humans. Such species include *C. zollingeri* and *C. ornatus*. Other species are better able to persist in places with dense tree cover, where the lack of light prevents fast-growing pioneer species dominating, for example *C. mindorensis* and *C. leptostachys* among many others.

The most common genus is *Ficus*, the figs. Species of fig were found in a wide variety of

Table 4. Palm species present in forest on various soil types.

Tree species	Soil Type			
	Calcareous	Non-Calc*	Ultrabasic	Chert
<i>Areca vestiaria</i>		×		×
<i>Calamus koordersianus</i>		×	×	×
<i>Calamus leptostachys</i>	×	×		
<i>Calamus macrosphaerion</i>		×		
<i>Calamus minahassae</i>	×	×	×	
<i>Calamus mindorensis</i>	×	×		
<i>Calamus ornatus</i>	×	×	×	
<i>Calamus pedicellatus</i>		×	×	×
<i>Calamus siphonospathus</i>	×		×	
<i>Calamus suaveolens</i>				×
<i>Calamus subinermis</i>	×	×		
<i>Calamus symphysipus</i>	×	×		
<i>Calamus zollingeri</i>	×	×	×	
<i>Caryota mitis</i>	×	×	×	
<i>Hydriastele selebica</i>		×		×
<i>Oncosperma horridum</i>		×		
<i>Pinanga rumphiana</i>	×	×	×	
<i>Saribus rotundifolius</i>		×	×	

* = Non-calcareous

habitats, including mature forest, secondary forest, roadsides, riversides and abandoned fields. A range of growth forms are present: free-standing canopy trees (8 species), small trees or shrubs (5 species), hemi-epiphytes (*i.e.* strangler figs, 14 species) and root-climbers (2 species). Position of syconia varied in the different species, from among the foliage (ramiflorous), to on the trunks (cauliflorous) and in the ground (geocarpic). In all, 29 species were recorded in Lambusango forest and its environs (roadsides and areas associated with farming). In addition, two further species were found on the nearby coral island of Hoga (*Ficus hombroniana* and *F. prasinicarpa*) and another species (*F. lepigarpa*) was found in forest in northern Buton near Ereke. These three species may also be present in Lambusango. It is probable that other fig species occur in Lambusango which were not recorded. In particular, root climbing epiphytes were probably under-recorded due to the limited amount of canopy surveying done during this work. Fig species were particularly diverse in areas with calcareous soils, presumably due to these soils providing relatively high levels of mineral nutrients. It is known that figs grow best on fertile soils, since their high assimilation rates and production of latex to protect against herbivores require such soils (Harrison, 2005). Another factor relevant to the high diversity of fig species is the reluctance, for cultural reasons, of local people to cut down fig trees (N. Priston, *pers. comm.*). Reasons for such reluctance are discussed by Berg and Corner (2005).

The different subgenera of *Ficus* were not equally represented in the species found. Table 5 shows the subgenera recognised by Berg and Corner (2005) and their breeding system (monoecious or dioecious). Also shown are the numbers of species in the subgenera identified in Lambusango, the numbers of species known from Sulawesi (Berg & Corner, 2005) and the proportion of Lambusango species as a percentage of Sulawesi species. The percentage figures vary considerably between subgenera, from 0% for subgenus *Ficus* to 67% for subgenus *Urostigma*.

Although the totals for the numbers of Lambusango species with the different breeding systems are similar, the percentage of monoecious species (58%) is considerably higher than the percentage of dioecious (26%). If the *Ficus* species found in northern Buton and the two found on Hoga (referred to earlier) together with the three separate varieties of *F. variegata* are included in the analysis the percentages show a similar discrepancy (65% for monoecious and 32% for dioecious). However, the difference in the proportions of the two breeding types present in Lambusango relative to the numbers in Sulawesi is barely statistically significant (goodness-of-fit chi-square test with Yates correction factor, degrees of freedom = 1, P = 0.050). Little of biological significance can be assumed from this statistical result since the addition of one more dioecious species would have given a non-significant probability value.

The apparent lack of dioecious species in

Table 5. Analysis of *Ficus* subgenera present on Buton and Sulawesi by breeding system.

Subgenus	Breeding system*	Buton species	Sulawesi species*	Percentage
<i>Ficus</i>	Dioecious	0	9	0
<i>Pharmacosycea</i>	Monoecious	2	7	29
<i>Sycidium</i>	Dioecious	5	22	23
<i>Sycomorus</i>	Monoecious	1	1	100
<i>Sycomorus</i>	Dioecious	7	16	44
<i>Synoecia</i>	Dioecious	2	6	33
<i>Urostigma</i>	Monoecious	12	18	67
Totals	Monoecious	15	26	58
	Dioecious	14	53	26

*Information from Berg & Corner (2005)

Lambusango may be a result of not finding all the root climbers in the subgenus *Synoecia*, due to lack of work in the canopy. Alternatively, the apparent excess of monoecious species can be attributed to the high proportion of species in subgenus *Urostigma* that are present. This might result from some aspect of their biology other than monoecy, such as the relatively small sizes of their syconia making them easily taken by flying animals which then disperse the seeds.

DISCUSSION

Many plants of Lambusango Forest belong to pan-tropical families, including Annonaceae, Euphorbiaceae, Leguminosae, Meliaceae, Moraceae, Myristicaceae, Palmae, Rubiaceae and Sapotaceae. These families are characteristic of SE Asian forests (Primack & Corlett, 2005). Genera and species of these families found to the east of Wallace's line are considered to have mostly or entirely colonised from the west (Primack & Corlett, 2005). The predominance of Asian families and genera is due to plants of these taxa being able to successfully colonise Wallacea across the relatively narrow water gaps from Asia and between the islands—tens of km, at least at times of low sea levels during the Pleistocene ice ages. Another possible reason for the predominance has been suggested by Morley (2003), namely that the south western arm of Sulawesi was attached to Borneo in the middle Miocene before moving to its present position. Flora on the arm would then have been able to colonise eastwards without having to cross Wallace's Line.

A few genera are considered to have colonised from the Australasian continent after it started to collide with the Philippine plate at the Oligocene-Miocene boundary (Morley, 2003), *e.g.* *Agathis* in Araucariaceae, *Gymnostoma* in Casuarinaceae, *Macadamia* in Proteaceae and *Xanthostemon* in

Myrtaceae. These genera are all represented by one species only. The Australasian continent, having moved northwards through temperate latitudes, did not have as many plant species adapted to tropical climates as Asia and therefore able to colonise lowland rain forests in Wallacea and compete with the Asian taxa (Primack & Corlett, 2005).

Lambusango Forest differs from typical SE Asian forests in the apparently complete lack of species of the family Dipterocarpaceae. This is due to two factors: the low number (six) of dipterocarp species that are present on Sulawesi (Keßler *et al.*, 2002) and the seasonal climate of Buton, which would be unsuitable for the many dipterocarp species that have evolved for ever-wet climates.

Of the woody species identified, 174 were checked against the compilation of trees known on the island of Sulawesi published by Keßler *et al.* (2002). This showed that 73% of the Lambusango species are also known to occur on Sulawesi. However, if the known distributions given for *Calamus* by Powling (2009) and for *Ficus* by Berg and Corner (2005) are used instead, then the figure becomes 83% of a total number of 176 species checked. This indicates that Buton can be considered to be a part of Sulawesi floristically, as might be expected given the close proximity and the land connection during the Quaternary ice ages.

Various factors influence the diversity of plants in Lambusango. Diversity is increased by the variable topology, with its flat areas, steep slopes, ridges and deep river valleys. These features produce many different habitats and microhabitats for plants to occupy. Many soil types are present, with their varying pH values, levels of mineral nutrients and water contents during the year, allowing species with different edaphic requirements to grow. Widayati and Carlisle

(2012) showed that tree species diversity in Lambusango increases with slope gradient and altitude, probably because of lower disturbance by humans in higher and steeper places, although steep gradients might also increase the variety of habitats available to trees. The work of Widayati and Carlisle (2012) indicated that soil chemical composition has little effect on tree diversity. The present work made no quantitative comparisons of overall diversity on different soil types, but it was observed that figs were very diverse on calcareous soils. The work showed that some dicotyledonous tree species and some palms (Tables 3 & 4) are restricted to certain soil types whilst others are able to grow on a wide range of soils. It is possible that some of the widespread species have different physiological races which are able to grow on different soil types.

The short dry season on Buton prevents the growth of some species that require an ever-wet climate, *e.g.* some Dipterocarp species. It must also restrict the number of species adapted to a longer dry season. However, the thin, dry soils in parts of Lambusango do permit the existence of some species adapted to a dryer climate, *e.g.* *Alstonia angustifolia*, *Buchanania arborescens* and *Cananga odorata*, which are characteristic of forests with drier, more seasonal climates than experienced by Buton (Whitten *et al.*, 2002). Another factor acting to decrease species diversity on Buton is relative isolation, it being an island off the coast of an island. It is possible that Sulawesi and Buton have experienced repeated loss of diversity during the succession of ice ages over the past two million years, when the climate became colder and dryer (Whitten *et al.*, 2002; De Deckker *et al.*, 2003), leaving few refugia for tropical lowland rainforest species. Local extinctions of species may have occurred but recolonisation not subsequently happened.

Some families and genera may be better able to colonise or recolonise than others, which could account for some genera being much richer in species than others. The two species-rich genera may be examples: *Calamus* (Palmae) with 18 species and *Ficus* (Moraceae) with 29 species (Table 2). Both genera are known to be very species-rich in SE Asia (Dransfield *et al.*, 2008; Berg & Corner, 2005), and their fruits are eaten by frugivorous birds (pigeons, hornbills, etc.) and fruitbats (Corlett, 1998; Shanahan *et al.*, 2001; Zona & Henderson, 1989) capable of flying across the sea from Sulawesi to Buton, carrying seeds in their guts. Species of other genera might be less likely to colonise due to their fruits being less

attractive to birds, on account of colour, nutritional value or size. However, it could be that other genera are more species rich than shown in Table 2, but their species were under-recorded because they received less attention. Possible examples include *Elaeocarpus*, *Macaranga* and *Syzygium*, which are known to be diverse in Borneo and Sulawesi (de Kok & Utteridge, 2010; Keßler *et al.*, 2002).

Only one species of conifer was found in the forest, *Agathis dammara* (syn. *A. celebica*). This was a single well grown individual at about 400 m asl. Species such as *A. dammara*, *Lithocarpus celebicus* and *Castanopsis buruana* occur at altitudes of 400 m to 600 m in Lambusango, although these species are normally components of the lower montane rain forest, which is considered to have a lower altitudinal limit of 1200–1500 m (Whitten *et al.*, 2002). However, on isolated, small mountains the lower limit is 700–900 m (Grubb, 1971). The reduced heights of vegetation zones on outlying mountains, compared with main ranges, is known as the ‘Massenerhebung’ effect, and the low altitudes of the three species mentioned may be an example of this effect. However, it has been reported that *A. dammara* occurs naturally at low altitudes in central Sulawesi, but only at higher altitudes on the peninsulas (Whitten *et al.*, 2002), which is contrary to expectations if the Massenerhebung effect applies. Clearly more information on the distribution of *A. dammara* is needed.

Many alien species flourish in and near the settlements surrounding the forest but few have colonised the intact forest. As noted above, some are able to colonise unstable shingles in open river valleys, but not invade the continuous forest. An introduced species that has become naturalised in the forest is *Areca catechu*, which persists at the sites of deserted settlements. Other non-native species which show some encroachment on the forest edges are *Muntingia calabura* and *Psidium guajava*, although there is little sign that they can naturalise in the continuous forest. Overall there are very few introduced species in the forest, despite the presence of many animals capable of transporting seeds, such as fruit bats, monkeys and pigs, which feed in cultivated land but spend much of their time in the forest. The continuous canopy cover in the forest results in low levels of light on the forest floor and it seems probable that competition for light prevents crop and weed species from establishing. It is noticeable that the three species mentioned above are plants of the forest understorey, so adapted to the lack of light

beneath a forest canopy.

The genus *Ficus*, the figs, was found to be the most species-rich of the plant genera on Buton. This high diversity is not a local phenomenon. There are about 735 fig species worldwide and 367 species in Malesia (Berg & Corner, 2005). Harrison (2005) has observed that *Ficus* is the most diverse genus in plant lists for many sites in the Indo-Pacific and African regions. His explanation is that the figs display evolutionary flexibility and morphological diversity, and have speciated to occupy many different ecological niches, some of which are rare. As a result figs can have a diversity of species in a small forest area, since they do not compete with each other. The variety of growth forms and morphologies of the figs on Buton suggests they do indeed occupy a variety of ecological niches.

As noted before, fig seeds are efficiently dispersed over long distances by birds and bats. A result of this is that a small forest area such as Lambusango might contain a large proportion of the fig species found in a much larger neighbouring area, in this case Sulawesi. In the present work this was found to be the case, with 29 species out of a Sulawesi total of 78 (Berg & Corner, 2005), that is 37%, found in Lambusango. Twelve species in the subgenus of *Urostigma* were present (67% of the Sulawesi total), suggesting species in this subgenus are particularly good colonisers. In addition, species in this subgenus are strangler figs, which must be able to survive dry conditions when they first germinate in the canopy of a host tree. This ability may allow them to survive the seasonally dry conditions in some of the soils of Lambusango.

Figs are pollinated by fig wasps which are often, but not always, species specific. This is a very effective mechanism which combines the advantages of wind pollination, since the wasps can be carried long distances by winds above the canopy, with the ability of insects to find rare individuals of a plant species, by responding to volatile chemicals released by the plant (Cook & Rasplus, 2003). Due to this mechanism pollen is not limited in most fig species in most environments and species are able to persist at low densities of individuals. As a result some figs are able to occupy rare ecological niches which have low competition due to limited recruitment opportunities (Harrison, 2005).

Lambusango Forest persists as a functioning forest ecosystem, with a degree of conservation protection. From an ecological point of view the forest needs to maintain a certain level of

intactness to function successfully as an ecosystem. If forest is lost due to human activities then ecological interactions will start to break down. If hornbills and pigeons were lost then rattan fruit would not be successfully dispersed and there would be less rattan for the local men to harvest. Hunting of animals and birds would result in less fig seed being dispersed and fig populations decreasing, with fewer figs for other forest animals. Indeed, figs have been shown to be 'keystone' species for the forest since so many animals rely on them as a source of food throughout the year (Kinnaird *et al.*, 1999), so loss of figs would cause many further detrimental changes.

The forest edge is under direct threat from human activities, such as encroachment by settlements and loss of peripheral areas to agriculture (Purwanto, 2008), but all the forest is affected to a greater or lesser extent by human actions, since access to the forest is very easy from the communities around the forest edge. Rattan canes are extensively collected by local men (Powling 2009; Widayati *et al.* 2010). Certain tree species, of which the most sought is *Vitex cofassus*, are felled for their timber. This is much in demand for local house and boat building, among other uses. At least one unidentified species of *Diospyros*, ebony, is taken (often illegally) because of the commercial value of the wood. It might be that *Agathis dammara* was once more common but has been extensively logged in the past.

Local people living on the periphery understand the importance of maintaining the forest as a reliable source of water for the rice padi fields on the flood plains of rivers leaving the forest. They also appreciate the forest as a source of rattan cane and honey, the two main non timber forest products. Ecotourism is presently bringing money to the people living near the forest. Their co-operation will be needed if the forest is to survive.

ACKNOWLEDGEMENTS

We thank Operation Wallacea for funding and logistics. We also thank BKSDA South-East Sulawesi for giving us permission to work in the Lambusango Wildlife Sanctuary and the Kakenauwe Nature Reserve. This work was done under a research permit issued by the Indonesian Institute of Sciences (LIPI). Sahimu, Tarahu, Kuseh, Imu and Mesilili, men of Labundo-bundo village, were essential guides in the forest. We thank the following people who have helped us with this work: Nenni Babo, W.J. Baker, D. Blakesley, Tharada

Blakesley, Marie Briggs, Eric Clement, J. Dransfield, Christopher Fraser-Jenkins, Stuart Frost, Graeme Gillespie, Grant Harris, Aelys Humphreys, Rogier de Kok, Rio Kornel, John Milsom, J.P. Moge, Patricia Moss, Titien Ng, Praptosuwiryo, Jean-Yves Rasplus, Alison Richardson, H. Rustiami, A. Schuiteman, D. Seymour, Steve Sudworth, Vicky Tough, T. Utteridge, the late Trevor Walker and Paul Wilkin.

REFERENCES

- BERG, C. C. & CORNER, E. J. H. 2005. Flora Malesiana Series 1 (Seed Plants) .17(2). 733 p.
- COOK, J. M. & RASPLUS, J. Y. 2003. Mutualists with attitude: coevolving fig wasps and figs. *Trends in Ecology and Evolution* 18: 241–248.
- CORLETT, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews* 73: 413–448.
- DE DECKKER, P., TAPPER, N. J. & VAN DER KAARS, S. 2003. The status of the Indo-Pacific warm pool and adjacent land at the last glacial maximum. *Global & Planetary Change* 35: 25–35.
- DE KOK, R. P. J. & UTTERIDGE, T. M. A. 2010. *A Field Guide to the Plants of East Sabah*. Richmond, Kew Publishing.
- DRANSFIELD, J., UHL, N. W., ASMUSSEN-LANGE, C. B., BAKER, W. J., HARLEY, M. H. & LEWIS, C. E. 2008. *Genera Palmarum*. Richmond, Kew Publishing.
- GRUBB, P. J. 1971. Interpretation of the 'Massenerhebung' effect on tropical mountains. *Nature* 229: 44–45.
- HARRISON, R. D. 2005. Figs and the diversity of tropical rainforests. *BioScience* 55(12): 1053–1064.
- KEBLER, P. J. A., BOS, M. M., SIERRA DAZA, S. E. C., KOP, A., WILLEMSE, L. P. M., PITOPANG, R. & GRADSTEIN, S. R. 2002. Checklist of woody plants of Sulawesi, Indonesia. *Blumea Supplement* 14: 1–160.
- KINNAIRD, M. F., O'BRIEN, T. G. & SURYADI, S. 1999. The importance of figs to Sulawesi's imperilled wildlife. *Tropical Biodiversity* 6: 5–18.
- MABBERLEY, D. J. 2008. *Mabberley's Plant Book* (3rd ed.). Cambridge, Cambridge University Press.
- MILSOM, J. 2000. Stratigraphic constraints on suture models for eastern Indonesia. *Journal of Asian Earth Sciences* 18: 761–779.
- MORLEY, R. J. 2003. Interplate dispersal paths for megathermal angiosperms. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 5–20.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION (USA) 2014. http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml
- POWLING, A. 2009. The palms of Buton, Indonesia, an island in Wallacea. *Palms* 52: 84–91.
- PRIMACK, R. & CORLETT, R. 2005. *Tropical Rain Forests*. Oxford, Blackwell Publishing.
- PURWANTO, E. 2008. *Lambusango Forest Conservation Project (LFCP), Southeast Sulawesi, Indonesia – Final Report (December 2008)*. Bau Bau LFCP.
- SHANAHAN, M., HARRISON, R. D., YAMUNA, R., BOEN, W. & THORNTON, I. W. B. 2001. Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. V. Colonization by figs (*Ficus* spp.), their dispersers and pollinators. *Journal of Bio-geography* 28: 1365–1377.
- VORIS, H. K. 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* 27: 1153–1167.
- WHITTEN, T., HENDERSON, G. S. & MUSTAFA, M. 2002. *The Ecology of Sulawesi*. Hong Kong, Periplus Editions (HK) Ltd.
- WIDAYATI, A., JONES, S. & CARLISLE, B. 2010. Accessibility factors and conservation forest designation affecting rattan cane harvesting in Lambusango Forest, Buton, Indonesia. *Human Ecology* 38: 731–746.
- WIDAYATI, A. & CARLISLE, B. 2012. Impacts of rattan cane harvesting on vegetation structure and tree diversity of Conservation Forest in Buton, Indonesia. *Forest Ecology and Management* 266: 206–215.
- WIDAYATI, A., CARLISLE, B., & SOEDRADJAT 2008. Trees of Lambusango Forest (ToLF). http://www.numyspace.co.uk/~unn_szbcl/butontrees/butontrees.html
- ZONA, S. & HENDERSON, A. 1989. A review of animal-mediated seed dispersal of palms. *Selbyana* 11: 6–21.