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Authors current email address for correspondence is engelhart@uri.edu

Mangrove Pollen of Indonesia and its suitability as a sea-level indicator

Simon E. Engelhart[a*], Benjamin P. Horton[a], David H. Roberts[b], Charlotte L. Bryant[c] and D. Reide Corbett[d]

[a] Sea Level Research Laboratory, Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, Pennsylvania 19104-6316, USA.

[b] Department of Geography, Durham University, Science Laboratories, South Road, Durham, DH1 3LE, UK.

[c] NERC Radiocarbon Laboratory, East Kilbride, G75 0QF, Scotland.

[d] Department of Geology, Coastal Resource Management Program, East Carolina University, Greenville, North Carolina 27858, USA.

*Corresponding author:
E-mail address: simoneng@sas.upenn.edu
Tel. +1 215 573 8372
Fax +1 215 898 5724

Abstract

We investigated the mangroves of Southeast Sulawesi, Indonesia, to assess their potential as proxies for reconstructing sea level during the Holocene. Initial investigations confirmed that the mangrove species demonstrate zonations parallel to the shoreline and are dominated by the family *Rhizophoraceae* with *Avicennia*, *Heritiera* and *Sonneratia* also important constituents of the mangroves.

We investigated the vertical distributions of pollen assemblages at three sites. Partial CCA analysis demonstrated that at all three sites, elevation was a significant control on the distribution of pollen assemblages in surface samples. We combined the three contemporary transects to develop a regional transfer function to explain the relationship between the surface assemblages and elevations using the Maximum Likelihood (ML) method. The developed transfer function indicated mangrove pollen can be used as a precise indicator of past sea levels with an error of ±0.22 m. The transfer function was applied to two fossil cores from the Wakatobi Marine National Park and evaluated using the Modern Analogue Technique. Both cores showed similar patterns in changes of palaeo mangrove elevation and had modern analogues in the contemporary training set. We conclude that mangrove pollen is a suitable proxy for reconstructing sea level in tropical environments.

Key words: Palynology, Sea level, Sulawesi, Indonesia, Mangrove, Palaeoenvironmental change

1. Introduction

Mangroves are an important aspect of the coastal environment and provide protection from tidal and wave action as well as acting as important nursery grounds for species of fish and shrimp (e.g. Martosubroto and Naamin, 1977; Turner, 1992; Sasekumar et al., 1992; de Graaf and Xuan, 1999). Mangroves are of prime economic importance with a UNEP report (UNEP-WCMC, 2006) valuing mangroves at up to $3.5 million per square km per year through a combination of coastal defences, tourism and farming. Furthermore, the trapping of waterborne sediment by mangroves reduces the turbidity of ocean waters (Bigelow et al., 1989), which is of essential importance to the development of coral reef systems (Kleypas, 1996). Research undertaken after the Indian Ocean Tsunami in 2004 shows that areas with well developed mangroves suffered proportionally less damage than those areas where mangroves had been replaced as a result of farming and other coastal development (Dahdouh-Guebas et al., 2005; Kathiresan and Rajendran, 2005; Bird et al., in review).

In view of the above, it is important to study contemporary mangrove systems and to understand their evolution under periods of sea-level rise and fall during the Holocene to provide a benchmark against which one must measure the additional sea-level rise that has occurred over the last 100 years. Sea-level changes in tropical environments are of further interest, as they provide one of the most robust constraints on the eustatic component of the sea-level signal (e.g. Nakada and Lambeck, 1989; Fleming, 1998; Lambeck, 2002; Milne et al., 2002; Peltier, 2002) and can be employed to constrain the source geometry of major meltwater pulses (e.g. Clark et al., 2002; Bassett et al. 2005). The use of coral reconstructions (e.g. Fairbanks, 1989; Chappell and Polach, 1991; Bard et al., 1996) has proved extremely valuable for reconstructions prior to the Holocene but the large error ranges (±2.5 m, Fairbanks, 1989; ±5 m Blanchon, 2005) limit their use for Holocene reconstructions where the error is often greater than the magnitude of the change being investigated.

In contrast to tropical environment relative sea-level reconstructions, reconstructions from temperate areas have been dominated by microfossil based reconstruction techniques (e.g. Scott & Medioli, 1978, 1980; Horton et al., 1999; Gehrels, 2000; Shennan et al., 2000; Campeau et al., 2000; van de Plassche, 2000; Horton et al., 2003; Horton and Edwards, 2005; Franceschini et al., 2005; Ruiz et al., 2005). Early sea-level research relied heavily on the use of pollen assemblages as a proxy for sea level with the first sea-level curve being produced by Godwin (1940) in the English Fenland. However, developments over the last three decades in the use of the vertical zonations of foraminifera (e.g. Scott and Medioli, 1978) and diatoms (e.g. Zong, 1997), and the perceived coarse resolution of pollen assemblages (e.g. Freund et al., 2004) have resulted in fewer pollen-based sea-level reconstructions. Furthermore, studies by Debenay et al. (2004), Horton et al. (2005a) and Horton et al. (in press) have shown that foraminifera and diatoms, respectively, have the potential to reconstruct sea level in tropical environments. The fossil record in tropical environments is however, especially prone to preservation issues. Debenay et al. (2004) state that foraminifera in mangrove environments are “dramatically affected by taphonomic processes”. Woodroffe et al. (2005) in Australia further demonstrate that foraminiferal preservation within mangrove sediments is problematic. Diatom preservation is also potentially problematic within fossil cores, due to the high salinity and temperature of the mangrove environments that promotes diatom dissolution (Barker et al., 1994).

Due to these preservation issues, mangrove pollen may have the greatest potential for accurately and precisely reconstructing sea level from mangrove environments (Horton et al., 2005b). The strong outer exine of the major mangrove pollen species should result in fewer taphonomic issues than affect foraminifera and diatoms. Indeed, palaeoenvironmental reconstructions using pollen have been produced from Australia (Grindrod, 1985, 1988; Kershaw et al., 2002), Tonga (Ellison, 1989), Borneo (Anshari et al., 2001), Irian Jaya (Ellison, 2005) and Thailand (Horton et al., 2005b). However, it must be noted that unlike foraminifera or diatoms, the pollen is not being deposited autochthonously but is subject to movement by distribution vectors i.e. wind, insects or tides. In spite of this, Grindrod (1985) describes mangrove taxa as having “highly localised pollen dispersal, despite the potential for tidal redistribution”. Despite this potential limitation, the use of mangrove pollen as a proxy for sea-level is supported by the coastline parallel species zonations demonstrated by mangroves (Grindrod 1985, 1988; Ellison, 1989; Kamaludin, 1993; Ellison, 2005) which suggest that species zonation is controlled primarily by tidal inundation (and thus elevation), which is essential for a proxy of past sea-levels. However, these previous pollen-based studies have relied on qualitative or semi-quantitative methods that potentially limit the accuracy and precision of the sea-level reconstructions. The development and application of quantitative methods such as transfer functions (e.g. Zong and Horton, 1999; Horton et al., 1999; Gehrels, 2000; Campeau et al., 2000; Edwards et al., 2004; Sawai et al., 2004; Patterson et al., 2004), potentially allows for the elucidation of past sea levels with improved precision and accuracy.

To address the above, we aim to document the characteristics of the dominant mangrove types of Southeast Sulawesi and to investigate the links between species composition and the surface pollen assemblages within three mangrove ecosystems. We will subsequently, use this pollen dataset to develop a pollen-based transfer function to quantitatively reconstruct former palaeoenvironments and palaeo mangrove elevations.

2. Study Area

The island of Sulawesi lies in close proximity to the quadruple junction of the Australian, Eurasian, Pacific and Philippine tectonic plates and has been subject to at least four major tectonic events during the Mid-Cretaceous, Oligo-Miocene, Middle Miocene and Early Pliocene (Villeneuve et al., 2002). Recent research on the geology of the area is limited (e.g. Wilson and Bosence, 1996; Ascaria et al., 1997; Wilson and Moss, 1999; Milsom et al., 1999; Hall and Wilson, 2000), and the majority of work focuses on developments on a geological timescale with an absence of work on tectonic movements during the Quaternary. This had led to a considerable amount of ambiguity in the present tectonic debate. This study is split between two distinct geographic locations, namely the Wakatobi Marine National Park (WMNP) and the island of Buton (Figure 1). Both locations share the same micro-tidal regime due to similar physiographic conditions, which is semi-diurnal with a range of 1.5m and tidal levels are highlighted for each site in the appropriate figures (2-4).

The WMNP occupies an area of 1.39 million hectares, making it the second largest marine protected area in Indonesia. The national park is comprised of the four principal islands of Wangi, Kaledupa, Tomea and Binongko, together forming the

Tukang Besi archipelago. The work of Escher (1920) describes the Tukang Besi archipelago as being situated in rows. He attributes the first row in the southwest to atoll development, the second row (location of present study sites) to elevated islands, the third row to atoll development and fourth row to elevated islands. This scenario can be attributed to the presence of anticlines and synclines.

Two study sites are located in the WMNP, both on the island of Kaledupa (5°30’04.11” S, 123°43’54.25” E). Laulua has an eastern aspect and is protected by a reef flat located 50 m from the shoreline. The study area at Laulua does not have a tidal flat due to the abrupt presence of a channel separating the mangrove from the reef flat. This study site is characterised by a belt of mangroves 100 m in width, with trees up to 8 m in height, although the majority of the vegetation reaches heights of between 2 and 3 m. The transect at Laulua was 92 m long and sampled every 4 m. Laulua does not have any freshwater input and shows a strong mangrove plant zonation parallel to the shoreline with a front zone of *Rhizophora* and *Bruguiera* (1.0-1.25 m IHD). This is followed landward by a pure *Rhizophora* zone (1.25-1.7 m IHD), a *Rhizophora* and *Avicennia* zone (1.7-2.0 m IHD), a zone of *Ceriops* (1.9-2.0 m IHD), a zone of *Avicennia* (~1.9 m IHD) and a back zone of mixed *Avicennia* and *Ceriops* species (1.9-2.1 m IHD). Silt is the dominant sediment substrate within the mangrove with the sand fraction increasing at the front of the mangrove. Organic content is highest at the front of the mangrove. Laulau shows a similar transition to that described by Matthijs et al. (1999), from a non mud substrate where *Rhizophora* is not present to dark muddy sediments where *Rhizophora* is present.

Mantigola is located on the western side of Kaledupa. The mangroves at this location are also protected by a reef flat 200 m from the shoreline. The transect was 144 m long and sampled every 6 m. In contrast to Laulua, Mantigola has a large tidal flat located in front of the mangrove (0.9-1.0 m IHD) that is exposed at low tide but it hosts no mangrove species. The fringing mangrove is exclusively *Rhizophora* (1.0-1.2 m IHD), which then moves into a dense mangrove composed of *Rhizophora* and *Bruguiera* species (1.2-1.95 m IHD), which accounts for over half of the 144 m transect. *Bruguiera* species presence declines with distance from the front of the mangrove in this section. The *Rhizophora* and *Bruguiera* mangrove is followed by a mixed zone of *Rhizophora*, *Avicennia* and *Ceriops* (1.95-2.15 m IHD) and then by a zone of *Ceriops* and *Avicennia* (2.15-2.25 m IHD). The final landward zone is composed of *Avicennia* and *Ceriops* (2.25-2.35 m IHD), with *Avicennia* becoming increasingly prevalent. The landward zone is also characterised by the presence of *Nypa* palms, isolated *Xylocarpus* and *Acanthus* species. The site has some freshwater influence with a 3m wide channel 50 m to the north of the transect and is located on a small channel that is dry at low tide. The vegetation reaches maximum heights of 10 m with an average of ~4 m. The substrate of the mangrove environment is predominantly silt. The abundance of sand increases towards the seaward edge of the transect. Conversely, the organic content of the transect increases towards the landward edge of the transect.

Buton Island (5°11’51.69” S, 122°55’57.76” E) is located off the southeastern tip of the Sulawesi coast and is outside the WMNP. Buton is 130 km long by 50 km wide and attains a maximum height of 1100 m above sea level. The site at Buton is located at Kakenauwe with an eastern aspect. The site is located in close proximity to a river, which provides freshwater input to the mangrove. The mangroves in this area range from 20 m to 100 m in width. The transect was 42 m long and sampled every 3 m. The transect is located in an area of mangrove 25 m wide, fronted by a large tidal flat, and extends from a mudflat zone (0.4-0.85 m IHD), into a zone of fringing *Sonneratia* and *Rhizophora* (0.85-1.35 m IHD) before reaching a landward *Rhizophora* zone (1.35-1.8 m IHD). A 1 m high coral terrace at the rear of the *Rhizophora* zone hinders back mangrove development. Here the species are considerably taller than those in the WMNP, as the average height of vegetation at this site is ~6 m, reaching a maximum of 12 m. The *Rhizophora* genus in particular are noticeably taller. A sandy substrate is found within the tidal flats, with the mangrove environment dominated by clay. Organic content gradually increases across the transect toward the landward edge.

3. Materials and Methods

We collected surface sediment samples at regular intervals along a transect perpendicular to the coastline. The transects began at the lowest exposed tidal flat during low tide and extended to the limit of mangrove vegetation at the landward extent of the transect. Sampling stations were demarcated at regular intervals along the transects, taking changes in topography and inundation regimes into account. Mantigola had twenty five stations, Laulua was marked with twenty four, and fourteen sampling stations were demarcated at Kakenauwe. For each modern sampling station and core we chose a temporary benchmark and calculated its height above sea-level using a staff and auto level, noting the time of the observation. Raw elevations were reduced to Indonesian Height Datum (IHD) by reference to the tidal predictions for each study site that were provided by the Proudman Oceanographic

Laboratory (Blackman, pers. comm.) following the methods of Horton et al. (2005a, in press). We monitored local sea level at hourly intervals over a twenty four hour period and the measurements suggested the elevation of the temporary benchmark relative to IHD is accurate to ±0.2 m. It is important to note that this error must be included in any relative sea-level reconstruction. The location of each TBM was determined using a Leica SR530 GPS system. Two fossil cores were collected from Ambeau and Llagiyye. A gouge corer was used at both sites to establish the consistency of stratigraphy before sampling with a Russian corer to reduce compaction effects. The cores were described using Tröels-Smith (1955), transferred into tubes, wrapped in plastic and refrigerated.

We collected one sample of 10 cm^3 (10 cm^2 surface sample by 1 cm thick) for environmental variable analysis and a second sample of 5 cm^3 (5 cm^2 surface sample by 1 cm thick) for pollen analysis. We mixed the samples to average seasonal effects following Zong (1997) and Sawai (2003). We prepared the samples for pollen analysis following the standard method of Faegri and Iversen (1989). Taxonomy was identified using the publications of Huang (1972) and Thanikaimoni (1987). The genera *Bruguiera* and *Ceriops* cannot be separated under light microscopy (Grindrod, 1985) and are grouped together as *Bruguiera/Ceriops*. Most fossil samples showed good preservation and were counted to at least 150 grains (Ellison, 1989; Patterson and Fishbein, 1989; Fatela and Taborda, 2002). Pollen results are represented as percentage relative abundance (Ellison 1989).

We recorded six environmental variables from each modern transect (elevation, distance from open water, grain size, organic content, salinity and pH). Salinity and pH measurements were recorded in the laboratory after the addition of 10g of sediment to 25ml of distilled water, allowing the samples to sit for four hours before measurements were taken. Grain size was undertaken using a Coulter counter laser granulometer. Samples were pre-treated with hydrogen peroxide to remove organic content. Organic content (loss on ignition) was calculated from the dry sample (dried overnight in an oven at 105°C) heated to 550°C for four hours (Ball, 1964).

3.1 Statistical Analysis

We used CONISS and unconstrained cluster analysis based on unweighted Euclidean distance and using no data transformation or standardisation to classify the stations into relatively homogenous clusters (Prentice 1986, van Tongeren 1987). Only those species that attained 2% abundance in any one sample were included for analysis. After clustering, the elevation of each sample was determined to identify elevational ranges for the zonations. Clusters were confirmed with detrended correspondence analysis (DCA) (Hill and Gauch 1980). The two techniques are complimentary (Birks, 1992), with cluster analysis splitting the samples into zones based on the pollen assemblages and DCA providing further information on the patterns and variations within and between groups.

Following Birks (1995), Detrended Canonical Correspondence Analysis (DCCA) is used to assess the length of the environmental gradient to determine if a linear or unimodal response model is appropriate. We assessed the performance of the transfer function using the coefficient of determination (r^2) and the root mean square error of prediction (RMSEP). We assessed the precision of the transfer function by employing jack-knifing (leave one out) and the modern analogue technique (MAT).

Jack-knifing removes one sample from the dataset and utilises the remaining dataset to predict its elevation (Birks 1995). The transfer function can then be assessed by considering the residuals between the observed elevation and the predicted elevation for the sample removed from the dataset. The RMSEP serves as a guide to the precision of the dataset. We ran the transfer function using bootstrapping to generate sample specific errors. MAT, whilst capable of predicting elevations, was employed in this study to check that each fossil sample had a modern analogue within the dataset. Following Birks et al. (1990), a fossil sample was considered to have a modern analogue in the training set if the minimum dissimilarity coefficient for the sample was within the 10th percentile of the dissimilarity range of the modern samples. We used five closest analogues following Southall et al. (in press) due to the small size of the contemporary dataset.

4. Results

Sixty three contemporary samples were analysed palynologically from the three transects. We identified forty one different pollen types from the three transects studied, consisting of sixteen mangrove taxa differentiated by species name with a further ten pollen types that were not identified as mangrove species in the identification literature but which were consistently present in the mangroves of Southeast Sulawesi. A further category of pollen grains includes those that were broken, corroded or hidden, thus hindering identification.

4.1 Laulua Pollen Assemblages

The pollen assemblages of Laulua are dominated by *Rhizophora*, *Bruguiera/Ceriops* and *Avicennia* with the relative abundances of these three species accounting for over

75% of the pollen in every sample (Figure 2). The transect is dominated by *Rhizophora* with relative abundances greater than 68% from 0 m to 44 m along the transect. Associated *Bruguiera/Ceriops* abundances above 10% and low *Avicennia* abundances never exceeding higher than 8% relative abundance also characterise the seaward aspect of the mangrove. The landward section of the transect (48 m to 92 m) is characterised by lower abundances of *Rhizophora* (22% at 88 m) with an associated increase to 60% abundance of *Bruguiera/Ceriops* at 84 m. *Avicennia* shows abundances varying between 8% and 38% in this section of the mangrove with the highest relative abundances at 88 m and 92 m. There is a relationship between the vegetation present at a sampling station and the dominance of the pollen within the surface sample. Where *Rhizophora* tree species are present on the transect, there is an associated high relative abundance of *Rhizophora* pollen within the surface sample. Peaks of *Bruguiera/Ceriops* in the surface samples are also associated with the appearance of this tree species at those sampling stations.

4.2 Mantigola Pollen Assemblages

The pollen assemblages of Mantigola are dominated by *Rhizophora*, *Bruguiera/Ceriops*, *Avicennia* and *Heritiera* with the relative abundances of these four genera accounting for at least 83% of the pollen in every sample (Figure 3). The transect is dominated by *Rhizophora* with relative abundances always exceeding 41% and greater than 62% from 0 m to 90 m along the transect. *Rhizophora* abundances are lowest in the rear mangrove (108 m to 144 m) where they range from 41% to 56%. *Bruguiera/Ceriops* relative abundances are similar along the transect and demonstrate no clear pattern. The relative abundances range from 6% to 20% for these genera. *Heritiera* is present throughout the transect, with a range of relative abundances from 3% to 24%. The relative abundances are higher in the landward section of the mangrove, which correlates with the presence of a number of *Heritiera* genus. Relative abundances of 20% and 24% occur respectively at 108 m and 114 m and coincide with a close proximity to this genus. *Avicennia* abundances are low throughout the mangrove, never exceeding 7% relative abundance except at 126 m where relative abundance is 22%. This may be associated with the location of the sampling site under a large *Avicennia* tree. The sample stations at 114 m and 120 m show an increase in *Avicennia* pollen, followed by a decrease at stations 132 m to 144 m along the transect.

4.3 Kakenauwe Pollen Assemblages

The pollen assemblages of Kakenauwe are dominated by *Rhizophora*, *Heritiera* and *Sonneratia*. The relative abundance for these three genera never accounts for less than 77% of the total pollen sum in any sample (Figure 4). *Rhizophora* is present on the entire transect ranging from 14% relative abundance at 6 m to a maximum of 72% at 39 m. *Sonneratia* is also ever present on the transect, with relative abundances ranging from 0.7% at 6 m to 11% at 39 m. *Heritiera* is the dominant genus on the tidal flat with a maximum abundance of 79% at 6 m and a minimum abundance of 11% at 39 m. The increase in *Rhizophora* abundance above 60% is correlated with entering a strip of mangrove vegetation.

5. The vertical distribution of mangrove pollen

The pollen compositions of the three mangroves studied are broadly comparable in terms of genera distribution and surface pollen assemblages. *Rhizophora* is the dominant species at all three mangroves and due to its pollen vector being wind

(Grindrod, 1985), is found in high abundances both in close proximity to its parent tree location as well as landwards and seawards of its position within the tidal frame. *Rhizophora* is dominant in the seaward mangrove at all three sites, accounting for over 80% of the trees within this zone. Whilst *Sonneratia* (Kakenauwe) or *Bruguiera* (Mantigola and Laulua) are present at the front of this zone, they are minimal components in comparison to *Rhizophora*. Kakenauwe differed from Laulua and Mantigola, as it did not have a back mangrove section with a raised coral terrace impeding further inundation. Mantigola and Laulua both show similar landward sections, although the zone of *Rhizophora* tree dominance is larger at Mantigola, a consequence of the difference in the elevation gradient at the two sites. The front of the mangrove at Laulua shows a rapid rise in elevation in the *Rhizophora* tree dominated zone whereas Mantigola demonstrates a constant rise in elevation across the mangrove. Both sites show mid and landward mangrove sections composed primarily of *Avicennia* and *Ceriops* trees with *Ceriops* generally showing more dominance in the mid to landward mangrove section with *Avicennia* dominance at the landward end of the transect. Mantigola was unique in the presence of mature *Heritiera* genus within the mangrove and is the only site that showed a species zonation above the limit of highest astronomical tide with *Acanthus* species present although these were poorly represented within the pollen assemblages.

Pollen assemblage zones L1, M1 and K3 show similar elevational ranges (and are representative of the seaward mangrove and are dominated by *Rhizophora* with the presence of either *Bruguiera/Ceriops* (Laulua and Mantigola) or *Sonneratia* (Kakenauwe) pollen. The elevation ranges of L1, M1 and K3 are 0.97 m to 2.02 m, 0.88 m to 2.18 m and 1.52 m to 1.66 m IHD, respectfully. Wijmstra (1969) and

Grindrod (1988) note the dominance of *Rhizophora* within the mangroves of Sumatra and Northern Australia, respectively. Both studies suggest that a relative abundance of ~ 90% is indicative of a *Rhizophora* stand. This is comparable to the zones of Laulua, Mantigola and Kakenauwe, which all demonstrate abundances of over 70% *Rhizophora*. The lower abundances of *Rhizophora* within Southeast Sulawesi is possibly due to the small size of the mangroves, not exhibiting a width greater than 150 m. Furthermore, numerous studies suggest that *Rhizophora* is the dominant seaward mangrove species (Macnae, 1968; Bunt et al., 1985; Grindrod, 1985; Ellison, 1989; Bunt, 1991; Kamaludin, 1989; Maloney, 1991; Tong Sa and Chow Hock, 1993; Matthijs et al., 1999; Ellison, 2005) with Kamaludin (1989) identifying 50% *Rhizophora* as indicative of a mangrove environment. It must be noted that a number of the above references (e.g. Maloney, 1991) identify a zone of *Sonneratia* or *Avicennia* trees seaward of the *Rhizophora* zone. In Southeast Sulawesi, this was only identified at Kakenauwe. The mangrove at Mantigola had an extensive tidal flat seaward of it and it is unclear why *Avicennia* or *Sonneratia* trees do not form a seaward zone at this site.

Zone L2 represents a mid mangrove environment of Laulua (1.86 m to 2.13 m above IHD) and is defined by a decrease in *Rhizophora* abundance from ~60% at the seaward section of the zone to ~25% at the landward section of the zone. This correlates with Kamaludin (1989) who states that *Rhizophora* abundances less than 40% is representative of a back mangrove environment. The increased presence (10 to 40%) of *Avicennia* is in line with Cantera et al. (1999) from Columbia who describe *Avicennia* as being more common in the central mangrove. The elevated

Bruguiera/Ceriops abundances are comparable to Bunt (1999) who places *Ceriops* behind the *Rhizophora* stands in Northeastern Australia.

Zone L3 of Laulua represents the rear mangrove (1.92 m to 2.01 m above IHD) and is associated with an increase in *Bruguiera/Ceriops* pollen to between 40% and 60% with an associated decrease in *Rhizophora* pollen to below 40% (Kamaludin, 1989). The stand of *Ceriops* trees identified at the rear of this zone and represented by an increase in *Bruguiera/Ceriops* pollen is also identified by Bunt (1999), Matthijs et al. (1999) and Ellison et al. (2000). Zone L3 also demonstrates the presence of *Heritiera* and *Lumnitzera*, genera identified as being indicative of landward mangrove communities (e.g. Maloney, 1991; Bunt, 1999) with firm soils. Zone M2 of Mantigola is similar to Zone L3 but with a higher elevational range (2.08 m to 2.37 m above IHD) and higher *Rhizophora* abundance (never greater than 60%). Zone M2 also shows an increase in the abundance of *Bruguiera/Ceriops* pollen though it is of less magnitude than in zone L3 due to the smaller size of the stand. The presence of *Heritiera* in the landward mangrove is also demonstrated by Bunt (1999).

Zones K1 and K2 of Kakenauwe are similar due to their location on the tidal flat. Zone K1 encompasses four samples (0.81 m to 0.89 m above IHD) and is represented by *Rhizophora* abundances of less than 30% and high *Heritiera* abundances. This is in agreement with Wijmstra (1969) who identifies 30% *Rhizophora* abundance as being indicative that the sample was immediately adjacent to a *Rhizophora* zone, such as on a tidal flat. Zone K2 represents the transition zone between the open tidal flat and the mangrove and demonstrates higher *Rhizophora* abundances (~50%) with an increase in *Bruguiera/Ceriops* and *Sonneratia* abundance, indicating that these genera are present in the fringing mangrove. The presence of *Sonneratia* trees in the front mangrove is also highlighted by Watson (1928), Maloney (1991) and Ellison et al. (2000).

6. Development and Analysis of a transfer function

To be useful as a sea-level indicator, microfossils must have a consistent relationship to a fixed position within the tidal frame (Thomas and Varekamp 1991). The mangroves of Southeast Sulawesi indicate species zonations parallel to the shoreline and the pollen surface assemblages relate closely to the tidal frame, making mangrove pollen suitable as a proxy for reconstructing relative sea-level. In support of this conclusion, the three transects were combined and analysed using canonical correspondence analysis (CCA). CCA axes one (eigenvalue = 0.135) and two (eigenvalue = 0.067) explain 31.1% of the pollen data. These two axes represent 88.8% of the species-environment relationship (Figure 5). There is a clear pattern with samples with low elevations and high sand, pH and organic content values plotting to the left and samples with high elevations, high salinities and high silt contents plotting to the right. The eight environmental variables account for 26.4% of the explained variance in the pollen data. This explained variance is composed of 14.5% (elevation), 7.8% (distance from open water), 6.3% (salinity), 6% (pH), 5.7% (organic content), 4.9% (silt), 2.3% (sand) and 1.3% (clay). The associated Monte Carlo permutations tests indicate that the elevation gradient accounts for a significant portion of the total variance in the pollen data ($p = 0.002$, 499 permutations under the reduced model). As such, a statistically significant transfer function quantifying the relationship between the pollen assemblages and elevation can be constructed. It must be noted that 59% of the explained variance is composed of intercorrelations between the environmental variables and therefore elevation cannot be considered to be completely independent of the other environmental variables. 71% of the total variation in pollen data is not explained by the eight environmental variables. This may be due to stochastic variation or temporal and spatial effects, which this study does not take into account. Nevertheless, the explained variance is similar to other datasets (e.g. Zong and Horton, 1999) and coupled with the information from partial CCAs, indicate that a statistically significant transfer function can be developed for elevation.

We subsequently developed a transfer function using the combined dataset of sixty three samples. The length of the environmental gradient (in this instance, elevation) for the combined dataset was assessed using DCCA and was 0.771 SD units, indicating a linear response model, so we chose the Maximum Likelihood (ML) transfer function, developed using C2 (Juggins 2005). ML is "the most statistically rigorous approach to environmental reconstruction" (Birks 1995), however it must also be noted that Birks (1995) also states that the model is rarely used in palaeoecology. The genus *Heritiera* was removed from the transect at Kakenauwe. The relative abundance of other pollen species is then calculated using total pollen sum. This genus was deemed to be allochthonous due to its non-presence in the mangrove but high abundances on the tidal flat. *Heritiera* was not removed from the entire dataset, as the genus is an important component of the landward mangrove in Southeast Sulawesi. Examination of the dataset reveals that allochthonous *Heritiera* can be identified in fossil cores by considering organic content and grain size analysis. If *Heritiera* occurs in high abundances and the organic content is below 10% with a percentage of sand greater than 40%, then the *Heritiera* in that sample can be concluded to be allochthonous and the *Heritiera* component removed from that sample using the same method as in the contemporary samples, outlined above. The dataset was screened to remove any samples with a residual greater than the standard deviation of the elevation in the dataset, resulting in a transfer function based on 55 contemporary samples. Using the diagnostic species *Rhizophora*, we noted that the tolerance changed from 0.45 before the screening of the dataset to 0.43 in the screened dataset with a change in the optima from 1.67 to 1.59, indicating that the removal of the samples had little effect on the predictions of the transfer function with the benefit of improved performance. The pollen based transfer function (Figure 6) shows a strong correlation between observed and predicted values, The transfer function has the potential to predict elevation with a statistical error of ±0.22 m with an r^2_{jack} of 0.8. These results suggest that precise reconstructions of sea-level are possible.

To test the applicability of the transfer function, two cores were taken from two different locations in the WMNP to generate palaeo mangrove elevations. The two sites are separated by 150 m along the coastline and both come from fringing mangrove environments immediately in front of the *Rhizophora* dominated seaward mangrove. Both cores come from sites which were not sampled by the contemporary transects but are proximal to the transect at Laulua on the east coast of Kaledupa (see Figure 1). The age of the cores is inferred from the widespread development of mangroves during the big swamp phase described by Woodroffe et al. (1989) which dates the commencement of mangrove development at between 6800 and 5300 cal yrs BP. Looking at the palynological content of the two cores, with the Ambeau core showing pre-mangrove environments, we conclude that the base of the Ambeau core is 500-1000 cal yrs BP older than the base of the core from Llagiyye. The transfer function generated palaeo mangrove elevations for seventeen samples. The base of the Ambeau core (Figure 7) is a stiff orange clay, which is then overlain by a tenacious blue-grey clay. This is in turn overlain by 1.5 m of peat sediments. The peat sediments are in turn overlain by clay sediments before a return to peat sediments at the top of the core. *Rhizophora*, *Bruguiera/Ceriops*, *Heritiera*, *Acrostichum aureum* and *Sonneratia* pollen dominate the core. *Heritiera* and *Acrostichum aureum* dominate the base of the core. The overlying unit is dominated by *Rhizophora* pollen at the expense of *Heritiera* and *Acrostichum aureum*. Toward the top of the core the pollen assemblages show an increase in the relative abundance of *Sonneratia* to 7.5%. The Llagiyye core (Figure 8) has a basal unit of tenacious blue-grey clay, which is overlain by 1 m of peat sediments. The peat unit is overlain by a series of increasingly clay dominated units, which is in turn overlain by the sand dominated surface unit. *Rhizophora* is dominant throughout the core with abundances exceeding 55%. *Heritiera* is present throughout the core but in greater abundance (~20%) at the base of the core declining to less than 5% at the top sample (0.53 m). *Bruguiera/Ceriops* is also present throughout the core in abundances greater than 10% but shows no general pattern of change through the core profile.

The Ambeau core palaeo mangrove elevations show a general pattern of decrease from 2.11 m ±0.68 m LAT at 3.99 m depth to 1.38 m ±0.22 m LAT at 0.77 m depth (Figure 7). Palaeo mangrove elevations in the samples dominated by *Rhizophora* with no *Acrostichum Aureum* are consistently ~1.5 m LAT with an increase to 1.75 m ±0.22 m LAT at 1.55 m depth associated with a change in core sediment from clay with some organics to an organic dominated layer. The two samples near the top of the core show decreasing palaeo mangrove elevations in keeping with the change in biostratigraphy to lower *Rhizophora* abundances and the presence of *Sonneratia* pollen, indicating a seaward mangrove depositional environment. The Llagiyye core (Figure 8) similarly shows a pattern of decrease over time from a maximum of 2.06 m ±0.22 m LAT at 2.08 m depth to 1.46 m ±0.24 m LAT at 1.05 m depth, associated with an increase in the abundance of *Rhizophora* and a decrease in *Heritiera* abundance.

The MAT results demonstrate that one of the samples from Llagiyye (Figure 8) and four of the samples from Ambeau (Figure 7) do not have modern analogues within the contemporary training set. With the exception of sample 0.77 m in the Ambeau core, the samples with no modern analogues are located in the deepest sections of the cores (Ambeau: 3.55 m, 3.7 m and 3.99 m, Llagiyye: 2.08 m) and are identified by high abundances of *Acrostichum Aureum* (Ambeau) and *Heritiera* (Llagiyye) with reduced abundances of *Rhizophora*. Ellison (1989) identifies samples with high *Acrostichum aureum* abundances as indicative of grassland above the mangrove forest, an environment that was not sampled within the transects. The predictions assigned to these samples must consequently be treated with caution. The sample at 0.77 m depth does not have a modern analogue due to the high abundances of *Sonneratia* and *Rhizophora*. Further sampling of mangroves in the region with *Sonneratia* as a seaward mangrove component will be necessary to clarify this issue, due to the fact that it is only a dominant genus at Kakenauwe.

Whilst we have demonstrated that the mangrove pollen transfer function can be used to reconstruct palaeo mangrove elevations, a number of factors must be considered when interpreting the pollen data. When dealing with pollen assemblages, spatial and temporal variability must be considered. Spatial variability within the contemporary transects is a possible factor with species represented within the mangroves but not on the transect, removed from the surface assemblages. For example, at Mantigola, *Sonneratia* pollen was found in small quantities within the surface assemblages even though there was only one *Sonneratia* tree identified within 100 m of the transect, suggesting that pollen vectors within mangroves diffuse the issue of spatial variability. However, Grindrod (1988) does state that *Sonneratia* pollen is overrepresented in mangrove sediments compared to its surface distribution and, as such, spatial issues may cause problems with less prolific pollen producers. As with all flowering plants, seasonal effects may affect the relative abundances of surface pollen assemblages with Tomlinson et al. (1979) suggesting that species in the family *Rhizophoraceae* have distinct flowering seasons in Queensland.

As demonstrated at the Kakenauwe contemporary transect, the introduction of an allochthonous component is a real possibility. Comparing the three sites, it would appear that the important factor in this introduction is the presence of a fluvial system within close proximity to the Kakenauwe transect, allowing the inwash of terrestrial pollen taxa onto the tidal flat. This is of some concern when considering reconstructions outside of the WMNP, as it is not possible to identify whether a sample within a fossil core was within close proximity to a similar system. The introduction of allochthonous taxa shows the highest potential on tidal flats with mangrove pollen production overwhelming the introduced taxa within the mangrove. The signature of the allochthonous component, with high abundances of *Heritiera* is not representative of a mangrove ecosystem within the region. Great care must therefore be taken when applying the transfer function with further analysis of the output to determine whether the predictions are realistic. This issue may be resolved through the use of multiproxy techniques such as organic content, grain size analysis and geochemical analysis as demonstrated in this study.

Whilst it has been highlighted that the use of mangrove pollen has potential problems for reconstructing palaeo mangrove elevation, the first ever mangrove pollen transfer function demonstrates that palaeo mangrove elevations can be reconstructed precisely. The statistical reconstruction errors are lower than those typically associated with tropical environment sea-level reconstructions using corals and qualitative pollen analysis (e.g. Ellison, 1989; Fairbanks, 1989; Chappell and Polach, 1991; Bard et al., 1996). The error in this study of 31% of the tidal range is a dramatic improvement on the errors highlighted by Ellison (1989) in Tonga of 100% of tidal range (±0.3 m). This allows for analysis of lower magnitude changes due to the precision of the transfer function (±0.22 m).

6. Conclusion

We demonstrate that it is possible to quantitatively reconstruct palaeo mangrove elevation by using mangrove pollen assemblages within a transfer function. The conclusions drawn from this study are:

1. The mangrove plants of Southeast Sulawesi show species zonations parallel to the shoreline. This species zonation is also reflected in the pollen surface assemblages. *Rhizophora* trees dominate the front of the mangrove ecosystem, often co-existing with *Bruguiera* or *Sonneratia*. The mid and rear mangrove is dominated by *Avicennia*

and *Ceriops* with *Heritiera* and *Lumnitzera* also showing localised distributions. The dominance of *Rhizophora* trees is reflected in the pollen assemblages. *Rhizophora* pollen is dominant in the seaward mangrove at all three sites. *Bruguiera/Ceriops* and *Avicennia* show higher abundances in the landward sections of the mangrove at both Laulua and Mantigola.

2. CCA analysis of the regional training set, comprising mangrove pollen assemblages from three coastal mangroves in Southeast Sulawesi, Indonesia, demonstrate a statistically significant relationship with elevation. Elevation accounts for 14.5% of the explained variance in the pollen assemblages with a p value of 0.002.

3. We developed the mangrove pollen transfer function for elevation using the Maximum Likelihood method. Statistical analysis of the transfer function suggests precise reconstructions of palaeo mangrove elevation are possible (±0.22 m). We applied the transfer function to two cores taken from the Wakatobi Marine National Park. We demonstrate that the mangrove pollen transfer function is capable of precise reconstruction of palaeo mangrove elevations. This transfer function has important implications for studies of mangrove reconstructions in the tropics, allowing for high-resolution reconstructions of palaeo mangrove elevations at study sites where foraminifera and diatoms are prone to post depositional errors. This technique also improves on the errors typically associated with tropical palaeoenvironmental reconstructions.

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Figure Captions

Fig.1 Location map of study areas showing a) Kaledupa b) Buton c) Kakenauwe d) Laulua e) Llagiyye and Ambeau f) Mantigola

Fig. 2 a) Unconstrained cluster analysis based on unweighted Euclidean distance showing the pollen assemblages versus order of samples on the dendrogram at Laulua excluding species under 2% b) DCA clusters c) Elevational range of zones identified by cluster analysis and DCA d)

	Schematic diagram of sample locations and vegetation distribution with tidal levels
Fig. 3	a) Unconstrained cluster analysis based on unweighted Euclidean distance showing the pollen assemblages versus order of samples on the dendrogram at Mantigola excluding species under 2% b)DCA clusters c) Elevational range of zones identified by cluster analysis and DCA d) Schematic diagram of sample locations and vegetation distribution with tidal levels
Fig. 4	a) Unconstrained cluster analysis based on unweighted Euclidean distance showing the pollen assemblages versus order of samples the dendrogram at Kakenauwe excluding species under 2% b) DCA clusters c) Elevational range of zones identified by cluster analysis and DCA d) Schematic diagram of sample locations and vegetation distribution with tidal levels
Fig. 5	Canonical correspondence analysis results for the combined mangrove dataset
Fig. 6	a) scatter plot and b) residuals showing the relationship between the observed versus the pollen predicted values using ML from the combined pollen dataset
Fig. 7	Stratigraphy, pollen assemblages, palaeo mangrove elevations, MAT results (no modern analogues highlighted in grey) and boundary conditions for the Ambeau core. Stratigraphy drawn according to Troels-Smith (1955)

Fig. 8	Stratigraphy, pollen assemblages, palaeo mangrove elevations, MAT results (no modern analogues highlighted in grey) and boundary conditions for the Llagiyye core. Stratigraphy drawn according to Troels-Smith (1955)
Table 1	Transfer Function Summary Statistics

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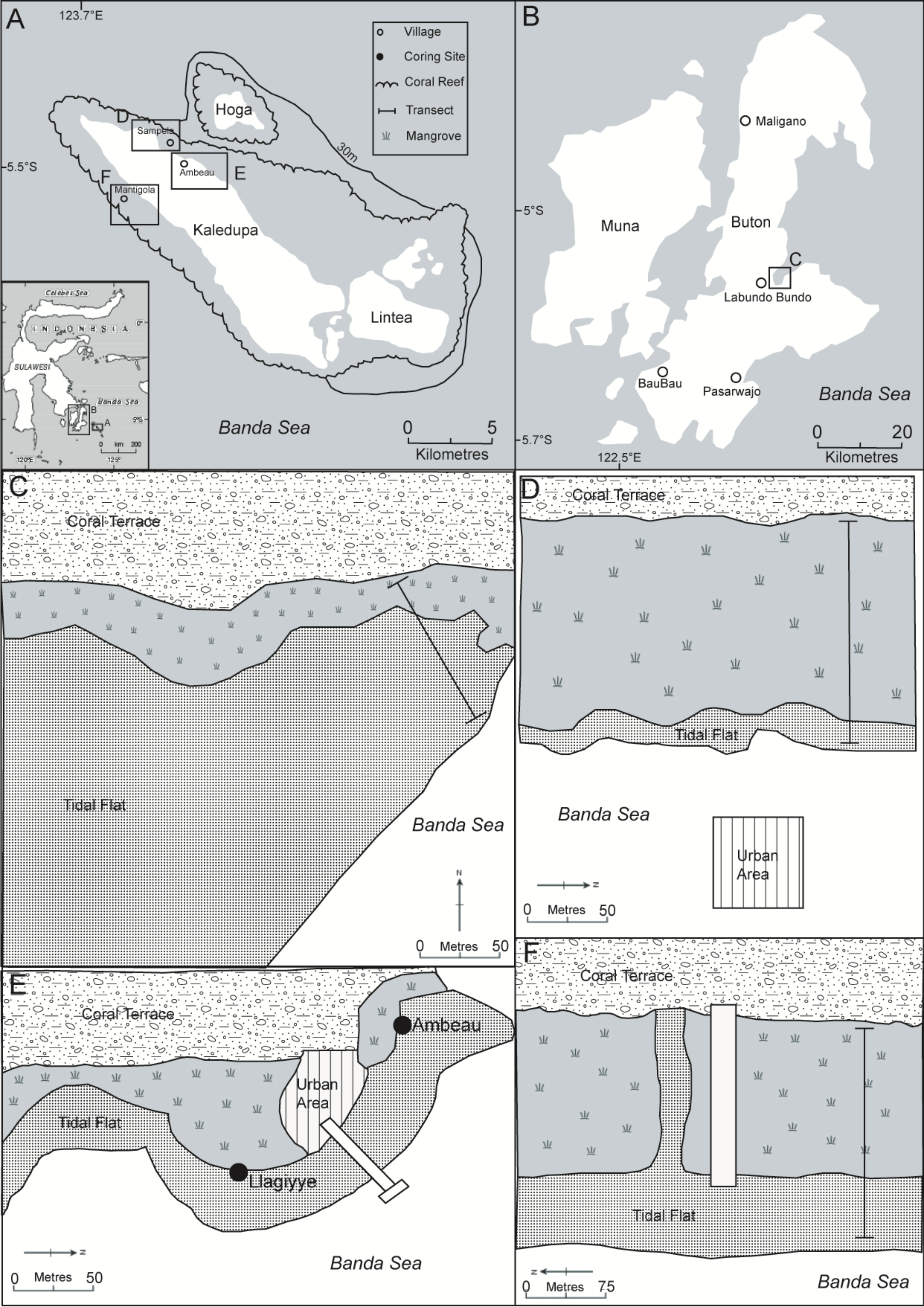
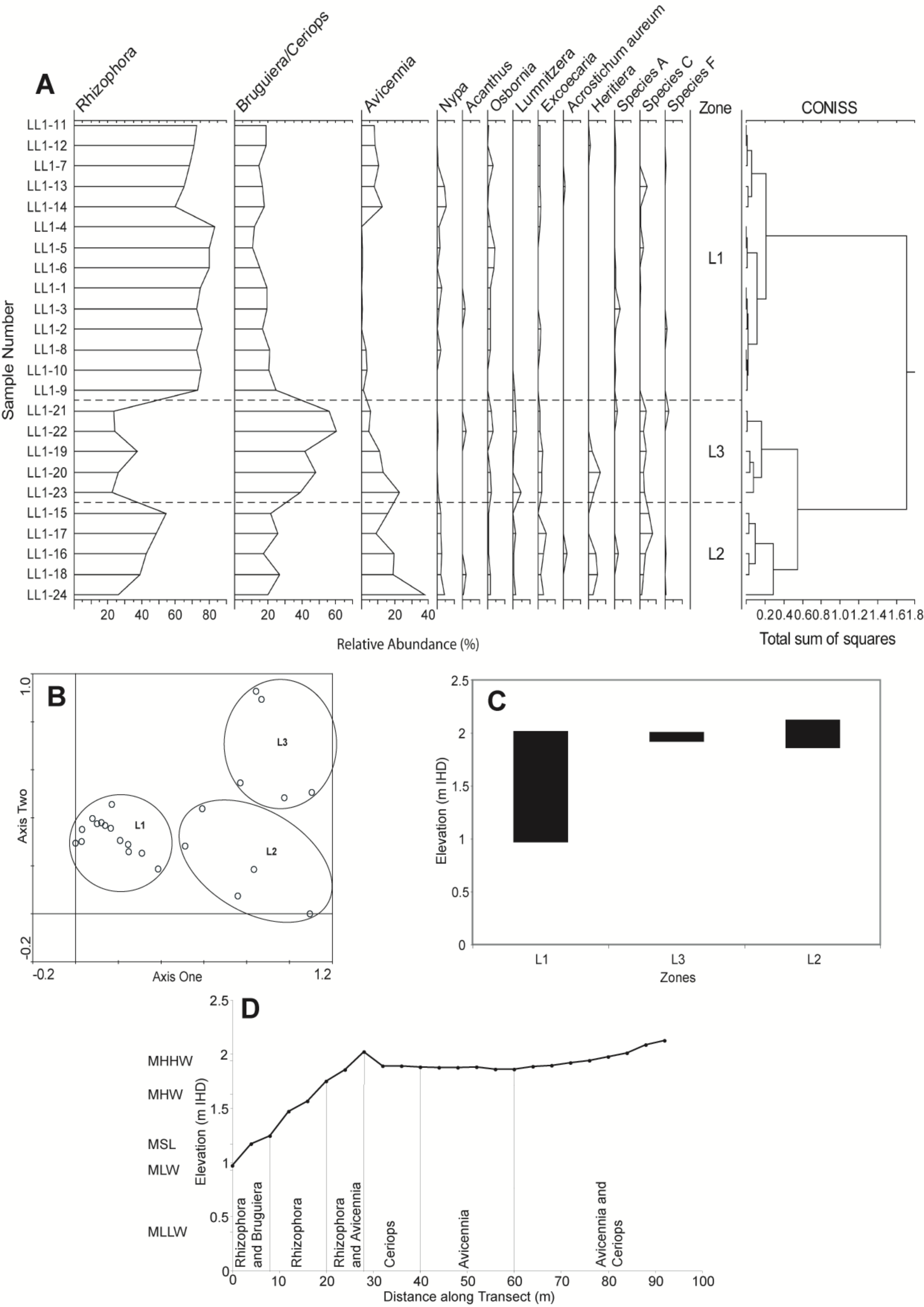
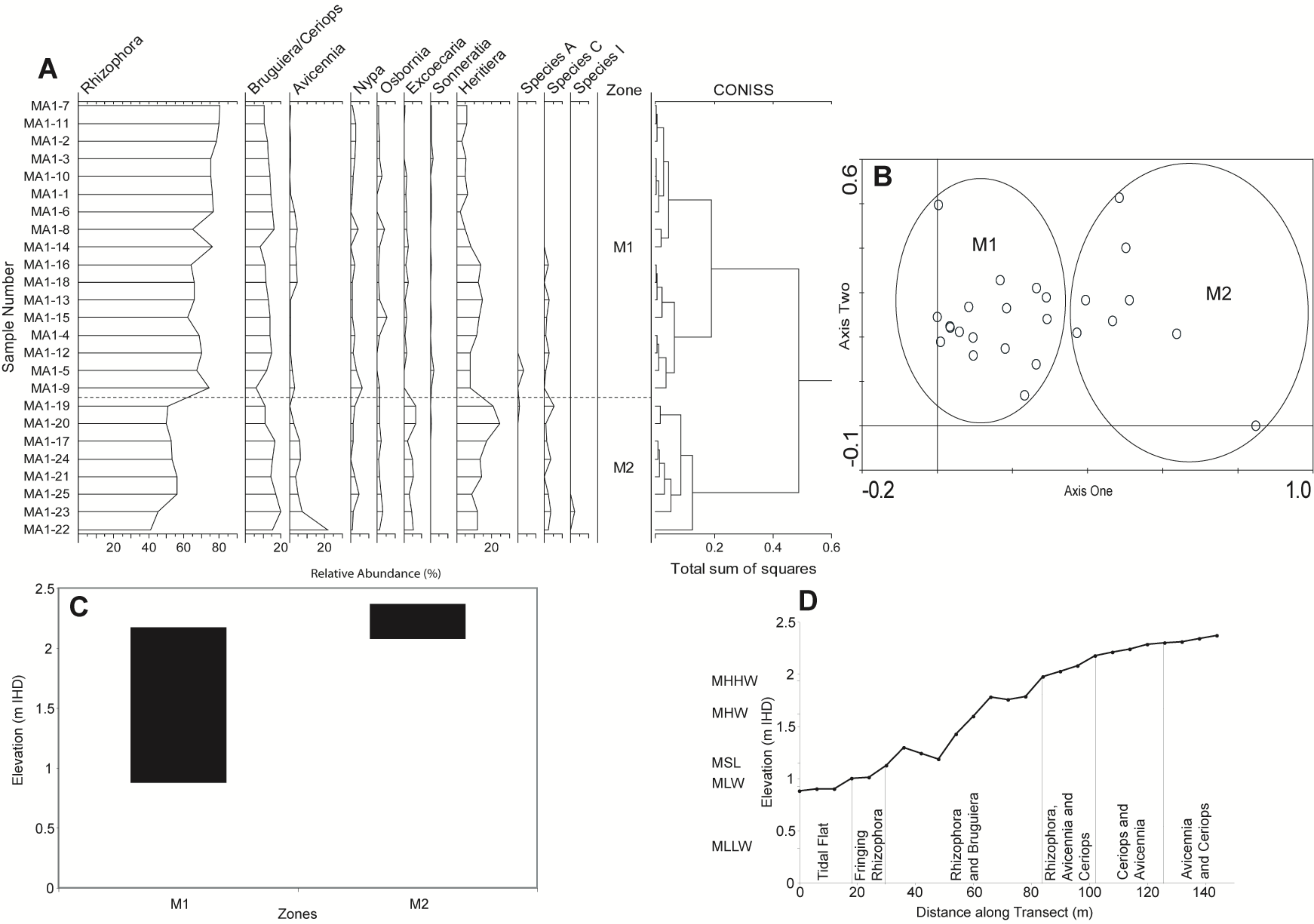
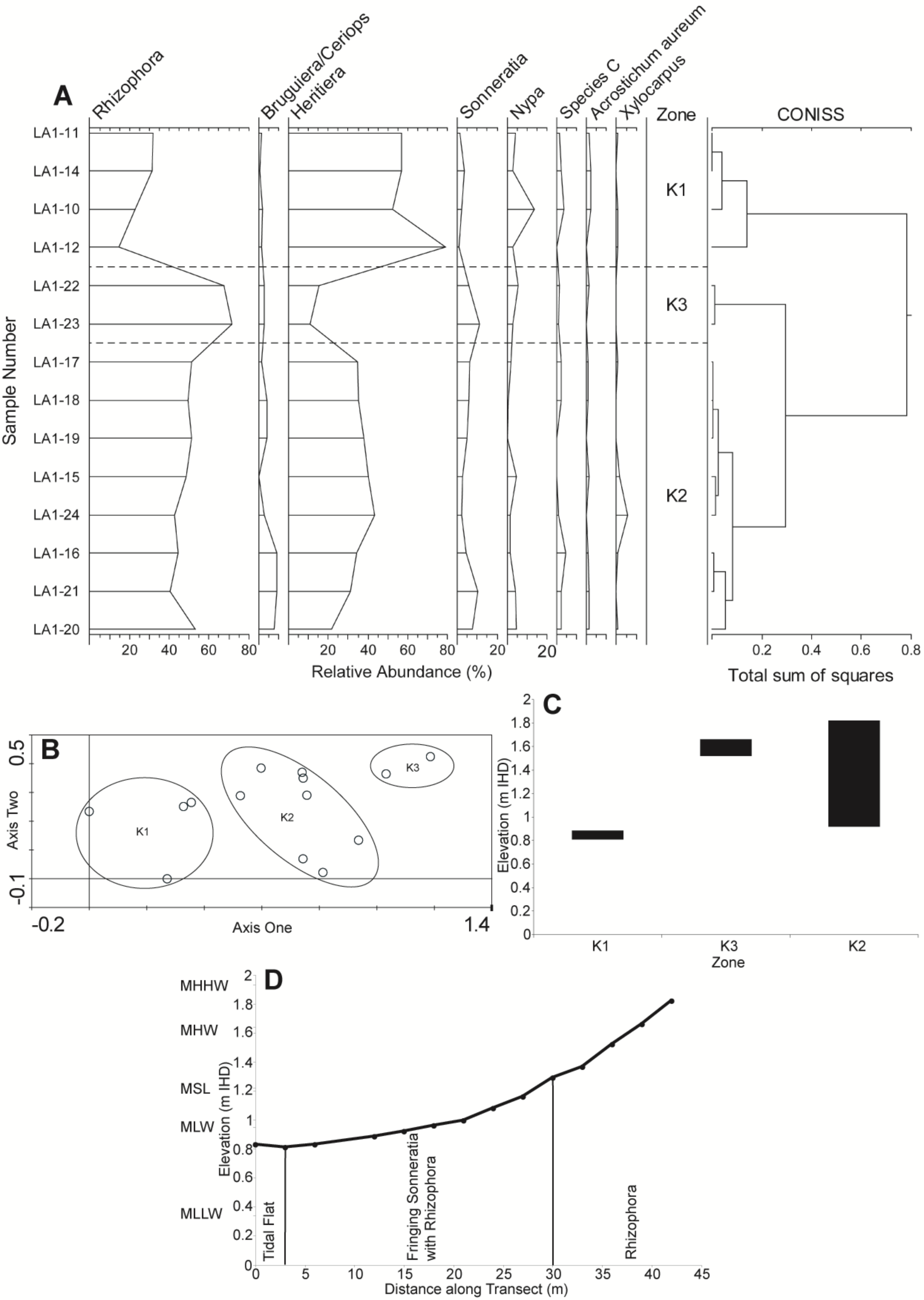
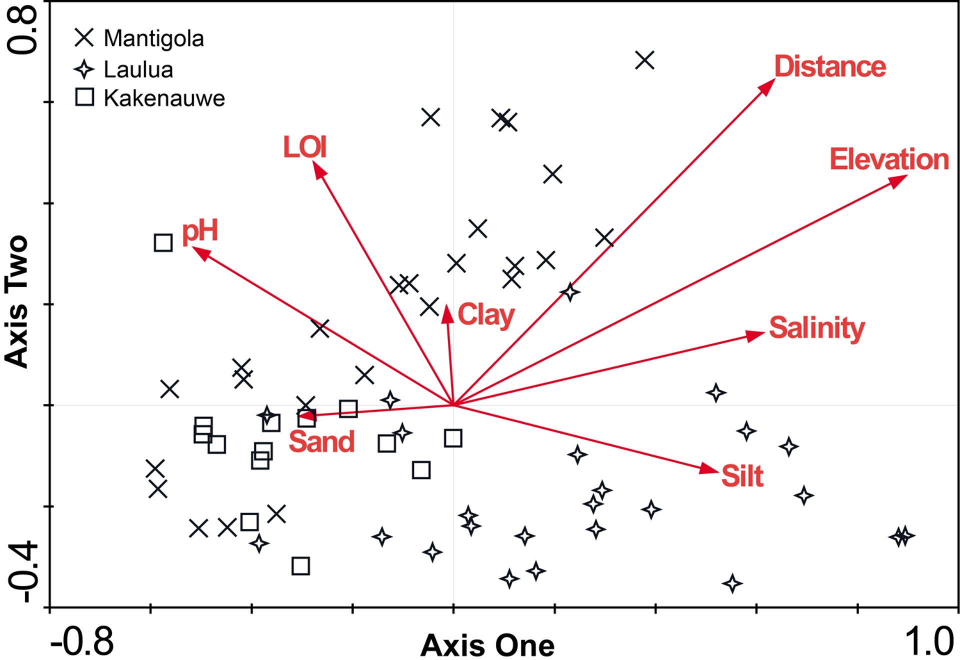
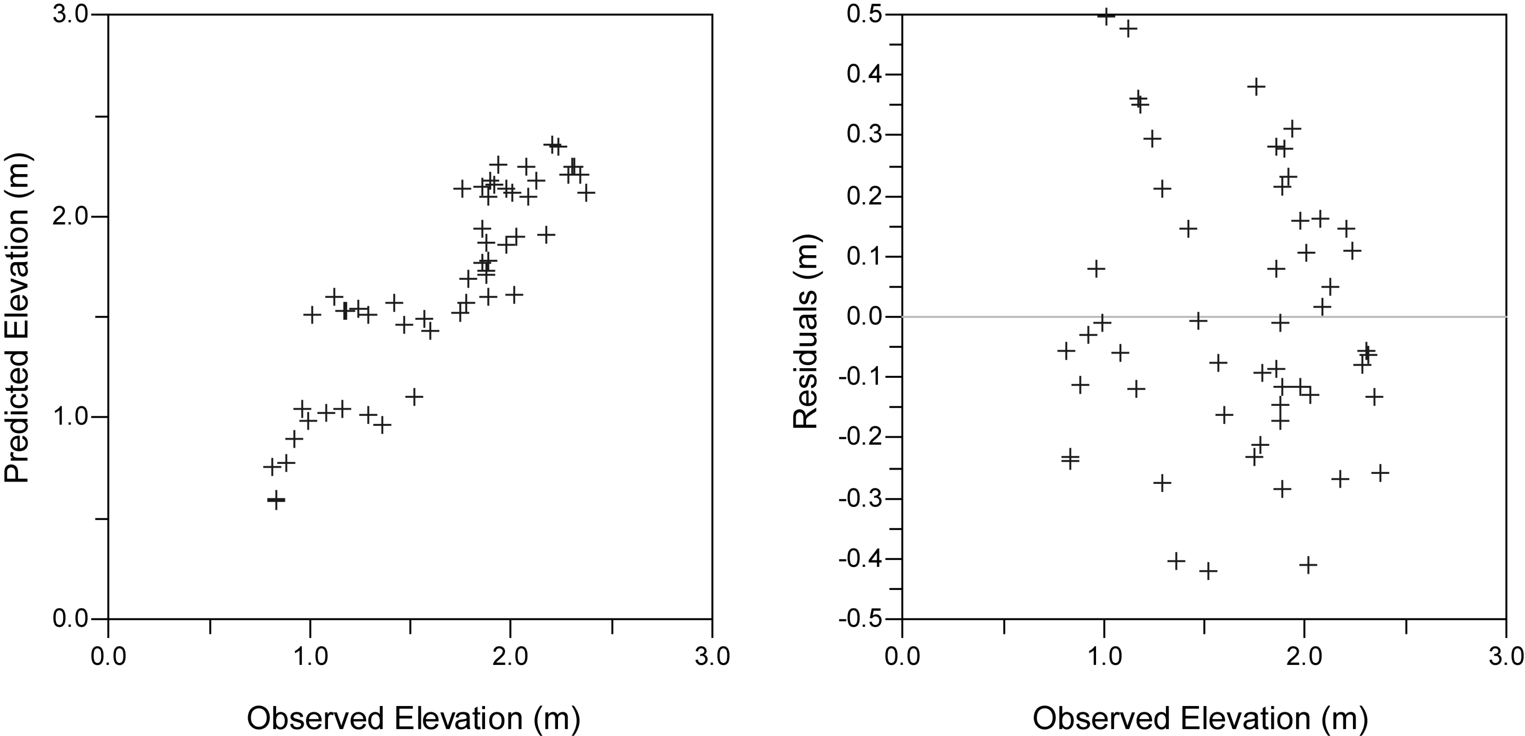

A
123.7°E
Village
Coring Site
Coral Reef
Transect
Mangrove
Hoga
D
Sampela
30m
-5.5°S
Ambeau
E
F
Mantigola
Kaledupa
Lintea
Celebes Sea
INDONESIA
0°
SULAWESI
Banda Sea
B
A
5°S
0 km 200
120°E
125°
Banda Sea
0 5
Kilometres
B
Maligano
-5°S
Muna
Buton
C
Labundo Bundo
BauBau
Pasarwajo
Banda Sea
-5.7°S
122.5°E
0 20
Kilometres
C
Coral Terrace
Tidal Flat
Banda Sea
N
0 Metres 50
D
Coral Terrace
Tidal Flat
Banda Sea
Urban Area
N
0 Metres 50
E
Coral Terrace
Ambeau
Urban Area
Tidal Flat
Llagiyye
N
Banda Sea
0 Metres 50
F
Coral Terrace
Tidal Flat
N
0 Metres 75
Banda Sea

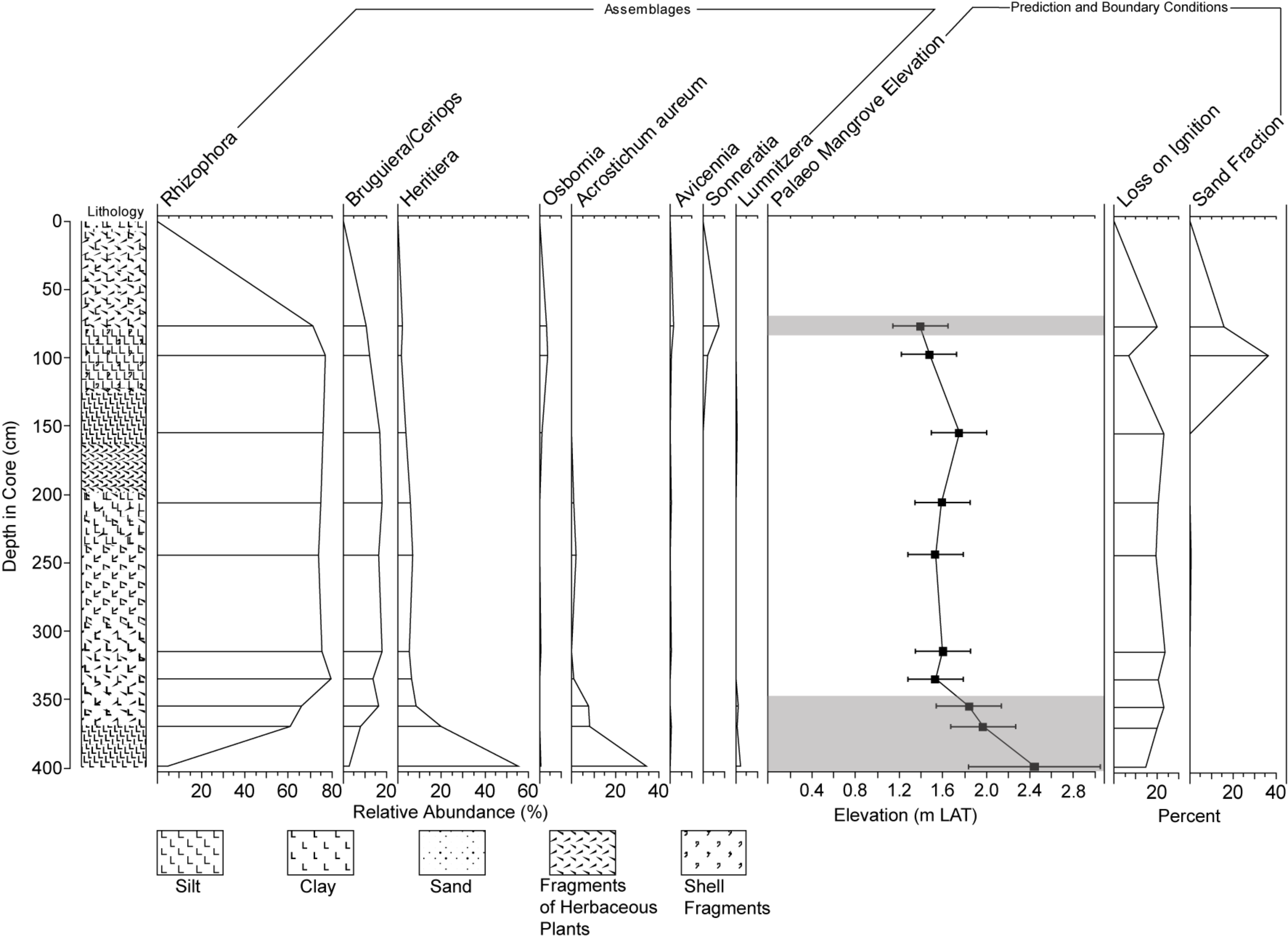

A
Rhizophora
Bruguiera/Ceriops
Avicennia
Nypa
Acanthus
Osbornia
Lumnitzera
Excoecaria
Acrostichum aureum
Heritiera
Species A
Species C
Species F
Zone
CONISS
Sample Number
LL1-11
LL1-12
LL1-7
LL1-13
LL1-14
LL1-4
LL1-5
LL1-6
LL1-1
LL1-3
LL1-2
LL1-8
LL1-10
LL1-9
LL1-21
LL1-22
LL1-19
LL1-20
LL1-23
LL1-15
LL1-17
LL1-16
LL1-18
LL1-24
L1
L3
L2
20 40 60 80
20 40 60
20 40
Relative Abundance (%)
0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6 1.8
Total sum of squares
B
Axis Two
Axis One
1.0
-0.2
-0.2
1.2
L1
L2
L3
C
Elevation (m IHD)
2.5
2
1.5
1
0.5
0
L1
L3
L2
Zones
D
Elevation (m IHD)
MHHW
MHW
MSL
MLW
MLLW
2.5
2
1.5
1
0.5
0
Rhizophora and Bruguiera
Rhizophora
Rhizophora and Avicennia
Ceriops
Avicennia
Avicennia and Ceriops
0 10 20 30 40 50 60 70 80 90 100
Distance along Transect (m)

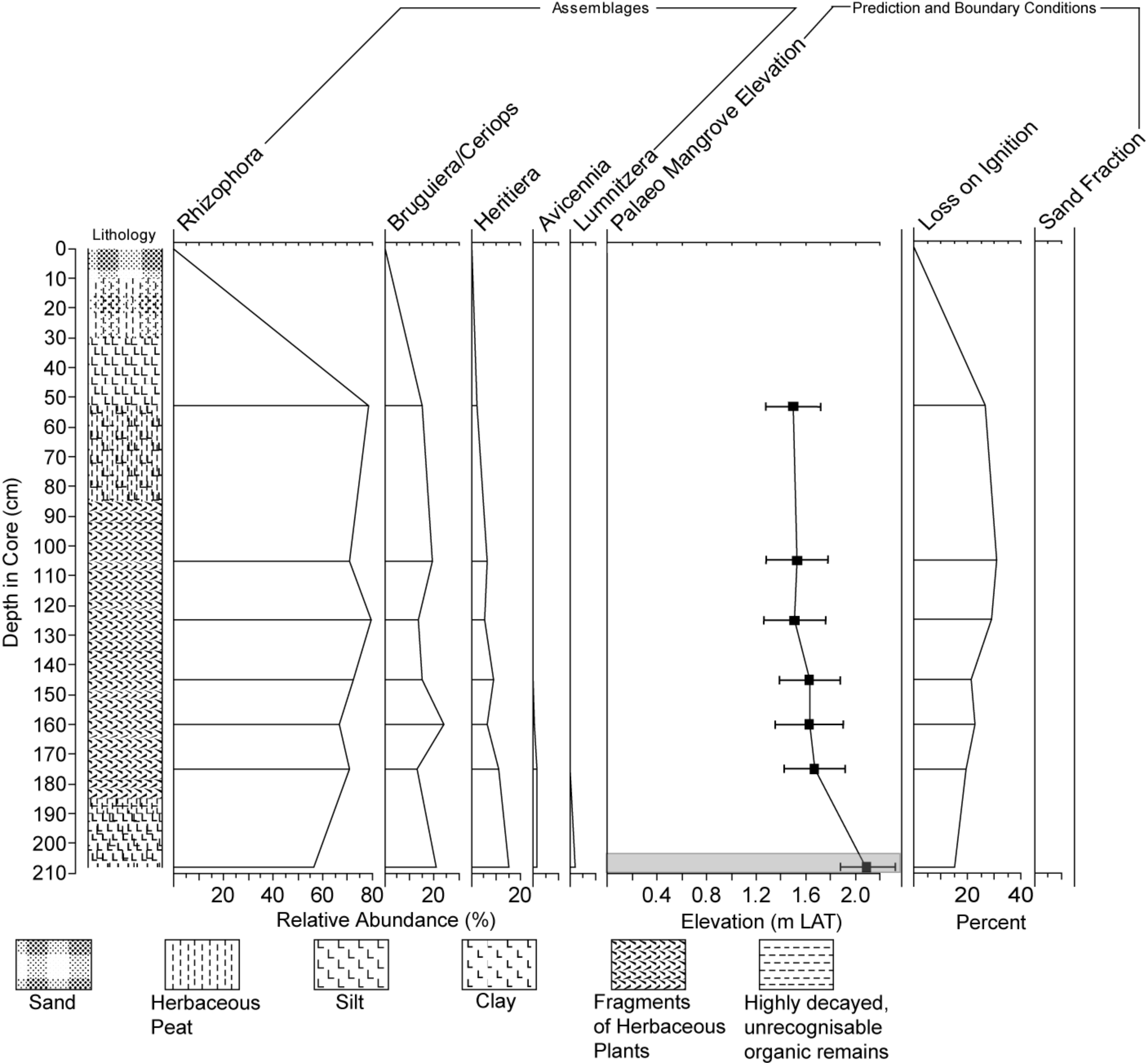

A
Rhizophora
Bruguiera/Ceriops
Avicennia
Nypa
Osbornia
Excoecaria
Sonneratia
Heritiera
Species A
Species C
Species I
Zone
CONISS
Sample Number
MA1-7
MA1-11
MA1-2
MA1-3
MA1-10
MA1-1
MA1-6
MA1-8
MA1-14
MA1-16
MA1-18
MA1-13
MA1-15
MA1-4
MA1-12
MA1-5
MA1-9
MA1-19
MA1-20
MA1-17
MA1-24
MA1-21
MA1-25
MA1-23
MA1-22
M1
M2
20
40
60
80
20
20
20
Relative Abundance (%)
0.2
0.4
0.6
Total sum of squares
B
0.6
-0.1
Axis Two
-0.2
Axis One
1.0
M1
M2
C
2.5
2
1.5
1
0.5
0
Elevation (m IHD)
M1
M2
Zones
D
MHHW
MHW
MSL
MLW
MLLW
2.5
2
1.5
1
0.5
0
Elevation (m IHD)
Tidal Flat
Fringing Rhizophora
Rhizophora and Bruguiera
Rhizophora, Avicennia and Ceriops
Ceriops and Avicennia
Avicennia and Ceriops
0
20
40
60
80
100
120
140
Distance along Transect (m)


A
Rhizophora
Bruguiera/Ceriops
Heritiera
Sonneratia
Nypa
Species C
Acrostichum aureum
Xylocarpus
Zone
CONISS
Sample Number
LA1-11
LA1-14
LA1-10
LA1-12
LA1-22
LA1-23
LA1-17
LA1-18
LA1-19
LA1-15
LA1-24
LA1-16
LA1-21
LA1-20
K1
K3
K2
20
40
60
80
20
40
60
80
20
20
Relative Abundance (%)
0.2
0.4
0.6
0.8
Total sum of squares
B
Axis Two
0.5
-0.1
-0.2
Axis One
1.4
K1
K2
K3
C
Elevation (m IHD)
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
K1
K3
K2
Zone
D
MHHW
MHW
MSL
MLW
MLLW
Elevation (m IHD)
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Tidal Flat
Fringing Sonneratia with Rhizophora
Rhizophora
0
5
10
15
20
25
30
35
40
45
Distance along Transect (m)


0.8
-0.4
Axis Two
-0.8
1.0
Axis One
× Mantigola
✧ Laulua
□ Kakenauwe
Distance
Elevation
LOI
pH
Clay
Salinity
Sand
Silt


Predicted Elevation (m)
3.0
2.0
1.0
0.0
0.0
1.0
2.0
3.0
Observed Elevation (m)
Residuals (m)
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
0.0
1.0
2.0
3.0
Observed Elevation (m)


Assemblages
Prediction and Boundary Conditions
Lithology
Rhizophora
Bruguiera/Ceriops
Heritiera
Osbornia
Acrostichum aureum
Avicennia
Sonneratia
Lumnitzera
Palaeo Mangrove Elevation
Loss on Ignition
Sand Fraction
Depth in Core (cm)
0
50
100
150
200
250
300
350
400
20 40 60 80
20
20 40 60
20 40
0.4 0.8 1.2 1.6 2.0 2.4 2.8
20
20 40
Relative Abundance (%)
Elevation (m LAT)
Percent
Silt
Clay
Sand
Fragments of Herbaceous Plants
Shell Fragments


Assemblages
Prediction and Boundary Conditions
Lithology
Rhizophora
Bruguiera/Ceriops
Heritiera
Avicennia
Lumnitzera
Palaeo Mangrove Elevation
Loss on Ignition
Sand Fraction
Depth in Core (cm)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
20
40
60
80
20
20
Relative Abundance (%)
0.4
0.8
1.2
1.6
2.0
Elevation (m LAT)
20
40
Percent
Sand
Herbaceous Peat
Silt
Clay
Fragments of Herbaceous Plants
Highly decayed, unrecognisable organic remains

RMSE (m)	R^2	Ave bias	Jack R^2	Jack ave bias	RMSEP (m)
0.2	0.83	0.007	0.8	0.004	0.22

Table 1. Transfer function summary statistics