Island ecosystem and biodiversity dynamics in northeastern Australia during the Holocene: Unravelling short-term impacts and long-term drivers
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The Holocene published online 25 April 2012
DOI: 10.1177/0959683612441840

The online version of this article can be found at:
http://hol.sagepub.com/content/early/2012/04/25/0959683612441840

>> OnlineFirst Version of Record - Apr 25, 2012

What is This?
Island ecosystem and biodiversity dynamics in northeastern Australia during the Holocene: Unravelling short-term impacts and long-term drivers

Ulrike Proske and Simon G Haberle

Abstract

Vegetation changes of tropical Lizard Island (Great Barrier Reef World Heritage Area, Australia) over the last 8000 years are derived from palaeoenvironmental analysis of a 475 cm long sediment core. During early-Holocene sea-level rise, flooding of the continental shelf and thus isolation of Lizard Island, the pollen record shows the gradual establishment of a mangrove forest paralleled by contraction of the near-coastal palm and grass-dominated vegetation. Subsequently, mid-Holocene relative environmental stability supported a diverse, Rhizophora-dominated mangrove and open, mixed sclerophyll vegetation inland. Around 6000 years ago, a profound disturbance of the mangrove is recorded by a siliciclastic layer and we hypothesise that this deposit documents the impact of a storm or cyclone. Postevent environmental conditions were strongly altered with enhanced estuarine conditions supporting a Sonneratia and Bruguiera-dominated mangrove forest. During late-Holocene sea-level fall and stabilisation, progradation and contraction of the mangrove forest was paralleled by the expansion of a palm-dominated swamp. Freshwater taxa continued to dominate the record, however, a distinct disturbance signal from anthropogenic activity is recorded in the last century. Although Sonneratia dominated the post-event mangrove, late-Holocene environmental instability led to the extinction of this genus on the island. Local environmental changes in the freshwater swamp and rainforest also led to the loss of Arenga and Ilex from the island’s ecosystems. Our record implies that long-term ecosystem and biodiversity change on Lizard Island is: (a) primarily reflected in the spatial extent of the island’s vegetation communities and the species dominance within them and (b) driven by an interplay between climate, sea-level and potentially human activity. In addition, a short-term impact provoked the reconfiguration of the mangrove, potentially causing long-term ecosystem instability and thus impacting on mangrove biodiversity development on the Great Barrier Reef islands.

Keywords

biodiversity, cyclone impact, Lizard Island, local extinction, mangrove development, Queensland

Received 16 August 2011; revised manuscript accepted 2 February 2012

Introduction

As a result of their geographical isolation from biotic source areas, limited habitat space and specialised dispersal pathways, Pacific Island plant ecosystems are particularly vulnerable to changes in sea-level and climate (Gillespie and Clague, 2009; Mueller-Dombois, 2009). Long-term and slow environmental changes usually lead to spatial adaptations and the extinction of species with narrow ecological tolerance ranges, implying that biodiversity decline is predominantly caused by habitat loss (Mueller-Dombois, 2009; Pitelka, 1997). In the short term, the Pacific Islands are affected by heavy storms and cyclones that can cause alterations in ecosystem structure which may lead to loss in island biodiversity (Blumenstock, 1961; Woodroffe, 1983). Late-Holocene human colonisation of the islands, however, impacted most profoundly on the vegetation through deforestation, soil degeneration, extensive burning of the landscape and disruptions of seed dispersal pathways (Burney et al., 2001; Fall, 2005; Haberle, 1996; Prebble and Dowe, 2008; Rolett, 2009; Rowe, 2007; Saez et al., 2009). This disturbance has led to the loss of both single species as well as whole plant communities and the promotion of disturbance-adapted plants.

Although long-term and abrupt vegetation changes have been studied on numerous Pacific Islands, mangrove ecosystems often have been given less attention particularly regarding their Holocene biodiversity development and the long-term impact of storms and human activity on these ecosystems. Mangroves are widespread along tropical and subtropical shorelines where they form the connecting ecosystem between land and ocean. Because of this position, mangroves play a major role in the coastal landscape by providing a nursery habitat for economically important marine organisms, protecting the shoreline from erosion and dampening the impact of storms and storms surges (UNEP-WCMC, 2006). Every year tropical storms devastate coastal areas around the world, with the degree of ecosystem damage varying from complete defoliation and uprooting of trees to minor damage in particularly vulnerable parts of the forest (Cahoon et al., 2003; Kauffman and Cole, 2010; Roth, 1992; Sherman et al., 2001).
Post-cyclone recovery patterns in the affected mangroves are species-dependent, site-specific, complex and controlled by the forest’s original structure which can lead to a completely altered species composition in the regenerating forest (Baldwin et al., 2001; Ferwerda et al., 2007). This implies that past cyclones and other natural catastrophic events such as tsunamis potentially played a major role in controlling the development of forest structure and composition as observed in the modern mangroves (Alongi, 2008). Today’s most diverse mangroves are located along the Indian and West Pacific Ocean with centres of high species numbers in Indonesia, Papua New Guinea and northern Australia (Spalding et al., 2010). One of northern Australia’s mangrove diversity hotspots is Queensland’s eastern coast with up to 30 species inhabiting one site (Duke, 2006). Queensland’s mangroves have been studied repeatedly with the majority of the research focusing on modern mangrove distribution (Bunt, 1996; Crowley et al., 1994) and the controlling factors of forest composition (Duke, 2006; Saenger, 1985). So far, however, only a few studies have investigated long-term mangrove development along this vast coastline.

The Holocene development of Queensland’s coastal ecosystems is mainly controlled by the variations in sea-level; the early-Holocene rise, the mid-Holocene highstand and the subsequent decline to its modern level. There is a lack of consensus regarding the extent and longevity of sea-level rise above its modern datum in the mid Holocene. Woodroffe (2009) argues for a 2.8 m highstand around 5000 cal. yr BP whereas others suggest that sea level did not rise above 1.5 m and declined from 6000 cal. yr BP onwards (Baker and Haworth, 2000; Chappell, 1983; Larcombe and Carter, 1998; Yu and Zhao, 2010). Irrespective of the differences in timing and elevation, during the sea-level highstand large parts of Australia’s coast and estuaries were flooded which created a new habitat for mangroves that were much more extensive than those seen today. This ‘big swamp phase’ (Woodroffe et al., 1985) is evident in mangrove deposits throughout northern Australia and nearby tropical regions, and is also observed in northeastern Queensland coastal sites such as Three-Quarter Mile Lake (Luly et al., 2006), the Mulgrave River region (Crowley et al., 1990) and Hinchinbrook Island (Grindrod and Rhodes, 1984). Subsequent to the highstand period, falling sea-level led to the progradation and contraction of the mangrove communities. Site-specific features such as geomorphology, substrate and freshwater input controlled the extent and composition of mangrove forests during this phase.

Queensland’s coast is repeatedly affected by cyclones and studies on cyclone activity show that these events have impacted on the coastal system throughout the Holocene. Extreme cyclones made landfall every c. 80 (Chappell, 1983) to 177 (Nott and Hayne, 2001) years along Princess Charlotte Bay, every 280 years on Curacao Island north of Townsville (Hayne and Chappell, 2001) and every 253 years on Lady Elliot Island south of Rockhampton (Nott and Hayne, 2001). These events would have affected the coastal ecosystems and although the majority of Holocene mangrove records document vegetation disturbance, these signals are rarely ascribed to past storm events (Grindrod, 1985). In addition, recovery patterns or impacts on ecosystem diversity are rarely discussed.

The only study detailing cyclone damage in Queensland’s mangroves is provided by Hopley (1974) who describes the impact of the 1971 Cyclone Althea on the coastal region of Townsville. He shows that large-scale damage due to sediment erosion and chenier progradation was observed in lagoonal Bruguiera and Rhizophora and in young mangrove stands (Hopley, 1974). Large parts of the forest exhibited no immediate damage but sediment deposition caused root burial especially in the Avicennia stands leading to mortality within 12 months post-cyclone (Hopley, 1974).

The study presented here is the first one to document the impact of a past catastrophic event on mangrove forest structure in Queensland and to detail the dynamics of post-event ecosystem recovery. In addition, causes for the extinction of three genera on the island are discussed and major driving mechanisms behind biodiversity development are outlined.

**Study area**

Lizard Island is part of the Great Barrier Reef World Heritage Area and is situated c. 93 km northeast of Cooktown and 30 km east from the Australian mainland coast. The reef-fringed island covers approx. 12 km² and rises to c. 359 m a.s.l. The drainage pattern is defined by the two NNW–SSE trending ridges (Figure 1a), however, there is no major river on the island. The yearly rainfall averages 1600–2000 mm which falls mainly during the austral summer wet season (Bureau of Meteorology, 2011). South-easterly wind directions dominate especially during austral winter whereas cyclones occur throughout the austral summer and early autumn. Between 1906 and 2007 six cyclones of varying categories crossed the Lizard Island region (Bureau of Meteorology, 2011), however, no reports are available on the degree of damage caused by these cyclone events. Annual air temperatures range between 20° and 34°C. The tides are semidiurnal and range between 2.5 (spring) and 0.3 m (neap).

**Geology and vegetation**

Lizard Island is composed of late Permian granite (Rees et al., 2006) that weathered into clastic sandy sediments depositing on and close to the island (Jones, 1984). These sediments form porous soils that can support a variety of vegetation types that are commonly found throughout northern Australia.

The first vegetation survey of the island flora conducted in the 1970s shows that approximately 60% of the island is covered by grassland (Figure 1b) dominated by kangaroo grass Themeda australis (Stapf 1918) and reedgrass Arundinella nephelensis (Trinius 1826) (Byrnes et al., 1977). Smaller patches are vegetated by closed forest (or rainforest), low closed forest (or semi-deciduous notophyll vine forest), closed shrub forest and heathland. Large parts of the central island are dominated by Thryptomene oligandra (Mueller 1858), Acacia crassicaarpa/A. humifusa (Bentham 1842) and Eucalyptus tesselaris (Mueller 1858) (Figure 1b). Permanently wet areas in the central valley are covered by Pandanus-dominated or grassy vegetation. The coastal and backriffs areas are vegetated by mangroves, dune and strand communities.

Mangroves on Lizard Island are found on Crystal Beach, Mangrove Beach and Watson Bay with the latter being the most extensive forest (Figure 1b). The mangroves in Watson Bay are located at the landward side of the sandy beach and dune complex and are sustained by regular tidal inundation via a small outlet (Byrnes et al., 1977). Compared with nearby mainland forests, mangroves on the inner Great Barrier Reef islands are reported to have fewer species and associates with Bruguiera pavilifora (Griffith 1836), B. sexangula (Poir 1816), Ceriops decandra (Ding Hou 1958), Acanthus ilicifolius (Linnaeus 1753), Acrostichum species (Willdenow 1810), Cynometra iripa (Kosteletzky 1835), Diospyros ferraea (Bakhuizen 1933), Heritiera littoralis [Aiton 1789] and Xylocarpus mekongensis (Pierre 1897) absent from many islands (Stoddart, 1980; Tomlinson, 1994). The mangrove assemblage on Lizard Island shows a slightly higher diversity than has been recorded for nearby islands (Stoddart, 1980) and the closest mainland site, Princess Charlotte Bay (Grindrod, 1985). Besides those species that are also common on the mainland (Avicennia marina var. australasica [Moldenke 1960], Bruguiera gymnorrhiza [Bentham 1864], B. exaristata [Ding Hou 1956], Ceriops tagal...
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[Robinson 1908], Excoecaria agallocha [Linnaeus 1759], Lumnitzera racemosa [Willdenow 1803], Osbornia octodonta [Mueller 1863] and Rhizophora stylosa [Griffith 1854]), the island’s mangroves also host Xylocarpus granatum [Koenig 1784], Aegialitis annulata [Brown 1810], Acrostichum speciosum and some associates such as the vine Derris trifoliata [Loureiro 1790], Rhizophora mucronata [Lamarck 1804] which is recorded from the mainland does not occur on the island.

Material and methods

In 2009 cores LIWB01 and 02 were collected at the landward edge of the mangrove swamp on Watson Bay which is located at the northwestern shore of Lizard Island (Figure 1). The core LIWB01 (14°40′4.50″S, 145°27′10.06″E) was hand-drilled with a 50 cm long d-section-corer close to the small drainage channel that connects the Pandanus and mangrove swamp with the sea (Figure 1). The top of the core is c. 3 m above modern sea level.
Subsequently the core was described in the field and sampled in the laboratory.

**Radiocarbon dating**

In order to obtain chronological control of the record, radiocarbon samples have been taken in a regular sampling interval. Additional samples were taken subsequent to the pollen analysis to date major ecological changes.

Owing to the absence of carbonate shells or large organic fragments, bulk samples that primarily consist of organic material (woody plant remains) were collected. These eight samples were submitted for radiocarbon dating at the ANU and Waikato Radiocarbon Dating Laboratory where all samples were treated with HCl and NaOH prior to analysis (see Table 1 and Figure 2). All radiocarbon dates were calibrated with Calib 6.0 (Stuiver and Reimer, 1993) using the terrestrial Southern Hemisphere Atmosphere calibration set (Mc Cormac et al., 2004).

**Grain size analysis**

The major part of the core consists of peat with varying but minor amounts of silt and clay (Figure 3a). Siliciclastic sediments occur between the base of the core to 340 cm, between 240–260, 105–170 and 70–0 cm. One Pandanus nut is documented at c. 340 cm.

![Figure 2. Age depth model.](image)

**Table 1.** Radiocarbon ages of core LIW801. The 2σ range of all samples is used in order to account for the variance of the calibration curve in the covered time span.

<table>
<thead>
<tr>
<th>Sample (cm)</th>
<th>Sample code</th>
<th>δ¹³C (%)</th>
<th>Uncalibrated ¹⁴C age</th>
<th>Calibrated age (yr BP) (2σ)</th>
<th>Dated material</th>
</tr>
</thead>
<tbody>
<tr>
<td>25–26</td>
<td>WK 30382</td>
<td>−27.2</td>
<td>189 ± 30</td>
<td>130–290</td>
<td>organic-rich sediment samples (bulk)</td>
</tr>
<tr>
<td>50–51</td>
<td>WK 30383</td>
<td>−27.2</td>
<td>1697 ± 30</td>
<td>1420–1620</td>
<td>organic-rich sediment samples (bulk)</td>
</tr>
<tr>
<td>90–91</td>
<td>ANU 18726</td>
<td>−26.4</td>
<td>5270 ± 45</td>
<td>5900–6120</td>
<td>organic-rich sediment samples (bulk)</td>
</tr>
<tr>
<td>136–137</td>
<td>WK 30384</td>
<td>−27.9</td>
<td>4834 ± 37</td>
<td>5450–5600</td>
<td>organic-rich sediment samples (bulk)</td>
</tr>
<tr>
<td>164–165</td>
<td>ANU 18723</td>
<td>−23.8</td>
<td>5650 ± 40</td>
<td>6300–6450</td>
<td>organic-rich sediment samples (bulk)</td>
</tr>
<tr>
<td>260–261</td>
<td>ANU 18731</td>
<td>−27.8</td>
<td>6095 ± 35</td>
<td>6780–7000</td>
<td>organic-rich sediment samples (bulk)</td>
</tr>
<tr>
<td>344–345</td>
<td>ANU 18023</td>
<td>−24.5</td>
<td>6400 ± 45</td>
<td>7170–7340</td>
<td>organic-rich sediment samples (bulk)</td>
</tr>
<tr>
<td>440–441</td>
<td>ANU 18732</td>
<td>−28.1</td>
<td>7250 ± 45</td>
<td>7940–8070</td>
<td>organic-rich sediment samples (bulk)</td>
</tr>
</tbody>
</table>

To determine the sedimentological properties of those core sections with a considerable siliciclastic portion, 36 samples of 1–3 cm thickness (c. 2.5–5 cm³ of raw material, Table 2) were analysed for their grain size distribution using the laser diffraction method. Prior to measurement all samples were treated with 30% H₂O₂ overnight to remove the organic fraction, sieved through a 2000 µm sieve to remove larger particles, treated with 10% HCl to remove any carbonates and transferred into calgon (Na₂O₁₈P₆O₁₆) to disperse any aggregates. In addition, every sample was physically dispersed using ultrasound for two minutes (Ryzak and Bieganowski, 2011). All samples were measured five times using the Malvern Mastersizer 2000 with Hydro MU attachment at the The Fenner School of Environment & Society at ANU. Subsequently the average of these five measurements was used to determine the grain size distribution for each sample.

**Pollen, spore and charcoal analysis**

Processing for pollen analysis was carried out on 43 samples and followed the standard KOH, HF, HCl and acetylation method (Bennett and Willis, 2001). Residues of each sample were mounted on slides and at least 300 pollen grains per sample were counted at 400× magnification. Pollen identification and nomenclature follows that set out in authored reference material (Huang, 1972; Thanikaimoni, 1987) and regional reference collections currently held at the Department of Archaeology and Natural History, Australian National University (see online collection at http://apsa.anu.edu.au/). Pollen taxa (Appendix 1) are divided into the following taxonomic or ecological groupings for pollen diagram representation: mangrove (Avicennia, Rhizophora, Sonneratia, Bruguiera and Ceriops), back mangrove (Lumnitzera, Excoecaria and Xylocarpus), Arecaceae/Pandanaceae (Pandanus, Cocos and Arenga), rainforest (characterized by a diversity of different genera, e.g. Barringtonia, Moraceae/Urticaceae and Euphorbiaceae), sclerophyll woodland (containing Myrtaceae, Casuarina, Dodonea and others) and herbaceous taxa (Poaceae, Euphorbiaceae), Acantaceae and Chenopodiaceae/Amaranthaceae). Three pollen types within the genus Sonneratia are recognised and separated in the analysis: Sonneratia x guingai, Sonneratia alba/caseolaris and Sonneratia ‘abnormal grains’ (see Appendix 2). The group ‘abnormal grains’ includes two types of pollen grains; those with excessive growths on their exine (Appendix 2, A and B) and grains that appear to be incompletely developed (Appendix 2, C). Such pollen grains of Sonneratia are described as being of ‘irregular shape’ though are rarely observed (Muller, 1969; Wright, 1977). Pollen counts are expressed as percentages of the total pollen sum, which in most cases reaches a minimum of 250 (excluding pollen of pteridophyte spores and aquatic vascular plants). Charcoal on the pollen slides (microcharcoal: black, opaque angular particles >10 µm) was also counted as an indicator for fire in the landscape (Whitlock and Larsen, 2001). 475
samples were subsampled (2 cm$^3$) for macrocharcoal analysis (>125 μm and >250 μm fractions) using the method employed at the Department of Archaeology and Natural History, ANU (Stevenson and Haberle, 2005). This includes bleaching overnight and sieving through a 125 μm and 250 μm sieve. The concentrations of fragments per unit volume were then counted under a Zeiss stereo microscope at 100× magnification and the data have been analysed using CharAnalysis (Higuera et al., 2009). The pollen diagram was constructed and the data analysed in psimpoll (Bennett, 2005). The stratigraphically constrained pollen data were divided into the maximum number of statistically significant zones using binary splitting by sum-of-squares analysis on taxa within the pollen sum and whose pollen values exceeded 5% at least once. Based on the distinct change in ecosystem dominance

![Figure 3](image-url)
The Holocene

Principal component analysis (PCA) was used to reduce the variability of the data set to two dimensions, using all pollen and spore taxa and charcoal concentration values. The calculation of palynological richness (rarefaction analysis) was developed as a way of comparing the diversity of pollen taxa in each sample by standardizing the pollen count between samples (Birks and Line, 1992).

Results

Chronology and sediment properties

Radiocarbon ages derived from bulk samples allow for the establishment of a basic chronology, however, older (reworked material) and/or younger radiocarbon (root contamination) might contaminate the selected material (Olsen, 1986; Tornqvist, 1992). Mainly samples with a high siliciclastic content can contain substantial amounts of reworked, older radiocarbon that has been transported into the site along with the minerogenic fraction (Tornqvist, 1992). The samples chosen here are of peaty character and primarily consist of organic material. Thus, contamination of these samples with older radiocarbon can be considered minimal. Introduction of younger radiocarbon by roots growing into the substrate appears to be the most likely source of error for the samples used here, though every effort was made to remove visible root matter prior to analysis (Tornqvist, 1992). To account for this uncertainty, all calibrated ages should be treated as estimates.

To determine a continuous age model for the core (Figure 2), a constrained least-squares cubic spline was fitted to the calibrated radiocarbon ages as a function of depth (de Boor, 1994). The spline was constrained to be monotonic (increasing age with depth) with the surface anchored to a modern age (2009). The spline was constructed with four knots, two fixed at the extremes of the depth scale and two interior knots with positions that were allowed to move in order to obtain the best fit to the data.

The calibrated dates show that the major part of the core is of mid-Holocene age (Table 1), a phenomenon which is observed in many coastal records that include Holocene mangrove deposits (Chappell, 1993; Clark and Guppy, 1988; Crowley et al., 1990; Woodroffe, 2000). The lowermost age at 440–441 cm (between the two basal sandy layers) dates into the early mid-Holocene at 7940–8070 cal. yr BP indicating an approximate maximum age for the record. The age reversal at 90–91 cm indicates that...
Three sections of core LIWB01 consist of a pronounced portion of siliciclastic material (Figure 3a). The basal part (from c. 470 to 370 cm) is characterised by a poorly sorted, primarily coarse sand-sized sediment that mainly consists of angular quartz and feldspar (Table 2). Gravel- and silt-sized particles occur commonly throughout this part of the record (Table 2). Towards the top of this section, a fining towards fine sand and ultimately silt grain size is paralleled by an increasing amount of organic matter.

The second portion of siliciclastic material occurs between c. 135 and 170 cm. This layer has a sharp boundary to the underlying peat and consists of poorly sorted, primarily fine sand to very fine silt-sized mica, quartz and feldspar (Table 2). Inverse grading is apparent in this layer.

The third section between c. 50 and 0 cm is characterised by poorly sorted, mainly fine to medium sand-sized quartz and feldspar grains with large amounts of organic debris.

Poollen, spores and charcoal

The pollen and spore distribution of core LIWB01 is shown in Figure 3a and b. The results of the micro- and macrocharcoal analysis are shown as concentration of particles in Figure 3a at the same depth intervals. The table in Appendix 1 lists all counted taxa and the corresponding species described on Lizard Island. In samples 445, 275, 265, 255, 125 and 75 cm, the pollen concentration is too low for an adequate pollen sum to be attained, which led to the exclusion of these samples from the record. To estimate whether the organic material in the sediments underwent postdepositional degradation, fungal spores have been counted in each sample. The abundance of fungal spores has been used as proxy for the active decomposition of buried organic matter (Almeida-Lenero et al., 2005). Relatively high values of fungal spore concentration, however, are generally paralleled by a high total pollen concentration in the core, which implies that decomposition of pollen by fungi was minimal. The lowest portion of the core consists of very coarse, clean sands that most likely deposited more rapidly than the clayey material. Thus the basal age of the lowest pollen zone remains an estimation.

Pollen zone 1 (475–311 cm, c. 8090–7130 cal yr BP). The lowermost zone 1a (475–420 cm, c. 8090–7870 cal yr BP) is characterised by Pandanaceae/Arecaceae (Pandanus 21–50%, Arecaceae type Cocos 3–38%) and herbs (Poaceae 1–21%, Cyperaceae 3–15%). Minor components are rainforest (Ulmaceae up to 7%), Ilex and Euphorbiaceae both up to 4%) and mangrove taxa (Rhizophora up to 10%, Bruguiera up to 4% and some back mangrove taxa). The spore association is dominated by Acorus (with minor occurrences of Cyclonurus- and Lygodium-type. The pollen concentration is low to moderate and charcoal concentrations are low. The rarefaction index is consistently high in this zone.

Zone 1b (420–311 cm, 7870–7130 cal yr BP) is characterised by the decrease in previously dominant components such as Poaceae, Cyperaceae and Arecaceae type Cocos. Simultaneously values of Rhizophora (22–38%), Arecaceae type Arenga (1–10%) and some back mangrove taxa increase. The spore concentration is relatively low with Davallia/Dynaria- and Cyclonurus-type dominating the assemblage. The pollen concentration remains on a moderate level and charcoal concentration increases. Micro-charcoal reaches a high peak in the lower part of this zone. The rarefaction index is variable but remains mostly high in this zone.

Pollen zone 2 (311–161 cm, 7130–6900 cal yr BP). This zone is dominated by relatively uniform values of mangrove (mainly Rhizophora 45–83%, Sonneratia up to 8% and Avicennia 1–2%) and back mangrove taxa (up to 3%). Freshwater vegetation is mainly represented by Pandanaceae/Arecaceae (Pandanus 4–17%, Arecaceae type Cocos 1–5%) and sclerophyll woodland (up to 8%). Spores of Davallia/Dynaria-, Cyclonurus- and Adiantum-type occur infrequently and concentration values are very low. In comparison with the previous zone the pollen concentration has slightly decreased and charcoal concentrations remain low to moderate throughout the zone. The rarefaction index is decreasing slightly in this zone.

Pollen zone 3 (161–140 cm, 6900–6000 cal yr BP). This narrow zone marks the abrupt increase of Pandanaceae/Arecaceae taxa (Pandanus 26–87%, Arecaceae type Arenga up to 12%) being paralleled by enhanced values of sclerophyll woodland (up to 10%), herbs (up to 8%) and rainforest taxa (up to 8%). A similar sudden increase is documented in the values of Davallia/Dynaria-type spores and the pollen concentration. charcoal concentrations increase slightly in this zone and the rarefaction index reaches a minimum in this zone.

Pollen zone 4 (140–50 cm, 6000–1470 cal yr BP). The fourth pollen zone documents the recurrence of mangrove taxa being dominated by either Sonneratia (up to 80%) or Rhizophora (up to 63%). Both mangrove taxa, however, show highly alternating values throughout the whole zone. The three Sonneratia taxa identified in this analysis all show peak percentage values, with the Sonneratia ’abnormal grains’ peaking first and immediately after the sand/silt layer recorded in zone 3. Macrocharcoal (>125 μm) concentrations are also high in the lower part of this zone. The Sonneratia peak is followed by a rise in Rhizophora and then a shift to dominance of Sonneratia x gulngai and Sonneratia alba/caseolaris. Other mangrove forest taxa also contribute to the signal (Avicennia up to 5%). The freshwater taxa signal is dominated by Pandanaceae/Arecaceae (up to 28%). Spores show low concentration values with Adiantum-type being the most dominant one. The pollen concentration falls back to very low values, whereas charcoal concentration remains low to moderate with the exception of peak values in macrocharcoal (>125 μm). The rarefaction index remains low to moderate in this zone

Pollen zone 5 (50–8 cm, 1470 cal BP to AD 1976). This zone is characterised by the abrupt decrease in all mangrove taxa, and in some samples the disappearance of mangrove taxa. The back mangrove taxa Exocoetaria remained prevalent with up to 8% representation. Pandanaceae/Arecaceae are dominating the assemblage (60–86%) with minor occurrences of sclerophyll woodland taxa (up to 15%) and herbs (Cyperaceae up to 7%, Poaceae up to 3%). Spore concentration values are highest in the whole record showing a strong signal from Cyclonurus- and Lygodium-type. The pollen concentration values rise to a moderate level and the microcharcoal concentration increases to peak.
levels, whereas macrocharcoal concentration remains low to moderate and the rarefaction index decreases.

**Pollen zone 6 (8–0 cm, AD 1976–2009).** The uppermost zone marks the rapid increase in sclerophyll woodland taxa with Myrtaceae pollen (63–69%) dominating the signal. Pandanaceae/Arecaceae are contributing with 11–14%, back mangrove (mainly *Excoecaria*) with up to 8% and rainforest taxa (mainly *Barringtonia*) with up to 4%. Spore concentrations decline with only low values of *Cyclosorus*, *Adiantum*- and *Lygodium*-type. The pollen concentration increases to very high values and charcoal concentration remain similar to the previous zone as does the rarefaction index.

**Macrocharcoal analysis**
Figure 4 shows the complete macrocharcoal data sampled at every centimetre, which has been analysed using CharAnalysis (Higuera et al., 2009). Figure 4a shows the peak fire event (+) reconstruction based on raw charcoal accumulation rate (black histograms) over interpolated 7 yr intervals with the background signal (Lowess smoothing, grey line) and global threshold (mean Gaussian model). Figure 4b shows the fire recurrence interval with fire events marked as grey boxes and the simulated fire frequency of 1000 yr intervals. The macrocharcoal record has been divided into two periods that are analysed independently, the lower one spanning the period of high sedimentation accumulation rate between 8090 and 5800 cal. yr BP and the upper spanning the period of low sedimentation accumulation rate from 5800 cal. yr BP to AD 2009. Charcoal accumulation rates are over 10× higher in the lower section of the record compared with the upper section. This is likely to be associated with different charcoal sources and taphonomic processes that influenced charcoal deposition at the site. CharAnalysis identifies a fire frequency of between 5 and 2 events per 1000 years during this period. There is a major peak in macrocharcoal accumulation rate immediately after 6000 cal. yr BP (the end of pollen zone L-3) and ending at 5800 cal. yr BP. Low levels of macrocharcoal persist for nearly the next 4000 years when fire event frequencies are <1 event per 1000 years. The fire frequency begins to increase after 1500 cal. yr BP and reaches a level of 3 fire events per 1000 years towards the present.

**Principle Components Analysis**
The Principle Components Analysis (PCA ordination biplot, Figure 5) shows the changes in assemblage composition through time. The ordination of pollen and spore types is dominated by the major mangrove forest and open grassland vegetation and charcoal, and illustrates the important roles of these taxa in characterising particular pollen zones. Axis 1 (PCA1) explains 33.6% of the variance, and primarily separates mangrove taxa (i.e. brackish water communities), with positive loadings, from grassland, palm and sclerophyll taxa (i.e. inland vegetation), with mostly negative loadings. Axis 2 (PCA2) explains less variance (15.7%), but distinguishes an undisturbed (negative loadings) environment from a disturbed environment characterised by higher micro- and macrocharcoal values (positive loadings).
The site could have induced a more effective burial of charcoal in dart, 1980). High charcoal accumulation values are recorded. The fern Arenga (Jones, 1996) is an example of such a compositional shift. Early-Holocene sea-level rise led to the retrogradation of the shoreline on Lizard Island which in turn caused the contraction of inland habitats and the gradual establishment of mangrove forests at the site between 7870 and 7130 cal. yr BP (Rees et al., 2006). This sandy substrate together with the moist conditions in the valley favoured the growth of palm swamps being dominated by Pandanus, Cocos and sedges. The presence of coconut for at least the last 8000 years implies that a viable population, being less abundant on the mainland coast of northeastern Australia (Dowe and Smith, 2002), persisted on the offshore islands prior to European arrival into Australia. The island’s hills were primarily covered by grasslands reflecting drier soil conditions in large parts of the island’s landscape and fires are likely to have occurred in this environment (L-1 in Figures 3a, 4). Rainforest was likely to be restricted to moist gullies and small valleys in the central ridge system (zone L-1a).

Early-Holocene sea-level rise led to the retrogradation of the shoreline on Lizard Island which in turn caused the contraction of inland habitats and the gradual establishment of mangrove forests at the site between 7870 and 7130 cal. yr BP (zone L-1b, Figure 3). Although freshwater-dominated habitats were receding, all previously recognized vegetation communities remain present and environmental changes are predominantly reflected by compositional shifts within these ecosystems. The decline in Cocos and increase in Arenga is an example of such a compositional shift here in the palm swamp complex. It appears that this shift is induced by a change in the depositional and hydrological setting; from a formerly very well-drained sandy substrate, being optimal for Cocos, to a moister, more fine grained sediment, being supportive for Arenga (Jones, 1996). This enhanced soil moisture is also documented by the increase in Davallia/Dynaria-type ferns that are associated with freshwater drainage features on Lizard Island (Byrnes et al., 1977). The palynological signal of the establishing mangrove forest is dominated by Rhizophora, however, minor occurrences of Sonneratia, Ceriops, Bruguiera, Exocoecaria and the fern Acrostichum indicate that a diverse mangrove community occupied the intertidal to supratidal zone (Stoddart, 1980). High charcoal accumulation values are recorded during the early phases of mangrove establishment around 7600 cal. yr BP (Figure 4). Changes in the depositional environment at the site could have induced a more effective burial of charcoal in the swampy sediment, however, simultaneously a high fire frequency of c. 4–5 fire events per 1000 years implies enhanced burning of the landscape. The transition from grassland dominance to a greater density of sclerophyll woodland underlines that high frequency burning and charcoal production was most likely occurring within the inland environment (Figures 4c, 5). This phenomenon of high frequency burning and high charcoal production coinciding with major vegetation shifts has been observed throughout mainland Australian tropical landscapes and appears to have been most prominent during the early Holocene (Haberle et al., 2010; Kershaw et al., 2002).

Mid Holocene: Mangrove forest dominance and disturbance

After c. 7000 years BP, when sea-level rise slowed down (Woodroffe, 2009; Yu and Zhao, 2010), environmental conditions appear to have been optimal for a thriving mangrove forest on Lizard Island (zone L-2, Figure 3a, b). Pollen from central and back mangrove taxa such as Avicennia, Sonneratia, Bruguiera and Lumnitzera document a distinct sea- and landward zone in the relatively diverse forest.

In the mid Holocene sea-level rise slowed down and culminated in a highstand of probably 1 m or more above modern datum. This led to the flooding of low-lying coastal and estuarine areas which created new mangrove habitats. Consequently large and diverse mangrove forests developed throughout tropical Australia but also in Southeast Asia and the Pacific (Ellison, 2008; Grindrod et al., 1999; Prose et al., 2010; Thampanya et al., 2006; Woodroffe et al., 1985). In these stable and favourable mid-Holocene conditions numerous mangrove species showed a wider longitudinal and latitudinal distribution than today (Crowley, 1996; Crowley and Gagan, 1995; Hashimoto et al., 2006).

Owing to the maximum expansion of the mangrove forest on Lizard Island, habitats for ecosystems in the valley appear to be further restricted. Less abundant occurrences from Arenga and Pandanus probably reflect these spatial limitations (zone L-2, Figure 3a, b). Taxa from sclerophyll woodland, however, continue to increase in this phase and their strong alignment with high values of charcoal accumulation (Figures 4, 5) indicates that continued burning of the landscape induced further changes in the dryland ecosystems (Figures 3a, 4).

Approximately 6000 cal. yr BP, the record shows a disturbance of the mangrove forest environment documented by the deposition of a c. 25 cm thick layer of silicilastic sediment (L-3, Figure 3a, Table 2). The grain size distribution (poorly sorted, predominantly very fine to fine sand-sized quartz, feldspar and mica grains) and the lack of carbonate particles suggest a close
terrestrial source of the deposited material whereas the sharp boundary to the underlying peat indicates rapid deposition. The unit’s palynological sign consists of pollen from proximal and distal inland ecosystems, predominantly *Pandanus, Avenga* and to a lesser extent sclerophyll woodland and rainforest taxa. The rapid deposition of clastic and allochthonous organic material with these characteristics requires a short but high-energy event impacting on the whole island.

The region of Lizard Island was affected by high-energy events, such as large storms and cyclones, throughout the Holocene (Hayne and Chappell, 2001; Nott et al., 2009). Cyclones are associated with high wind speeds, wave run-up and heavy rainfall that usually cause large-scale erosion of morphologically exposed features and often produce characteristic sediment units in coastal and shallow-marine areas (Carter et al., 2009; Castaneda-Moya et al., 2010; Nott, 2006; Swiadek, 1997).

In the case of Lizard Island we hypothesize that such an event triggered the deposition of the siliciclastic material in the central valley. The thickness, poor sorting, inverse grading, allochthonous content and location of the deposit within the coastal area are typical for storm deposits (Morton et al., 2007). Other characteristic features such as sets of graded planar mud laminae and foresets (Morton et al., 2007), however, have not been observed which could be ascribed to the environment in which the material was deposited. The high density of roots and stems in mangrove forests creates only small spaces for the deposition of mud laminae which subsequently can be destroyed and incorporated into the underlying sediment through bioturbation (Rhodes et al., 2011). Thus, deposits from high-energy events rarely exhibit the full suite of characteristic sedimentary features in these environments (Rhodes et al., 2011).

Following this event, mangrove forest taxa continue to dominate the pollen signal (L-4, Figure 3a), however, with a shift in species dominance. *Sonneratia* dominates directly after the event indicating the genus’ fast recovery probably by epicormic resprouting from damaged trees (Saenger, 2002). The large percentage of incompletely developed pollen grains and grains with disturbed exine ornamentation (Appendix 2), however, implies regrowth under considerable environmental stress (Foster and Afolin, 2005; Koti et al., 2005). The slower and stepwise recovery of the *Rhizophora*-signal is probably due to a more severe damage of these trees and the dependence on regrowth from seedlings and saplings (Bardsley, 1985; Woodroffe and Grime, 1999).

Subsequent to the initial phase of mangrove re-establishment, *Rhizophora* and *Sonneratia* dominate the mangrove assemblage together. The occurrence of the hybrid *Sonneratia* x *gulngai* [Duke 1984] necessitates both *S. alba* and *S. caseolaris* on-site (Duke, 1984; Duke and Jackes, 1987), implying that all three species were part of the late-Holocene mangrove community (Appendix 2). These three species, however, occupy different parts of the mangrove system with *S. alba* being most frequently observed on the landward edge of *Rhizophora* stands in the central mangrove (Stoddart, 1980) whereas *S. caseolaris* and *S. x gulngai* are dependent on more estuarine conditions (Duke, 2006). Together with a marked abundance of *Bruguiera*, the presence of *S. caseolaris* and *S. x gulngai* indicates that the coastal region experienced enhanced freshwater conditions during this phase (Figure 3b) (Duke, 2006).

In the early part of zone L-4, high fire occurrence being reflected in peak deposition rates for macrocharcoal documents enhanced environmental stress in the dryland ecosystems (Figure 4). The sharp drop in charcoal accumulation values around 5800 cal. yr BP could reflect the onset of wetter conditions as documented in the increase of fern spores and the stronger presence of less salt-tolerant mangrove taxa (Figure 3). Alternatively, lower fire frequencies may be the result of increasing isolation of the island from mainland Australia sources of fire ignition.

### Late Holocene: Contraction of mangroves and recent human impact

Optimal conditions for extensive mangrove growth ceased with the onset of late-Holocene sea-level fall to its modern datum (Baker and Haworth, 2000; Chappell, 1983; Larcombe and Carter, 1998; Yu and Zhao, 2010). Approximately 2000 cal. yr BP the pollen signal from the mangroves on Watson Beach declines indicating mangrove forest contraction and probably progradation of the shoreline (L-4, Figure 3). The change in sedimentary environment from effective particle trapping under the forest to enhanced sediment bypassing in the inland ecosystems is reflected in the sharp drop rather than gradual decline of mangrove pollen abundance values. The parallel increase and later dominance of *Pandanus* (L-5, Figure 3b) together with swarm-associated taxa such as *Lygodium*-type spores indicate the expansion of the central palm swamp forest. Back mangrove taxa such as *Excoecaria* continue to be present until today underlining the marginal character of mangroves at the coring site.

In the late c. 3000 years *Cyclosorus*, which has been reported as a disturbance indicator in tropical eastern Australia (Haberle et al., 2006), becomes more abundant. Together with increasing fire frequency and rising charcoal accumulation values from c. 1500 cal. yr BP onwards, more abundant *Cyclosorus* ferns imply enhanced vegetation disturbance in the late Holocene (Figures 3, 4). A highly variable climate related to the establishment of the modern ENSO-mode has affected tropical northeastern Australia during the last c. 5000 years with an intensification of ENSO around c. 3000 cal. yr BP (Gagan et al., 2004; Haberle et al., 2010; Shulmeister and Lees, 1995). This less stable climate could have caused prolonged drought periods leading to greater ignition potential of the predominantly grassland and sclerophyll vegetation.

The sharp increase in sclerophyll woodland in the uppermost part of the core (L-6, Figure 3) dates into the AD 1700s. Increased human activity on the island’s northern shores associated with increased tourism may have caused the deposition of eroded material from sclerophyll-vegetated slopes in the lowland area (Figure 1).

### Storm impacts on mangrove dynamics

The degree of damage caused by large storms and cyclones varies considerably in mangroves and is dependent on both the characteristics of the forest (width, ‘health’, composition, internal structure, etc.) as well as local abiotic factors (site elevation, soil characteristics, etc.). A general pattern, however, seems to emerge when comparing observations after recent storm damage from northern Australia, the Pacific and Caribbean. *Rhizophoraceae* are in most cases immediately and most extensively damaged by wind stress whereas dwarfed or shrubby trees appear to be more protected because of their compact growth form (Bardsley, 1985; Hopley, 1974; Roth, 1992; Smith et al., 1994; Stocker, 1976; Swiadek, 1997; Woodroffe and Grime, 1999). Species of *Avicennia* and *Sonneratia* seem to be mainly affected by sediment deposition on aerial roots causing the long-term mortality of these trees (Hopley, 1974; Paling et al., 2008; Sherman et al., 2001). From our record we cannot reconstruct mechanisms and degree of forest damage, however, the delayed post-disturbance event increase in *Rhizophoraceae* pollen could indicate that trees of this family were severely damaged on Lizard Island during the 6000 cal. yr BP event.

Forest regrowth patterns after storms or cyclones are driven by various factors: initial degree of tree damage, spatial extent of forest damage, soil characteristics, species-specific regrowth strategies (epicormic resprouting or via seedlings) (Bardsley, 1985; Piou et al., 2006; Stocker, 1976). The pollen signal from
Lizard Island shows immediate post-disturbance event presence of flowering *Avicennia* and *Sonneratia* trees implying that damage was minimal in this part of the forest or a relatively fast recovery through epicormic resprouting. The pollen record supports the notion that those mangrove species with the capacity for epicormic resprouting are likely to be advantaged over other mangrove species, leading to their dominance in a post-disturbance recovering forest (Stocker, 1976; Woodroffe and Grime, 1999). Despite *Sonneratia’s* strong post-disturbance event presence it appears that altered environmental conditions, possibly an excess of fresh water in the coastal system (Ball and Pidsley, 1995), caused physiological stress in this genus leading to the production of abnormal pollen grains. This phenomenon is not observed in the post-disturbance event *Avicennia*-pollen which can be ascribed to the robustness of *Avicennia* and its tolerance to a wide range of environmental conditions (Duke, 2006).

The recovery of Rhizophoraceae relies on seedlings and saplings, a much slower process that requires the presence of intact, flowering trees. The delayed but strong postdisturbance event signal from Rhizophoraceae on Lizard Island implies that only partial damage was caused in the forest and few intact trees could have supplied saplings for regrowth. Recolonization from stands on neighbouring islands such as the Nymph and Turtle Islands (c. 11 and 14 km to the west, respectively) could have been possible as well. The weak but present signal of Rhizophoraceae directly after the disturbance event, however, indicates the presence of at least a small flowering stand on Lizard Island. Our record further implies that long-term tree mortality caused by alterations in soil chemistry or root burial was probably minimal since all mangrove species continue to be present after the event.

**Mid- and late-Holocene decline in island biodiversity**

Holocene climatic and sea-level changes induced ecosystem adaptation on Lizard Island. Spatial and compositional variations in the vegetation communities reflect this environmental change, however, only three local extinctions (*Ilex, Sonneratia* and *Arenga*) are recognised so far which implies a general resilience of the island’s vegetation.

**Arenga.** During the early and mid Holocene the palm *Arenga* was a considerable part of the island’s inland palm swamp community (Figure 3b, Appendix 2). Two species of *Arenga* occur naturally in Australia, *Arenga australasica* [Moore 1963] and *Arenga microcarpa* [Beccari 1889], though the latter is restricted to small populations in the Northern Territory. *Arenga australasica* (Appendix 2) is recorded to have its last significant occurrence in the mid Holocene (c. 5800 cal. yr BP) and is not part of today’s island vegetation (Byrnes et al., 1977; Department of Environment and Resource Management Wildlife Online, 2010). The palm’s decline occurs at a time of less stable climatic conditions and high fire event frequencies. *A. australasica* is sensitive to poor drainage and fire (Jones, 1996), suggesting that strong seasonal fluctuations in the water-table and increased burning might have led to the palm’s extinction on the island.

**Sonneratia.** After the impact of the mid-Holocene (6000 cal. yr BP) disturbance event, *Sonneratia* was a major component in the mangrove forest until its late-Holocene contraction. Three different taxa of this genus have been recognised in this phase; *Sonneratia alba, S. caseolaris* and their hybrid *Sonneratia x galngai* (Appendix 2). None of these species, however, are reported from the modern island mangrove community today (Byrnes et al., 1977; Department of Environment and Resource Management Wildlife Online, 2010; C Lovelock, personal communication, 2010). The last significant occurrence of *Sonneratia* dates into the late Holocene (c. 1500 cal. yr BP); a phase during which enhanced landscape disturbance is documented in the record (see discussion above, Figures 3, 4, 5). Probably during this time of general landscape change which includes the contraction and seaward movement of the mangrove forest, *Sonneratia* is likely to have been outcompeted by the more robust *Rhizophora stylosa* and *Avicennia marina* in the increasingly restricted coastal environment.

**Ilex.** The genus *Ilex* was a common component of the island’s rainforest patches until the late Holocene (c. 1100 cal. yr BP). The most widespread species in northern Queensland is *Ilex arnhemensis* subsp. *ferdinandi* which thrives in a wet habitat within the understorey of the forest (Hyland et al., 2010). Increased disturbance and probably enhanced ENSO-related climate fluctuations could have led to drier and more open conditions which might have caused the decline and local extinction of this genus.

**Human impact?**

Holocene human colonisation of the Pacific Islands is strongly correlated with broad landscape disturbance that has led to the loss of both single species as well as whole plant communities and the promotion of disturbance-adapted plants.

Our record from Lizard Island shows no evidence for late-Holocene loss of major vegetation communities. Human impact, however, could have played a role in the local extinctions of *Arenga, Sonneratia* and *Ilex*. Particularly the final occurrence of the latter two is immediately followed by an increase of microcharcoal which indicates enhanced disturbance of the broader landscape. Late-Holocene Aboriginal occupation of coastal environments is recorded from the island’s south side with an increase in activity at around 1880–1580 cal. BP (Mills, 1992).

Environmental change including the local extinctions could be ascribed to these activities, however, more archaeological research in particular in the northern part of the island is required to support this hypothesis.

**Conclusions**

The reconstruction of Lizard Island’s Holocene vegetation development has unravelled spatial and temporal ecosystem dynamics and identified driving mechanisms behind ecosystem change on a tropical island of high conservation significance. Fluctuations in sea-level led to the shifting, expansion and contraction of the habitats for mangroves, freshwater swamps, grasslands, sclerophyll woodland and rainforest. On shorter timescales, a disturbance event (possibly a cyclone at c. 6000 cal. yr BP) and subsequent landscape burning induced fundamental changes in the ecosystems’ composition and diversity.

Our record showing the extinction of numerous species from different ecosystems on the island gives new insights into dynamics of northeastern Australia’s floral biodiversity. Mangrove species that are now only reported from the mainland might have had a much wider distribution during the early and mid Holocene. Restrictive environments such as offshore islands host a smaller and narrower range of habitats and small shifts induced by environmental changes affect the vegetation more severely. Increasing landscape disturbance together with weather extremes eradicate species with limited ecological tolerances and new colonisation by these species from external sources is hindered by spatial isolation. These selective extinctions ultimately lead to the dominance of more robust plants on these islands.
Acknowledgements

Dr Jo Palmer and Dr Andrew Thornhill from the Australian National Herbarium are thanked for helping UP with pollen reference sample collection and Dr Janelle Stevenson (ANH) for helping with the identification of Areguia pollen. We thank Dr David Reslop (RSES at ANU) for developing the age model and Andrew Higgins (Fenner School, ANU) for access to the Malvern Mastersizer. Phil Roberts counted the macrocharcoal samples and radiocarbon analysis was conducted at Waikato Radiocarbon laboratory and the ANU Radiocarbon Lab. We wish to thank the support of the Dingaag traditional owners and representative Mr Jonathan Charlie for permission to work on their traditional land and for help in the field. We are grateful to two anonymous reviewers whose constructive comments helped to improve the manuscript.

Funding

UP acknowledges the German Academic Exchange Service (DAAD) for funding her Postdoctoral Visiting Fellowship at the Australian National University (ANU). The project was conducted in association with an archaeological research project led by Dr Matthew Felgate (funded through the Australia and Pacific ed in association with an archaeological research project led by Dr Matthew Felgate (funded through the Australia and Pacific

References


### Appendix 1:
List of all taxa counted in core LIWB01 and the corresponding species occurring on the island today.

<table>
<thead>
<tr>
<th>Group</th>
<th>Pollen/spore taxa</th>
<th>Species occurrence on Lizard Island</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mangrove</td>
<td>Avicennia</td>
<td>A. marina subsp. australasia</td>
</tr>
<tr>
<td></td>
<td>Rhizophora</td>
<td>R. stylosa</td>
</tr>
<tr>
<td></td>
<td>Sonneratia x gulngai*</td>
<td>not recorded</td>
</tr>
<tr>
<td></td>
<td>Sonneratia albo/ caseolaris*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sonneratia 'abnormal grain'*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ceriops</td>
<td>C. tagal</td>
</tr>
<tr>
<td></td>
<td>Bruguiera</td>
<td>B. exaristata, B. gymnorrhiza</td>
</tr>
<tr>
<td>Back mangrove</td>
<td>Lumnitzera</td>
<td>L. racemosa</td>
</tr>
<tr>
<td></td>
<td>Excoecaria</td>
<td>E. agallocha</td>
</tr>
<tr>
<td></td>
<td>Xylocarpus</td>
<td>X. granatum, X. rumphi</td>
</tr>
<tr>
<td>Arecales/</td>
<td>Pandanus</td>
<td>P. salmslaubachii, P. tectorius</td>
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<td>Arecalesae type</td>
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<tr>
<td></td>
<td>Arecalesae type</td>
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</tr>
<tr>
<td></td>
<td>Arecalesae type</td>
<td>C. nuclera cv. domesticated</td>
</tr>
<tr>
<td>Rainforest</td>
<td>Barringtonia</td>
<td>B. asiatica, B. calyprata</td>
</tr>
<tr>
<td></td>
<td>Flagellaria</td>
<td>F. indica</td>
</tr>
<tr>
<td>Moraceae/</td>
<td>Ficus congesta var. congesta</td>
<td>F. obliqua var. petiolaris, F. opposita, F. racemosa,</td>
</tr>
<tr>
<td>Urticaceae</td>
<td>F. obliqua var. petiolaris, F. opposita, F. racemosa, F. sepica var. caulisflora, F. virens var. sub lanceolata, Trophi scandin, Pipturus argenteus,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ilex*</td>
<td>not recorded</td>
</tr>
<tr>
<td>Ulmaceae</td>
<td>Celtis paniculata, C. philippensis var. philippensis, Trema aspera, Trema tamentosa var. tamentosa, T. tamentosa,</td>
<td></td>
</tr>
<tr>
<td>Rainforest</td>
<td>Euphorbiaceae type Mal步步 been</td>
<td>Mal步步 beenosa, M. Clara</td>
</tr>
<tr>
<td></td>
<td>Euphorbiaceae</td>
<td>Chamaesyce atata, C. bifilo, C. hirta, Cadiaem variegatum var. moluccanum, Crotan arnhimic-</td>
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<td>Euphorbiaceae</td>
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<td>T. ari...</td>
<td>T. ari...t...</td>
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<tr>
<td></td>
<td>Eugenia/ Syzygium</td>
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</tr>
</tbody>
</table>
| Sclerophyll 10 – 20 μm | Myrtaeae 10 – 20 μm | Eucalyptus t...</p>
Appendix 2