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Holocene lowland vegetation change and human ecology in Manus Province, Papua New Guinea

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Introduction

This paper concerns evidence for past human impacts on the environment in the lowland tropical New Guinea region. Against a background regional overview, we consider two sequences, one archaeological, the other palaeoecological, from opposite ends of Manus Island, the largest island of the Admiralty Islands that now constitute Manus Province, Papua New Guinea. Contrasts in these local sequences prevent their easy alignment with grand narratives of regional prehistory. We show instead that closer examination of local contexts, especially the nature of agroecosystems, gives useful insights that help to disentangle natural processes of forest vegetation change and the effects of human activities. We consider aspects of the ecology of the tree genus *Calophyllum* L. (Clusiaceae), which occurs in both sequences, to assess the possibility of a human role in the dynamics of forest dominated by *Calophyllum euryphyllum* Lauterb. (Clusiaceae).

I. People and environment in the New Guinea region: An overview

Palaeoecological context

In the New Guinea region, the late-Quaternary environment since humans arrived 40,000-60,000 years ago was affected by altitudinal fluctuations of vegetation zonation in the highlands and sea-level changes around the coasts, both linked to the glacial cycle, with significant changes around the Last Glacial Maximum and less dramatic adjustments consequent on the high-sea-level stand in the mid Holocene.

Ecological mechanisms for vegetation change on tropical islands include competing species interactions, abrupt natural events (such as volcanic ash falls, tsunamis or cyclones), climate change, changing terrestrial insularity associated with geological activity and eustatic or isostatic sea-level fluctuations, and human interference. Palaeoecological data, particularly spanning the Holocene, have established partial chronological frameworks for these processes by recording ecological trends in different local contexts. Fine-scale vegetation changes can be measured from subfossil proxies (e.g. microfossil and macrobotanical analyses) and then used to infer conditions under which certain plant taxa have responded to disturbance. Similarly, palaeoclimatic patterns can be inferred from a number of subfossil, chemical and sedimentary proxies from the same archives. Surprisingly little evidence of this kind has been identified from the northern New Guinea lowlands and adjacent islands. Here we summarise the palaeoecological context for past vegetation changes in the region.

The Pleistocene

In New Guinea, investigating the role of humans in vegetation change is complicated by the lack of palaeoecological records that show changes before and after human colonisation, about 40,000-60,000 yr BP. Palynological records from mainland New Guinea that adequately represent these shifts have been reviewed recently by Hope (2007, 2009). The sites are mostly in basins in the high-elevation New Guinea ranges (Haberle 1998; Hope 2009). Archaeological evidence suggests people must have been in these areas since around 40,000 yr BP but sustained impacts on forest vegetation did not occur until around 30,000 yr BP at Kosipe and around 21,000 yr BP at Haeapugua.

Despite the growing evidence of Pleistocene occupation of the lowlands and coasts of New Guinea and its offshore islands (Allen 2003; O'Connor and Chappell 2003; O'Connell and Allen 2004), little palaeoecological evidence is available. Hope and Tulip (1994) summarised the main complicating factors that make the lowland tropics a challenge for palaeoecologists. Because rapid organic accumulation rates of between 10 cm and 80 cm in 100 years are not uncommon for both lakes and swamps, sections of peat or organic muds rarely exceed Holocene ages (Walker and Chen 1987; Hope and Tulip 1994; Osborne et al. 1996). Hope and Tulip (1994) point out that this problem is compounded by the low deposition rate of pollen in the humid tropics (after Kershaw and Hyland 1975). High local floristic diversity with a bias towards entomophilous and low pollen-producing taxa is a characteristic of the lowland tropical floras. Even when pollen preservation is high and deposition is continuous, many New Guinea palaeoecological records show marked transitions in forest vegetation during the Pleistocene but reveal no indication of ecological forcing factors, disturbance or anything else.

The pollen record from Hordorli, a swamp basin at 780 m altitude in the Cyclops Mountains near Lake Sentani, West Papua/Irian Jaya, Indonesia (Figure 1), is unique in that it provides a 50,000-year record of lowland vegetation change (Hope and Tulip 1994; Hope 1996). The suite of palaeoecological evidence that should mark initial human colonisation,
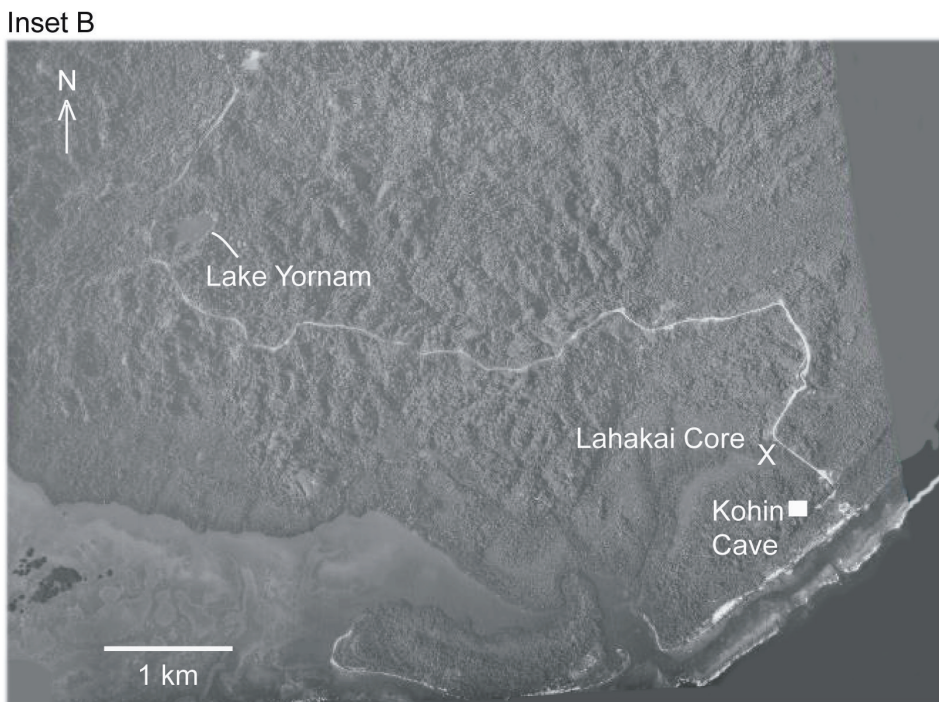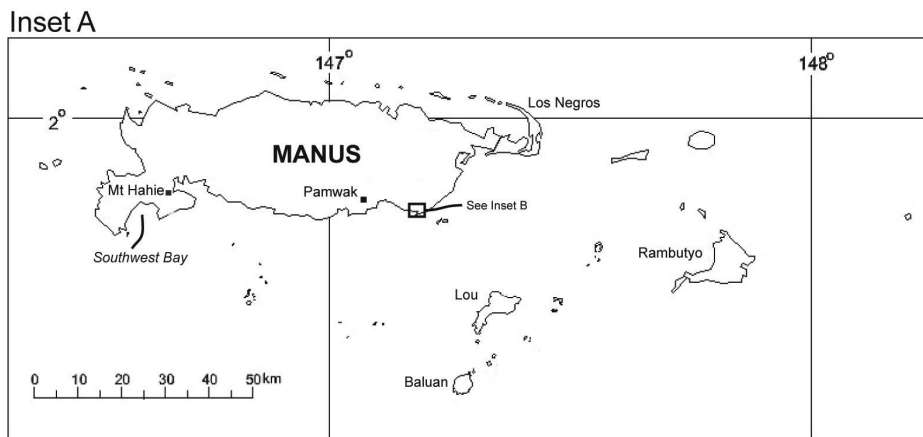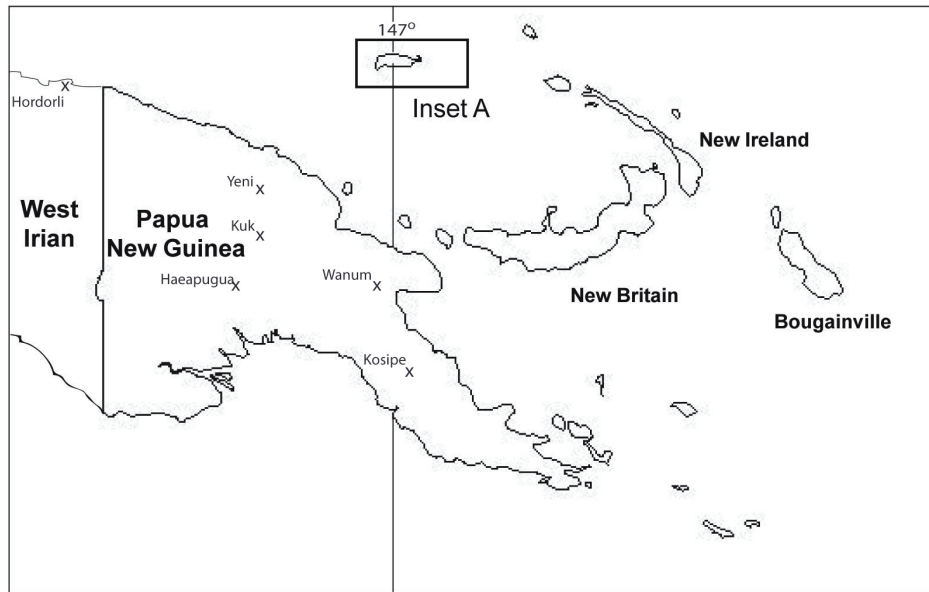
Figure 1. Map of Papua New Guinea, showing sites, the location of Manus Province and Lahakai Swamp in southeast Manus

such as increased fire frequency and increases in the abundance of secondary vegetation, is not conclusively represented at Hordorli until the Holocene. The Hordorli record also shows that closed tropical and lower montane forests have continuously occupied many areas despite human occupation. Hope and Haberle (2005) suggest that the lack of fire signals recorded at sites such as Hordorli may represent delayed intensive occupation of wetter sites.

There are no palaeoecological archives that span the Pleistocene from the tropical New Guinea islands. Given that the flora of these islands represents a subset of the mainland, there is no reason to presume that past vegetation change would be very different. Hope and Haberle (2005) suggest that the coastal lowland catchments of the Popondetta, Markham, upper Ramu and Sepik areas may have been drier during the Pleistocene than at present, dominated by *Nauclea* woodlands and possibly subject to natural fires, further complicating any palaeoecological signature of human presence. Such a model of vegetation change may also apply to the New Guinea islands.

The Holocene

Human influence on New Guinea vegetation change becomes more apparent in palaeoecological records of the Holocene, and can be correlated with archaeobotanical evidence for the beginning of plant domestication and agriculture (Yen 1996; Denham et al. 2004; Fairbairn 2005; Haberle 2007). Again, records are concentrated in the highlands of Papua New Guinea. Haberle and David (2004) have argued that increases in charcoal particles and *Casuarina* pollen, a secondary forest indicator, represented in a number of New Guinea highland palaeoecological records may signal the expansion of active and fallow cultivation areas during the mid Holocene.

In the coastal tropics of New Guinea, little palaeoecological research has concentrated on resolving questions of subsistence practice. Most pollen records have been retrieved in an effort to map the extent of mangrove sediments and the response of vegetation to coastal progradation and sea-level change. Mangrove sediments have been found hundreds of kilometres upriver in the Ramu and Sepik (Swadling and Hope 1992; Chappell 2005), indicating that a large estuary existed in the early mid Holocene before coastal progradation formed the present backswamp complex. Rapid siltation and coastal progradation has been demonstrated from mangrove sediments and geomorphological features found along the southern coast of New Guinea (Ellison 2005) and along the Fly-Digul platform, suggesting that the available land area for human occupation was limited during the early Holocene (Chappell 2005).

The pollen record from Lake Wanum, a lowland tropical lake in the Markham Valley, northern Morobe Province, Papua New Guinea (Figure 1) (Garrett-Jones 1979), provides the most continuous Holocene record so far of lowland vegetation change for mainland New Guinea. The lake has a rapid accumulation rate of organic-rich sediment during the Holocene. The record shows that an open sedge swamp surrounded by riparian forest/woodland persisted throughout the Holocene with an increase in dry-land grassland, secondary forest (including *Nauclea* and *Macaranga*) and burning after about 5500 yr BP.

In the Hordorli pollen record, charcoal particles first appear after 10,900 yr BP, and probably indicate a minor level of human activity. An increase in secondary forest species after 7000 yr BP may be a result of minimal human activity or, as Hope and Tulip (1994) suggest, may be the result of warmer conditions and shorter tree life in the lower montane forests.

The Wanum and Hordorli records both fail to provide any direct palaeoecological evidence for the initiation of root/tuber cultivation complexes and tree crops. Garrett-Jones (1979:295, 329) identified taro (*Colocasia esculenta*) pollen in the basal pollen zone of a 20 m deep core (core LWII), dated to around 9000 yr BP (identification confirmed by Haberle 1995). This represents the earliest subfossil record of *C. esculenta* from New Guinea, but the vegetation represented by the sample containing it appears to be a sedge swampland with riparian forest

and grasslands present on the dryland slopes. Prebble et al. (In prep.) consider the early Holocene *C. esculenta* to represent most likely a wild form present as part of the natural distribution in marginal swampy habitats, or less likely, a feral population escaped from earlier human introductions.

Human prehistory of the northern New Guinea lowlands and adjacent islands

People reached New Britain and New Ireland around 35,000 yr BP, and Manus more than 20,000 yr BP. Although lowered Pleistocene sea levels never brought the islands of the Bismarck Archipelago significantly closer to each other or to the main Sahul landmass, New Britain and New Ireland could be reached by crossing between intervisible islands, distances shorter than those already accomplished through Wallacea. Manus, in contrast, has always been a very small target, far below the horizon from any direction.

Excavated sites are too few and scattered to provide a clear picture of the earliest human phase in the Bismarck region. The New Ireland Pleistocene sites suggest small groups, mobility, foraging for resources of land and sea, and a mixed diet (Gosden 1993, 1995; Allen 2000, 2003; Specht 2005).

In Manus, the basal occupation of the Pamwak rock shelter may be significantly older than the oldest ^{14}C date of 21,000 yr BP. Carbonised *Canarium* nut shell and faunal remains dating to the terminal Pleistocene have been interpreted to represent human introductions from mainland New Guinea (Fredericksen et al. 1993). Undated, but probably also of Pleistocene age, are flaked stone tools salvaged from southwest Manus open sites destroyed by logging (Kennedy et al. 1991; Kennedy 1992, 1997, 2002; Ambrose 2002a).

By the end of the Pleistocene, an emergent pattern of movement of resources across the Bismarcks suggests that people had begun modifying their environments and making use of inter-island connections to supplement locally available resources. Obsidian and animal translocations suggest people made interisland crossings between mainland New Guinea, New Britain, New Ireland and Manus (Flannery and White 1991; Gosden 1992; Allen and Gosden 1996; Heinsohn 2003; Specht 2005).

Archaeological sites of the early to middle Holocene in the Bismarcks have yielded material from wider catchments than before, and in larger quantities. There is a greater range of artefacts and manufacturing techniques, including grinding of both shell and stone axes (Spriggs 1997; Allen 2000; Specht 2005). Food remains at several sites where conditions favoured preservation include fruit, nuts and other useful trees, most of them familiar in gardens today.

Although the record for Manus in the early to middle Holocene is very thin, the general pattern of resource use is consistent with the rest of the Bismarcks. Whether tree crops were important in early to middle Holocene Manus is unknown, but it seems likely they were, given their earlier presence and prominence elsewhere in sites in the Bismarcks (Gosden 1995; Specht 2005).

From about 3500 years ago, sites of the Lapita cultural complex extend from the Bismarck Archipelago east to Tonga and Samoa. The nature of these sites and their relationship to earlier sites in the southwest Pacific region and further west has been the subject of extended debate (Spriggs 1997; Terrell and Welsch 1997; Kirch 2000; Green 2003; Terrell 2004). The standard interpretation sees Lapita sites as the settlements of immigrant agricultural people, who spread relatively rapidly from Southeast Asia through the Bismarck archipelago and further east, and whose descendants include the Polynesians. In extreme forms of this view, these new settlers have been distinguished from earlier-established inhabitants of the southwest Pacific by sharply defined cultural and technological contrasts, including in particular the introduction of agriculture. Current debate reflects more subtle positions about the relative contributions of

putatively Southeast Asian and Melanesian subsistence practices and technological traditions (Green 2003; Golson 2005; Lilley 2006).

Manus does not fit neatly into a regional synthesis of intercommunicating Lapita peoples, for unequivocally Lapita material from Manus consists of only eight sherds from three sites, none of them in the beach locations typical of Lapita sites elsewhere. Thus, what part Manus played in the Lapita phenomenon is problematic (Kennedy 1981, 1982, 2002; Allen 1991; McEldowney and Ballard 1991), although obsidian from Lou Island occurs in Lapita sites throughout the Bismarks, and beyond. The Lapita-phase archaeological data from Manus are too tenuous to support arguments for local transformation of the patterns of settlement or subsistence (Kennedy 1983, 2002).

The end of the Lapita phase in the Bismarcks, North Solomons, Vanuatu and New Caledonia region has been characterised as a shift away from the regional interaction implied by the relative homogeneity of the Lapita cultural complex (Spriggs 1997; Bedford and Clark 2001, 2003), resulting in the present-day cultural diversity for which Melanesia is noted.

Again, the small number of excavated sites is inadequate to outline the post-Lapita period of Manus. Although the quantity and diversity of material and numbers of sites are greater than in preceding periods, much is from contexts which do not allow reliable dating. In general, the material suggests widening connections, throughout Manus and beyond.

The big picture: Changing subsistence and settlement patterns

Because people have been in the New Guinea islands region since the late Pleistocene, it is reasonable to expect that archaeological and palaeoecological sequences should register the shift from mobile foraging to more settled life based on agroecosystems. But because of the variability and flexibility of current subsistence practices, it is less clear what sort of changes might be expected. Despite the strongly asserted association of the shift to agroecosystems with the Lapita horizon, direct archaeobotanical or palaeoecological evidence is lacking, and change is inferred from proxies, such as the presence of pottery, shifts in settlement location, density and size, and linguistic reconstructions of plant and garden-related lexicons. Although this inferred subsistence change at present dominates the grand narrative of regional prehistory, the nature of emergent Holocene subsistence is open to question.

There is growing biogeographic and genetic evidence that important components of southwest Pacific agroecosystems are indigenous domesticates (e.g. bananas, breadfruit, *Pandanus* and sago; Yen 1991, 1996; Kennedy and Clarke 2004). The importance of the tree crops that form an integral part of the regional subsistence pattern, extending back at least to the middle Holocene, and probably to the late Pleistocene (Fairbairn 2005), has been underestimated. The significance of tree crops in mid-Holocene, pre-Lapita times is part of continuing debate about the Lapita cultural complex (Gosden 1992, 1995; Yen 1996; Kennedy and Clarke 2004).

The tree-crop-based systems of the present day, unlike the wide-ranging foraging of the earlier Pleistocene sites, involve significant alteration of natural forests, although this does not necessarily entail major disturbance. They show considerable regional variation in crop mixes and cultivation practices, and allow very rapid change in response to localised exigencies. As a result, local sequences may be quite disparate, and involve subtle changes difficult to detect in palaeoecological data.

II. Manus Island: Local cultural and environmental sequences

As sketched above, the archaeological record of Manus is meagre. Table 1 shows the excavated sites for which there is a reasonable assessment of radiocarbon ages or distinctive typology. There is a chronological bias towards the late Holocene, and a geographical one towards Lou Island and the eastern end of Manus. This largely reflects interest in the obsidian sources on Lou Island, shared by archaeologists and local sponsors of field work, as well as prehistoric inhabitants of the area. Historical records of European contact with Manus Province show a similar geographical bias (Kennedy et al. 1991).

Table 1. Archaeological sites of central/eastern Manus Province

Site	Pleistocene	Early-mid Holocene	Late Holocene		References
			Lapita	Post-Lapita	
Pamwak[a]	X	X		X	Fredericksen et al. 1993, Spriggs 1997, Ambrose 2002a
Peli Louson[a]		X		X	Kennedy 1983
Father's Water[a]		X		X	Kennedy 1983
Kohin[a]			X	X	Kennedy 1981
Mouk[b]			X	X	McEldowney and Ballard 1991
Sasi (Baun)[c]				X	Ambrose 1988, 1991, 2002a
Emsin[c]				X	Ambrose 1991, 2002a
Pisik[c]				X	Ambrose 1991, 2002b
Umleang[c]				X	Fullagar and Torrence 1991, Ambrose 2002a

a. Manus Island, b. near Baluan, c. Lou Island

The eastern half of Manus Island has villages and hamlets scattered throughout the interior, as well as along the coasts, with associated gardens and tree crops including planted sago stands. Tree crops are very important in village environs, and scattered throughout gardens and fallow. Garden clearance usually does not involve burning. The island's western half, in contrast, has neither settlements nor garden areas in the interior. The relatively few villages are coastal, and depend largely on sago (Hide et al. 1996). The contrast implies different local histories of settlement and subsistence, and requires a much finer focus of inquiry than the regional big picture.

Southwest Manus archaeological sequence

In southwest Manus, despite the absence of recent interior settlement, salvage archaeology during logging recorded more than 100 settlement sites. These are concentrated on high ground, especially ridge crests and their intersections, and marked by large quantities of pot sherds and worked obsidian (Kennedy et al. 1991; Wadra 1991; Kennedy 1992, 1997). The number and scale of these sites, exposed, recorded and then obliterated within a relatively short period, provide information difficult to integrate with that from the controlled conditions and close-up view of archaeological excavation, providing very detailed information about a tiny sample of the past. While archaeologists dissect a small part of a site, relatively modest logging and other industrial operations can simultaneously expose and destroy whole archaeological landscapes.

Despite destruction of the stratigraphic integrity of the southwest Manus sites, a few chronological and other inferences can be made from the salvaged artefacts. First, most of the sites are older than the forest, which can be no more than a few hundred years old: they are under, not in it. There is very little artefactual evidence referrable to the last few hundred years. Much of the distinctive pottery is not matched elsewhere in Manus or beyond. Since Lapita-style sherds are lacking, on conventional grounds the entire corpus may be characterised as post-Lapita, though quite what that means in Manus is unclear.

At least 25 sites contain distinctive, elaborately retouched obsidian points, technologically identical to those from a Lou Island site dated about 1720 yr BP (Kennedy 1997; Ambrose 2002a). Whether the southwest points are of imported obsidian is not clear, since there is a local southwest Manus obsidian source associated with Mount Hahie (Figure 1). But quite apart from intriguing questions of the geopolitics of resource acquisition and technological skills that these artefacts raise (Kennedy 1997), they imply a horizon during which settlement density was at least as high as the present-day pattern of eastern Manus. And this, in turn, suggests a similar subsistence base, with taro gardens and extensive tree crops.

At a few southwest sites, distinctive large retouched flakes similar to artefacts dated at Pamwak to the late Pleistocene/early Holocene suggest earlier occupation.

The archaeological evidence from under the forest of southwest Manus thus suggests people have been present there since the Pleistocene. At some point, they began to make and/or use pottery. About 1700 years ago, relatively intensive agriculture can be inferred. There is no direct evidence of what was grown, or when this phase ended. However, the lack of recent artefact types suggests that population decline and shift from inland to coastal settlement had occurred well before the period of European contact. Both the location and density of past settlements contrast with the present-day pattern. Since the growth of a forest dominated by *Calophyllum* spp. constitutes the most recent phase of the local sequence, understanding the dynamics of the forest is a necessary part of interpreting the human history of the southwest.

Logging in southwest Manus, begun in 1988, was prompted by the existence of a timber resource in a largely unpopulated area (Freyne and Bell 1982). In keeping with the aims of national forestry policy at the time, the Manus Provincial Government hoped the southwest Manus logging project would reduce the imbalance between the eastern and western halves of the island, bringing urban development and new technology to the west by construction of a township and veneer mill. Neither has eventuated. Appearances to the contrary, many of the trees are too old to yield useful timber, much less the peelable logs anticipated, and the project has been beset by long-running disputes (O'Collins and Lamothe 1989; Kennedy 1991; Ghai and Regan 1992:328; Anon. 2004). Logging proceeded despite recognition that the southwestern Manus *Calophyllum*-dominated forest is ecologically unusual, and that its dynamics are obscure (Kerenga and Croft 1984/85; Stevens 1995:63). While the archaeological record does not directly elucidate these dynamics, some relationship with preceding human activity is implied. Nevertheless, prominent NGO commentary on the timber resource insists it was in pristine condition before logging began (e.g. World Wildlife Fund 2001; Seacology 2008; National Geographic 2009). This is a familiar theme in critiques of forest resource use throughout the tropics (e.g. Bayliss-Smith et al. 2003; Willis et al. 2004).

Southeast Manus palaeoecological sequence: Lahakai Swamp

A preliminary palaeoecological investigation of Lahakai Swamp in southeastern Manus was undertaken with the aim of documenting Holocene vegetation change, in particular evaluating human impact and other disturbances on Manus (Southern 1987). After a broad survey of sites, Lahakai Swamp was chosen for its proximity to recent gardening and sago processing,

and to Kohin Cave, an excavated archaeological site occupied intermittently from 3400 yr BP to the present (Kennedy 1981). It is worth noting that nearby Lake Yornam (Figure 1), formed probably within a karst sinkhole deposit, revealed alkaline conditions unsuitable for the preservation of pollen (Southern 1987).

A series of raised Plio-Pleistocene fringing reefs, now forming karst cliffs along part of the southeast coast of Manus, have blocked the drainage of many south-facing valleys. Diverted creeks are visible behind the cliffs (see Figure 1) and swamp deposits have accumulated large amounts of organic material suitable for palaeoecological analyses. In 1987, when the site was cored, this swamp was maintained as a sago plantation and was intensively exploited by local landowners. The vegetation was dominated by a spineless form of sago palm (*Metroxylon sagu*) which formed nearly monotypic stands with few other plant taxa present (Figure 2). The surrounding hill slopes behind the swamp were heavily gardened. Some areas were recently cleared for new gardens, and adjacent areas remained in fallow secondary forest regrowth that included many exploited fruit and nut trees.

Figure 2. Coring the Lahakai Swamp site. Jack Golson watching Wendy Southern and local assistants. Photograph by W. Ambrose, 1987

Methods

Lahakai Swamp was cored using a Russian D-Section corer, collected in 40 cm length sections to a depth of 9.6 m, at which point basal estuarine/marine-shell debris was encountered. The core was sampled at 10 cm intervals down to 630 cm and processed for palynomorphs using standard procedures (10% HCL, hot 10% KOH, 40% HF and acetolysis for all samples) as described by Faegri and Iversen (1975). Samples were then washed in alcohol followed by tertiary butyl alcohol to dehydrate them, before suspension in a recorded volume of silicon oil (2000 centistokes). This was used as an equivalent measure of pollen concentration, counter to more familiar techniques of adding a known number of *Lycopodium* marker spores to a sample. For microscopy, all counts were aimed at >150 pollen per sample. Fern and fern ally spores were also recorded but were not included in the total palynomorph sum. The palynomorphs were identified using the reference collection of what is now the Department of Archaeology and Natural History, ANU (see www.palaeoworks.anu.edu.au). All microscopic charcoal

fragments were counted using the point-count method of Clark (1982), calculated as mm^2 cm^{-3}. The percentages of selected palynomorphs (major taxa >2% of total sum and a select range of indicator taxa), charcoal and total palynomorph concentration data were placed into stratigraphic diagrams using the program C2 Data Analysis version 1.5.2 (Juggins 2005).

Results and interpretation

The stratigraphy of the core is presented in Figures 3a, 3b and 3c, and divided into zones on the basis of the main vegetation signals and charcoal particle concentrations. The AMS radiocarbon dates from the bulk samples from the core are presented in Table 2, with the key features of each record and their palynological zones described in Table 3. Three phases of vegetation change are defined by the sequence from southeast Manus, demonstrating coastal edaphic changes in response to mid-Holocene sea-level fluctuations, followed by freshwater swamp forest development, and increasingly dryland forest dominance in the late Holocene. This later swamp forest-dryland phase is critical in that it allows some definition of land-use practices demonstrated by the presence of both horticultural (*Colocasia*) and tree-crop (e.g. *Metroxylon* and *Aleurites*) components.
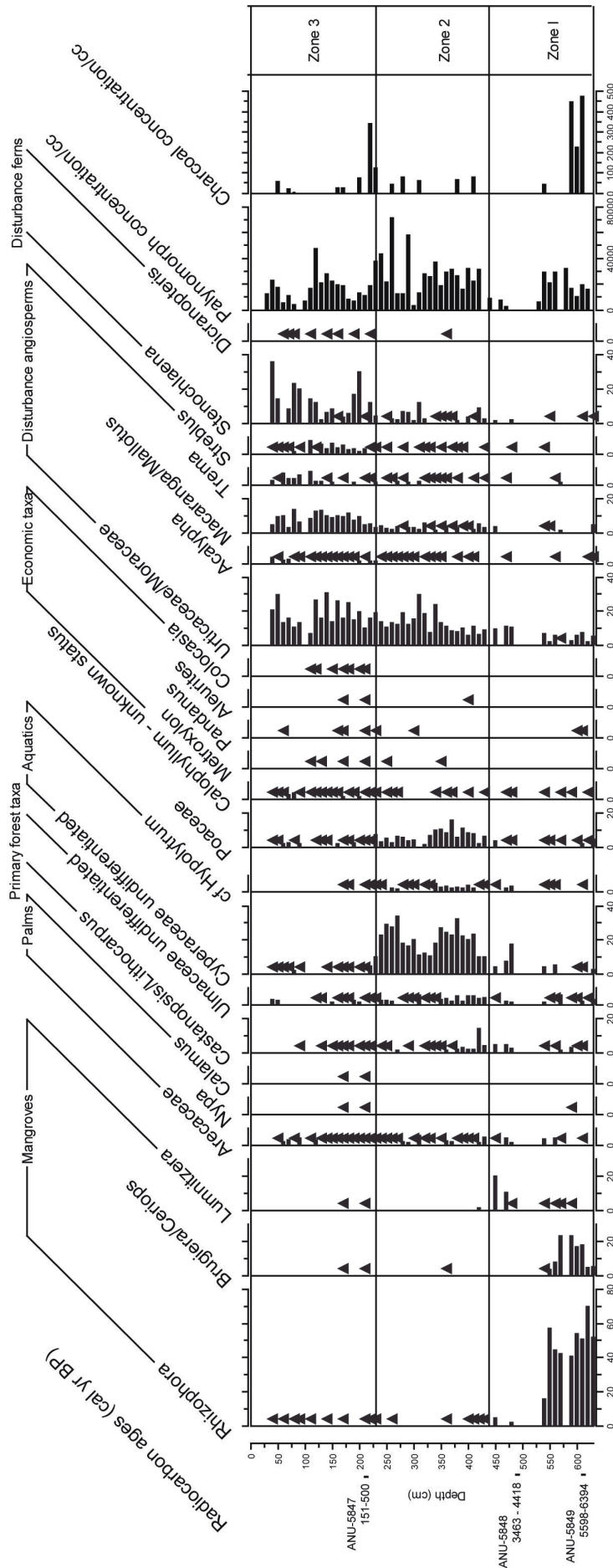
Table 2. Radiocarbon ages from Lahakai core

Sample name	Depth cm	Radiocarbon age BP	Calibrated age 2σ
LKAI 1	210-220	340±70	151-500
LKAI 2	480-495	3654±185	3463-4418
LKAI 3	615-630	5280±185	5598-6394

All dates on bulk sediment. All ages calibrated using Calib v. 5.1.

Table 3. Palynological zones represented in the Lahakai Swamp sequence, Manus, and outlined on the basis of changes in dryland, wetland and human-impact signatures

Zone	Dryland	Wetland	Interpretation of human impact and other disturbances
5500-3000 cal. yr BP Zone I	Most common taxa recorded are Urticaceae/Moraceae, Arecaceae (which increases towards the top of the zone) and Myrtaceae.	High but declining values of mangrove taxa *Rhizophora* and *Brugiera/Ceriops*, with minimal representation of *Pandanus* and Centrolepidaceae/Restionaceae. Cyperaceae and cf *Hypolytrum* increase towards the top of the zone, as does *Lumnitzera*.	Micro-charcoal particles high at around 5000 cal. yr BP. Macro-charcoal band at around 4000 cal. yr BP particles.
3000-500 cal. yr BP Zone II	Characterised by the secondary taxa Ulmaceae, Poaceae and *Castanopsis/Lithocarpus*. *Macaranga/Mallotus* (also secondary forest taxa) and Urticaceae/Moraceae increase towards the top of the zone.	Mangroves largely absent, dominated by Cyperaceae.	Fern spores increase in this zone, with *Lygodium* showing a small peak. Two bands of macro-charcoal particles at around 1000 cal. yr BP.
500-present Zone III	Several taxa increase in this zone, including *Calophyllum*, *Elaeocarpus*, *Endospermum*, Myrtaceae, while the secondary forest taxa common in Zone II decrease.	Cyperaceae is represented in much lower proportions than in the previous zone. Most wetland taxa are poorly represented.	*Polypodium* increase and *Dicranopteris* appears consistently for the first time. Micro-charcoal particles high at around 500 cal. yr BP. Two macro-charcoal bands represented in this zone. Possible and probable plant cultigens including *Colocasia* and *Aleurites* are first represented in this zone.

Figure 3a. Palynological diagram for the Lahakai core, Manus. The key abundant taxa are presented in bars (samples with taxa representing >2% of total sum) and triangles (samples with taxa representing <2% of total sum). Taxa are sorted within these groups in stratigraphic succession using the sort function in C2 Data Analysis. Taxa are grouped according to their respective vegetation associations as follows: Trees and shrubs; pteridophytes and bryophytes; sedges and other aquatics; grasses; economic taxa; unknown palynomorphs. Palynomorph concentrations are presented as grains/cm^3 x 10^4; charcoal concentrations are presented in mm^2 cm^{-3} x 10^2
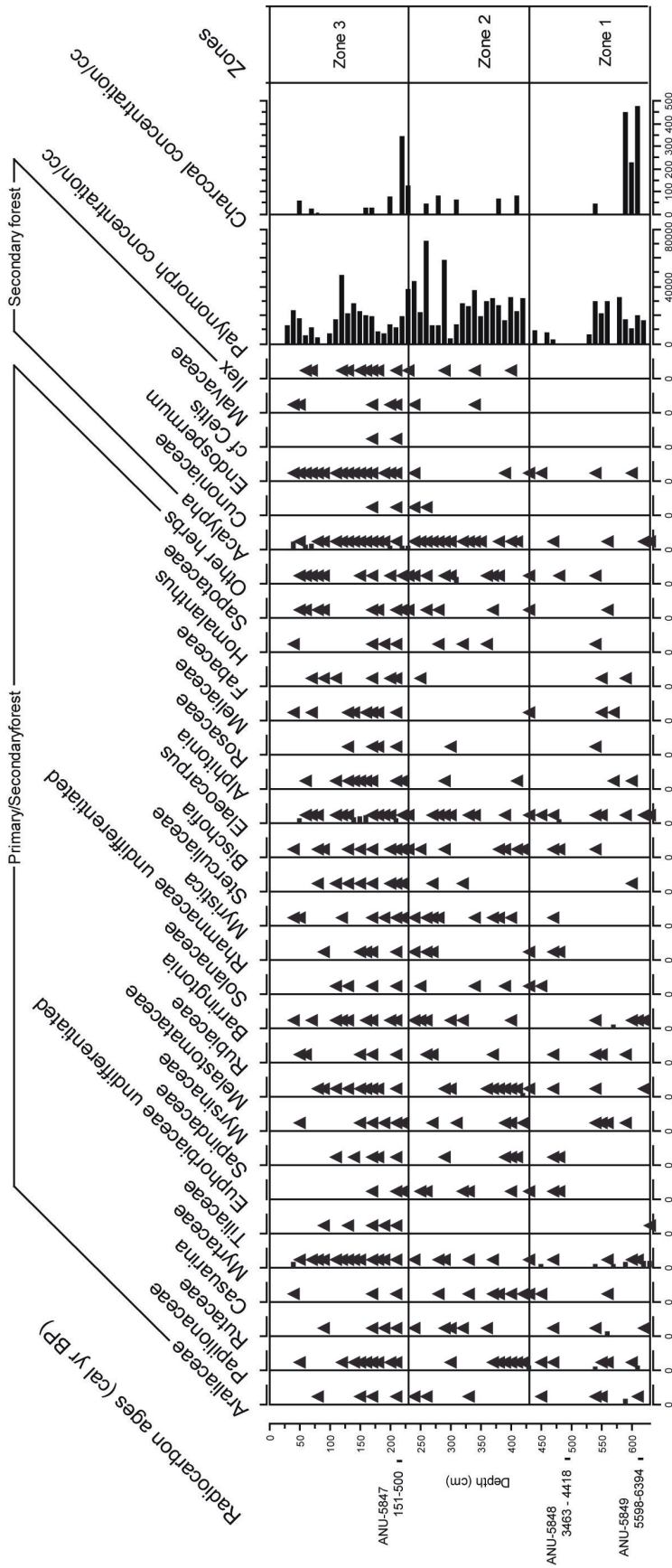
Analyst: W. Southern

Figure 3b. Palynological diagram for the Lahakai core, Manus. More rare angiosperm tree, shrub and herb taxa are presented in bars (samples with taxa representing >2% of total sum) and triangles (samples with taxa representing <2% of total sum). Sorting, grouping and concentration as for Figure 3a

Figure 3c. Palynological diagram for the Lahakai core, Manus. More rare fern and aquatic taxa are presented in bars (samples with taxa representing >2% of total sum) and triangles (samples with taxa representing <2% of total sum). Sorting, grouping and concentration as for Figure 3a
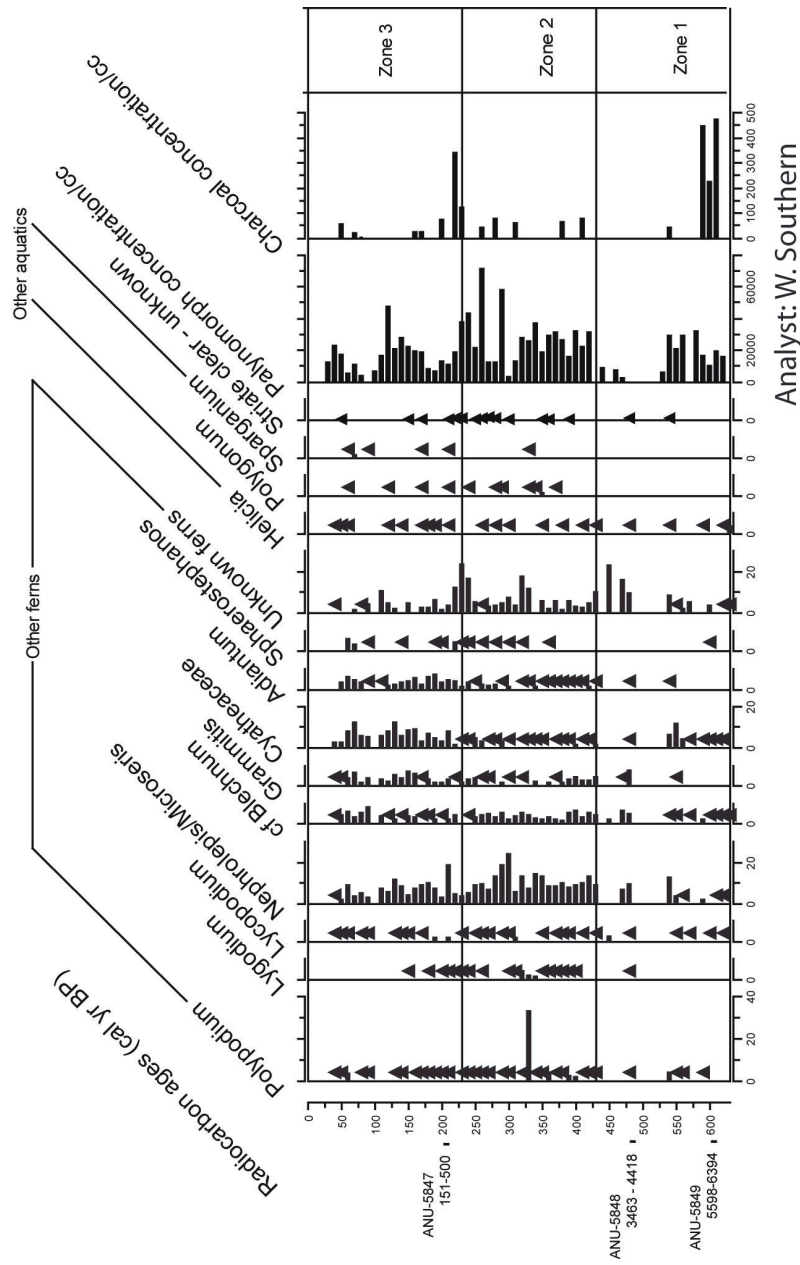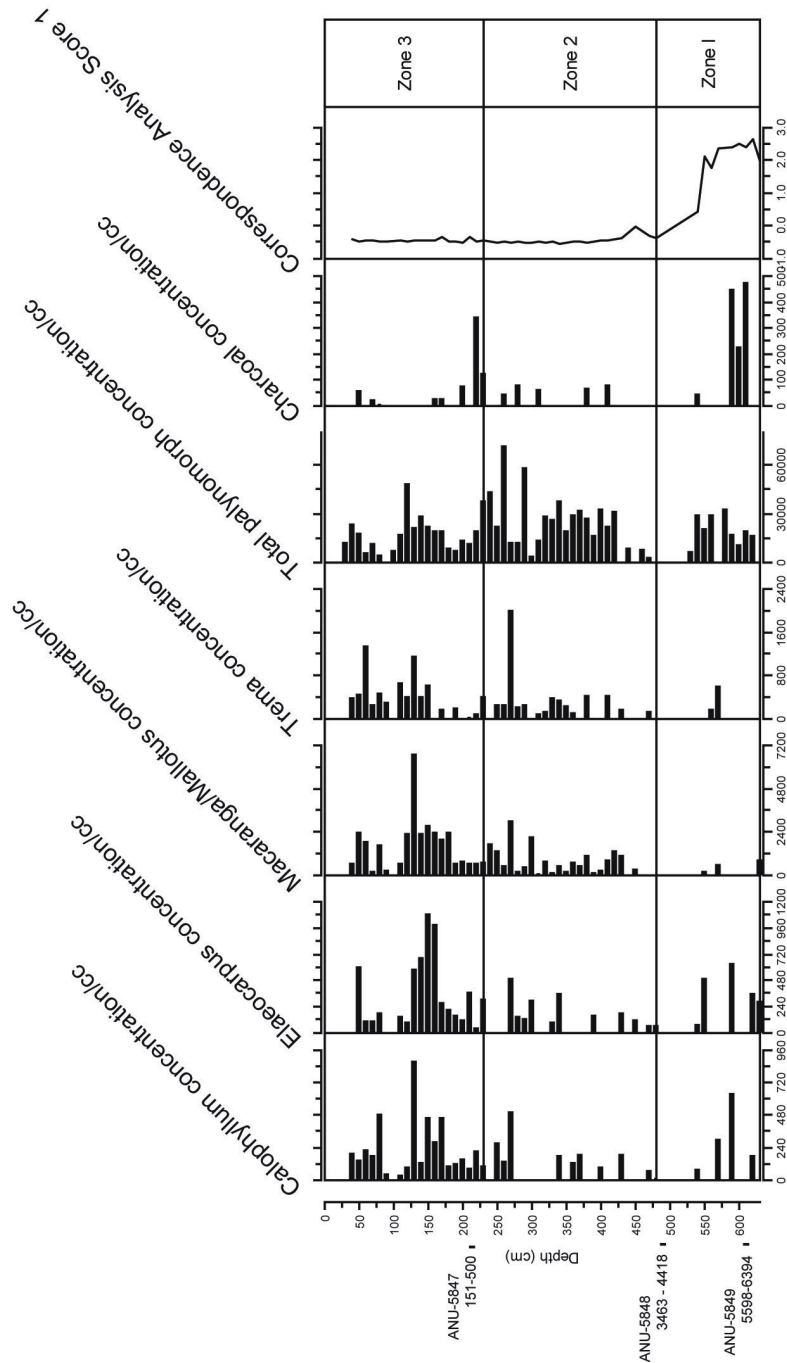
Figure 4. Palynomorph concentrations (grains/cm³ × 10⁴) of select taxa (including *Calophyllum*) and Axis 1 results of a Correspondence Analysis (CA) of the entire dataset from the Lahakai sequence are presented. Data were centred and standardised for the analysis and the Axis 1 results show 61% of the variance in the dataset. The plot and Correspondence Analysis were produced using the Program C2 Data Analysis version 1.4.3. (Juggins 2005)

One of the most striking features of this record is the lack of *Metroxylon* sago pollen in the upper part of the sequence, despite the core site being intensively managed for sago production in 1987. One explanation for the lack of sago pollen in the upper sequence of this core is that most trunks of this hapaxanthic (monocarpic) tree have been harvested before flowering. An alternative, that pollen production in sago is low, is ruled out by modern pollen assemblages from surface swamp soils from under sago stands in other parts of Papua New Guinea (M. Prebble unpublished data). This discrepancy in pollen representation highlights the complexity of the interpretation of fossil pollen data. Pollen representation of *Calophyllum*, important for the southwest Manus sequence, presents another complex case.

Calophyllum *at Lahakai*

Although few data are available on the pollination ecology of *Calophyllum*, some taxa in the genus are known to be entomophilous (Stevens 2007) and thus probably do not produce high concentrations of pollen. It is very difficult to gauge from the percentage data presented from the Lahakai record the magnitude of the response of *Calophyllum* to any ecological changes, including human impact. To address the problem of pollen representation, in Figure 4 we show pollen concentration data for *Elaeocarpus*, a primary forest tree, *Calophyllum*, and the two key disturbance taxa, *Macaranga/Mallotus* and *Trema*. These data mitigate the proportional bias imposed by anemophilous (wind dispersed) and locally abundant taxa.

In Zones 1 and 2, *Calophyllum* is represented in similar concentrations to *Elaeocarpus* but is not consistently represented across all of the samples, suggesting that both these taxa were ephemeral in the Lahakai environment at this time. These data contrast with *Macaranga/Mallotus* and *Trema* pollen, which are poorly represented in Zone 1, but are consistently represented across samples in Zone 2. All of these taxa are represented in all samples in Zone 3 and show similar changes in concentration across the zone. In Zone 2, the *Calophyllum* and *Elaeocarpus* concentrations are almost complementary, which suggests rapid changes in forest structure.

In order to assess whether these variations reflect changes exhibited across the entire record, correspondence analysis was performed on the percentage data of all pollen and spore taxa identified and all the samples analysed from the Lahakai core. Eigen values (Axis 1) generated for each sample are presented as proportions of the total variation in the dataset shown in Figure 4. These values account for 61% of the variation in the entire dataset, and are primarily controlled by the proportions of mangrove pollen in each sample. The greatest variation exhibited in this core occurs in Zone I. These data emphasise the point that variation in Zones 2 and 3 is minimal.

This raises the question of why *Calophyllum* behaves like a primary forest taxon in Zones 1 and 2 and a disturbance taxon in Zone 3.

III. *Calophyllum* forest in Manus and the Pacific

We have suggested that understanding the earlier settlement sequence of Manus requires understanding the dynamics of the forest. Since the growth of a forest dominated by *Calophyllum* spp. constitutes the most recent phase of the local sequence in southwest Manus, we consider what role this genus played in the southeast sequence represented at Lahakai. First, we review what is known of the ecology of *Calophyllum* in Manus and the wider region.

Information about the southwest Manus *Calophyllum* forest is limited but striking. Brief forestry and botanical surveys before logging began in 1988 highlighted its value for timber on the one hand, and ecological rarity on the other (Freyne and Bell 1982; Kerenga and Croft 1984/85; Stevens 1995:63). The area includes a very peculiar forest type, consisting of extensive plantation-like tracts in which large, even-sized *Calophyllum euryphyllum* Lauterb. (Clusiaceae) are almost the only tree, with abundant seedlings but virtually no saplings.

This monotypic forest type also occurs on Rambutyo Island in Manus Province (Figure 1), on Mussau and on small islands off New Ireland, growing on a range of different soils and substrates (Kerenga and Croft 1984/85:46). There are no detailed descriptions or maps of the extent of the monotypic *Calophyllum* stands in southwest Manus or elsewhere.

C. euryphyllum has a scattered distribution on the Aru Islands, the islands of Geelvink Bay and the Vogelkop peninsula of Irian Jaya, the north coast of New Guinea from Jayapura to the Sepik, the Bismarck Archipelago (except New Ireland) and in the Central and Milne Bay provinces of Papua New Guinea (Stevens 1995). *C. euryphyllum* is the dominant species of the monotypic forest, but it is not the only *Calophyllum* species on Manus. *C. soulattri* and *C. waliense*, the latter an endemic Manus species, are also recorded. Although detailed distributions are lacking, it is likely these three species grow together (Stevens 1974:355). *C. inophyllum*, a widespread Malesian strand species, is also indigenous to Manus, but is primarily adapted to the coastal fringe, though it can grow on wetland substrates (Stevens 1974, 1980, 1995, 2007).

Apart from the monotypic stands of *C. euryphyllum*, *Calophyllum* spp. are common trees in the rainforest canopy throughout Manus (Kerenga and Croft 1984/85). In central and south-central Manus, moderately rich mixed forest including *Calophyllum* spp. showed no distinct dominants (Kerenga and Croft 1984/85:44-46). In the survey of Manus forest resources that led to logging in western Manus, Freyne and Bell (1982:32-33) estimated that *Calophyllum* (species not identified, but probably mostly *C. euryphyllum*) comprised about 50% of the largest size class (dbh <70 cm) of trees in two out of three sampled rainforest blocks, and 84% in the third, the western Manus block that includes monotypic stands.

In a subsequent preliminary study in the southwest Manus logging area, O'Collins and Lamothe (1989) identified 11 forest associations including canopy, subcanopy and regenerating vegetation in logged, unlogged and burnt forests. Three forest types were also identified from an old coconut (*Cocos nucifera*) plantation. *Calophyllum* (cf. *C. euryphyllum*) dominated all forest types with the exception of logged sub-canopy forest and the canopy and sub-canopy forests of an old coconut plantation, where this tree forms a minor component of the vegetation.

In eastern Manus, *Calophyllum* is absent from forest regrowth in lowland areas heavily disturbed by human interference (Kerenga and Croft 1984/85:45). In interior eastern Manus, Rooney (1982) reported that *Calophyllum*-dominated rainforest forms a late stage of succession after clearance for taro (*Colocasia*) cultivation. He suggested that the conversion of earlier woody fallow to forest dominated by '*Calophyllum* and tropical hardwood species', which local inhabitants consider undesirable for taro gardens, resulted from management failure caused by labour shortage, following a modernisation movement in the 1940s that halved the local population (Rooney 1982:275). Though details of the species composition of this forest are unclear, Rooney's comment does not suggest monotypic *Calophyllum* stands.

Despite the scarcity of quantified descriptions, it seems that the frequency of *Calophyllum* spp. in Manus forest is variable, and that the monotypic stands of western Manus, Rambutyo and small islands off New Ireland represent a rare occurrence of hyper-dominance, the dynamics of which are unknown.

The survey of forest resources of Manus asserts that *Calophyllum* (species not stated) is a pioneer (Freyne and Bell 1982:29, 34). The basis for this statement seems to be the observation of seedlings in disturbed areas, but perhaps also the assumption that the even size of trees in the monotypic stands translates to even age. There is no comment about the absence of saplings in these stands noted by Kerenga and Croft (1984/85). Freyne and Bell's (1982:35) stand table showing regeneration of saplings, the only such data available for Manus, relates to more typical rainforest, in which large *Calophyllum* trees constitute about half the volume of usable timber, rather than the much higher figure for the western Manus block containing the

monotypic stands. Freyne and Bell (1982:29) attribute this peculiar formation to catastrophic destruction, citing a Manus colleague's account of an oral tradition about a tidal wave and strong wind, thought to have occurred in the early 19th century (see also Johns 1986).

If the monotypic *C. euryphyllum* forest of southwest Manus was composed of a pioneer species in even-aged stands, the timing of forest initiation could be estimated, and suggest a terminal date for the shift from a pattern of inland villages most likely supported by taro gardening and tree crops to a smaller population living in exclusively coastal villages supported by sago and other tree crops.

This explanation for the southwest Manus monotypic forest lacks evidence. The argument from oral history fails on a number of grounds. There has been no comprehensive study of Manus oral history, available information being anecdotal at best. Attributing damage throughout the uplands of southwest Manus, or Rambutyo, to tsunamis lacks credibility, given the elevation of the terrain. Stories of catastrophes, including earthquakes, darkness and drought as well as high winds and tsunamis causing forest, garden and village destruction, are commonly recounted throughout Manus (J. Kennedy pers obs. 1977-1991). They are undoubtedly based on observation, but a widely repeated story does not account convincingly for peculiar effects of a localised catastrophe. In central Manus, where villagers tell a very elaborate account of how a tidal wave and wind long ago destroyed the local forest, leaving only one tree, a large *Ficus*, still standing, there are no dense *Calophyllum* stands (J. Kennedy pers obs. 1981). There is no reliable support from oral history for a local catastrophe in southwest Manus that might account for natural disturbance-mediated establishment of *Calophyllum* forest.

As to even age of the trees, the foresters' assumption that fairly uniform diameter translates to even age has not been borne out since logging began in southwest Manus. Many trees are too old to be any use (Anon. 2004). Age variation both within and between stands suggests more complex dynamics of establishment, as do other traits of the species.

Elsewhere on Manus, *C. euryphyllum* is a common component of rainforest. Its local value as timber, especially for canoe hulls, makes it likely that trees would once have been protected or conserved. Although there is little in the literature about its ecology, Rooney's (1982:275) comment about its role in late-stage fallows is suggestive. A recent forestry development program to propagate genetically improved seed for community tree-planting programs (Gunn 2007) shows that the seed has very high moisture content and is unlikely to retain viability for long. It is eaten by birds, bats and phalangers (Anon. n.d.).

Although *C. euryphyllum* is distributed from the Aru Islands and the Vogelkop, along the north coast of New Guinea to the Bismarck Archipelago, occurrences of monotypic stands are restricted to a few areas in Manus, Mussau and islands off New Ireland. Yet throughout the species' range, large-scale disturbance is common. This includes the eastern half of Manus, which lacks monotypic *Calophyllum* stands despite being closest to the volcanic eruptive centres of Lou Island and the St Andrew Strait that are the most potent source of disturbance in the region. In eastern Manus, fallow gardens support a familiar range of large-leaved, fast-growing pioneer species, in which *Calophyllum* is not prominent, if present at all (Rooney 1982; Kerenga and Croft 1984/85). While the reported distribution of monotypic stands of *C. euryphyllum* might well reflect incomplete knowledge, this is unlikely in the case of eastern Manus, or the case of New Britain, an island that has been thoroughly explored for its timber potential, and also has a rich recent history of natural catastrophes and widespread gardening.

Although there is little direct evidence of the ecology of *C. euryphyllum*, there is information to suggest its likely characteristics. All except one of the Papuasian species of *Calophyllum* surveyed in Stevens' (1980) systematic treatment of the genus are shade-tolerant rainforest trees (the exception is the common coastal/strand species *C. inophyllum*), with no evidence of pioneer habit. In Whitmore's (1989) expanded classification along a gradient from pioneers to progressively more shade-tolerant species, the Solomons *Calophyllum* species (*C. neo-ebudicum*

and *C. peekelii*) both fall towards the shade-bearing end. Seeds have no dormancy and are poorly dispersed. Seedlings germinate readily in light or shade, but with high early mortality. Survivors grow up in high forest or small gaps (see also Greig-Smith et al. 1967; Whitmore 1984:89; Burslem and Whitmore 1996).

C. euryphyllum probably behaves in a similar fashion, with regeneration dependent on a population of seedlings rather than a seed bank. Thus, distribution of the trees may reflect conditions promoting the persistence and onward growth of seedlings into saplings, rather than the dispersal and germination of seeds (Bazzaz and Pickett 1980:293, 303). The monotypic *C. euryphyllum* forest is clearly a special case, requiring explanation of how other species are excluded. The absence of saplings noted by Kerenga and Croft (1984/85) suggests that the formation of monotypic stands involves peculiar dynamics in which on-growth of seedlings is suppressed, and that these may persist. It has been shown that in Bornean forests, most shaded seedlings of canopy tree species are at least 10 years old, and some may be much older (Delissio et al. 2002).

Ecological studies have examined forests where stands of *Calophyllum* spp. dominate, further east in the Pacific. *Calophyllum neo-ebudicum* occurs throughout Vanuatu in moist forest, but is most abundant in the southern islands of Erromango and Aneityum (Wheatley 1992; Mueller-Dombois and Fosberg 1998). On Aneityum, the natural vegetation is dense mixed lowland forest with a canopy of *C. neo-ebudicum* and *Agathis obtusa*, but much of this forest has been extensively logged, leaving much of the island in secondary scrub (Hope pers comm.). *C. neo-ebudicum* is the most common canopy associate in Erromango.

Drake et al. (1996) documented four types of forest on the raised limestone island of 'Eua, Kingdom of Tonga, two dominated by *C. neo-ebudicum*. The key feature of this study is the recognition that regeneration of disturbed areas in these forest types is not dominated by *C. neo-ebudicum*, but *Dendrocnide harveyi* (Urticaceae), *Bischofia javanica* (Euphorbiaceae) and *Rhus taitensis* (Anacardiaceae) in the mixed forest, and *Alphitonia zizyphoides* (Rhamnaceae) and *Elattostachys falcata* (Sapindaceae) in the upland *Calophyllum* forest. This suggests that disturbance has not maintained *C. neo-ebudicum* dominance, but instead supports a more diverse mixed forest assemblage.

Whitmore's long-running study of the regeneration of forests on Kolombangara, in the Solomon Islands, monitored all age classes of 12 canopy species on a range of sites and under disturbance conditions which included cyclone damage and gardening clearance, as well as small natural gaps (Whitmore 1989; Burslem and Whitmore 1996, 1999). Burslem et al. (2000) discuss forest regeneration after cyclone damage, to evaluate the suggestion that community composition of tropical forests may be influenced strongly by rare but large-scale disturbance events. They conclude that the relative abundance of common tree species on Kolombangara is only briefly disrupted by such events, and that a better explanation for spatial differences in the island's forest composition is provided by different histories of human disturbance. Bayliss-Smith et al. (2003) reach a similar conclusion for the Marovo lagoon area, and argue the value of interdisciplinary studies for understanding of rainforest dynamics.

As Whitmore (1989) showed for Kolombangara, the considerable spatial and temporal differences in population size and turnover of tree species following canopy disturbance make generalisations about forest dynamics unsafe. The functional and life-history characteristics of tree species vary independently across multiple parameters, which dichotomous typologies cannot reflect (Baker et al. 2003; Kraft et al. 2008; Zimmerman et al. 2008:111). Studies of relative species abundance and distribution in tropical forests, based on repeated censuses of large plots, have highlighted the difficulties of testing competing theories of the maintenance of the species diversity of tropical forests (Chave 2004, 2008; Carson and Schnitzer 2008). Notably, seedling-to-sapling stages of tropical forest dynamics have not yet been satisfactorily investigated (Zimmerman et al. 2008:108).

The high diversity of tropical forests is the central focus of studies of their ecology and dynamics. Recent approaches have shifted from relatively simple deterministic models to more sophisticated theoretical models, which integrate ideas from island biogeography and population genetics and have greater analytical power, especially capability to handle large datasets at multiple scales. A central issue generating much debate is whether stochastic dispersal-dependent sampling effects and demographic processes are sufficient to account for community structure, and the extent to which species-level differences in ecological strategy contribute to this structure (e.g. Connell 1978; Denslow 1987; Hubbell 2001; Potts et al. 2002; Chave 2004; Svenning et al. 2004; Wills et al. 2006; Carson and Schnitzer 2008; Kraft et al. 2008; Stokstad 2009). Recognition that tropical forests often have a few common species and a large number of rare ones has become central to the development of these insights in forest community ecology. Dealing quantitatively with spatial patterning of the rare species has required new approaches to both data collection and analysis, especially to measures of biodiversity (Chave 2004, 2008).

Monodominant tropical canopy species

High diversity notwithstanding, at the other extreme of the range of relative species abundance, dominance of the canopy by single species, ranging from 50% to 100% of individuals, is common throughout the tropics and has drawn extended commentary. Connell and Lowman (1989) classified these forests into two types, on the basis of whether or not the monodominant species persists beyond one generation. Stands of short-lived, light-demanding species with well-dispersed seeds capable of long dormancy do not regenerate in situ. Persistent dominance of the canopy by one species, they suggest, could arise in two ways: by colonisation of large gaps and subsequent regeneration, or by gradual replacement of other species. They proposed ectomycorrhizal association as one possible mechanism for such replacement and listed species which show persistent dominance from the families Dipterocarpaceae, Fagaceae, Lauraceae and Leguminosae (subfamily Caesalpinioideae), from Malesia and the New World.

Subsequent research has shown that monodominant canopy species do not share a simple set of causative traits or mechanisms. They may form at early or late successional stages after clearance, and this does not predict whether they regenerate or not. Those that form persistent stands of long-lived trees may or may not depend upon ectomycorrhizae or poor soils. Examples have expanded to include more species of the families Leguminosae, Guttiferae, and notably New Guinea and New Caledonian *Nothofagus* species (Connell and Lowman 1989; Hart et al. 1989; Hart 1990; Read et al. 1995, 2000; Torti et al. 2001; Potts et al. 2002; McGuire 2007).

C. euryphyllum on Manus provides another example of monodominance in a family (Clusiaceae) not included in recent discussions. Forest in which *C. euryphyllum* constitutes about 50% of canopy trees appears to be quite widespread throughout Manus. *Calophyllum* species further east in the Pacific seem to follow a similar pattern. The restricted patches in which *C. euryphyllum* reaches much higher proportions, in the west of Manus, on Rambutjo and elsewhere, we have singled out above as monotypic, emphasising not only the species' dominance but also the distinctive lack of growth stages between seedlings and mature trees.

Research on tropical canopy monodominance establishes the multiplicity of possible causal mechanisms, rendering generalisation unsafe. We need more evidence to explain both the widespread pattern of *Calophyllum* spp. dominance on Pacific islands, and especially the hyperdominance of the monotypic *C. euryphyllum* stands. On present evidence, it is impossible to decide whether the Lahakai pollen data might represent the more widespread, c. 50% dominance of *Calophyllum* spp. on Manus, or the rarer patches of monotypic stands.

Conclusion

The *Calophyllum*-rich forests of Manus are part of an island landscape that has supported a human population since the Pleistocene. We lack the detailed evidence necessary to show how people have impacted forest vegetation and vice versa. Nevertheless, *Calophyllum* spp are represented in both our local sequences, one based on a phase of human occupation on top of which has grown a distinctive monotypic forest, the other on palaeoecological signals from an area which archaeological evidence shows was well populated. In the most recent phase of both sequences, *Calophyllum* is somewhat anomalous, represented by a peculiar forest in the west, and a divergent pollen signal in the east.

Since we lack the observational data crucial for understanding the ecology of these trees and their community dynamics, we cannot make direct causal links between the former human settlement of the interior of southwest Manus and the succeeding monotypic forest, nor between the palynological record of Lahakai Swamp and the human activity represented by the nearby archaeological site. Nevertheless, the southwest Manus archaeological landscape makes it clear that the absence of human settlement in the recent forest of western Manus was not a permanent condition, and that the forest almost certainly post-dates agricultural disturbance. On the other hand, in eastern Manus, agricultural activities have continued to the present. This contrast in the history of human activity might be correlated with the distribution of monotypic *Calophyllum* forest. One possibility is that the monotypic stands formed after a pattern of moderate-scale, relatively frequent disturbance initiated by agriculture was interrupted by a gradual cessation of garden clearance, so that both frequency and scale of disturbance decreased. Tests of this hypothesis are offered by the unstudied archaeological potential and as yet undescribed ecological characteristics of other occurrences of monotypic *C. euryphyllum* forest, on Manus, Rambutyo and elsewhere. Further efforts to understand the phylo- and phytogeography of *Calophyllum* spp. in the southwest Pacific are warranted, including palaeoecological research focused on mapping the temporal and spatial distribution of *Calophyllum* from local sequences.

We conclude by noting that the benefits of interdisciplinary research include rephrasing and refocusing complex questions, such those posed by the ecological histories of islands, as much as answering them.

Acknowledgements

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