



Threshold response of Madagascar's littoral forest to sea-level rise

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ABSTRACT

Aim Coastal biodiversity hotspots are globally threatened by sea-level rise. As such it is important to understand how ecosystems resist, respond and adapt to sea-level rise. Using pollen, geochemistry, charcoal and diatom records in conjunction with previously published palaeoclimatic records, we investigated the mechanism, interactions and ecosystem response and resilience of Madagascar's littoral forest to late Holocene sea-level rise.

Location Sediment sequences were collected along the south-east coast of Madagascar in two adjacent habitats in Mandena; the highly diverse littoral forest fragment and species-poor *Erica*-matrix.

Methods We used a multi-proxy approach to investigate the relative influence of environmental changes on the littoral ecosystem. We reconstructed past vegetation and fire dynamics over the past 6500 years at two sites in the littoral forest using fossil pollen and macrofossil charcoal contained in sedimentary sequences. Alongside these records we reconstructed past marine transgressions from the same sedimentary sequences using geochemical analyses, and a salinity and drought index through the analysis of fossil diatoms.

Results Our findings indicated that it was the synergistic effect of sea-level rise coupled with rainfall deficits that triggered a threshold event with a switch from two types of littoral forest (an open *Uapaca* forest and a closed littoral forest fragment) to an *Erica*–*Myrica* heath/grassland occurring in approximately less than 100 years. Resilience to sea-level rise differed in the two adjacent habitats, suggesting that the littoral forest fragment was more resilient to the impacts of sea-level change and aridity than the open *Uapaca* woodland.

Conclusions We demonstrated that the littoral ecosystem was influenced by late Holocene sea-level rise and climatic desiccation. While climate change-integrated conservation strategies address the effects of climate change on species distribution and dispersal, our work suggests that more attention should be paid to the impacts of interactive climatic variables that affect ecosystem thresholds.

Keywords

Aridity, climate refugia, coastal ecology, ecosystem dynamics, environmental fluctuations, resilience, resistance, recovery, soil salinity.

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INTRODUCTION

Most climate-change scenarios predict an increase in the frequency and magnitude of extreme climatic events, but little information is currently available as to how ecosystems might respond and adapt to these events. Many ecosystems, however, have experienced rapid climatic changes and severe disturbances

within the last few thousand years (Overpeck, 1996; Overpeck & Webb, 2000; Willis *et al.*, 2004), providing an opportunity to study the response and recovery rate of vulnerable ecosystems in the long-term ecological record. Comparing ecosystem responses to past climate changes has important implications for climate change-integrated conservation strategies, especially in habitats classified as vulnerable biodiversity hotspots most

susceptible to future climate changes, e.g. coastal systems (Willis *et al.*, 2007). As global warming proceeds, sea-level rise is predicted to increase rapidly and dramatically during this century due to thermal expansion of water and glacial melting (Meier & Wahr, 2002; Meehl *et al.*, 2005). The extent to which sea level will rise is controversial, and estimates range from 18 to 59 cm (IPCC, 2007) to up to 163 cm (Rahmstorf, 2007; Rohling *et al.*, 2008) in this century.

There are a number of biodiversity hotspots with coastal ecosystems that are predicted to be under threat from this predicted sea-level rise (Willis *et al.*, 2007) but to date there has been relatively little work to examine what the impact will be on their extent and composition. The littoral forest of Madagascar, which occurs on the sandy coastal plains of eastern Madagascar, is one such ecosystem. It is one of the smallest and most diverse habitats in Madagascar (De Gouvenain & Silander, 2003; Ganzhorn *et al.*, 2001) and has been identified nationally as a top priority for conservation due to its limited extent, high concentration of local endemics and its taxonomically distinct assemblages of plants, ants and vertebrates (Ganzhorn *et al.*, 2001). The littoral forest, however, is under future threat from sea-level rise and current threat from human activities, including a large mining project and illegal charcoal production.

Previous work on the littoral forest has hypothesized that its fragmented nature is as a result of previous anthropogenic activity (Ganzhorn *et al.*, 2001; De Gouvenain & Silander, 2003; Consiglio *et al.*, 2006). It has also been hypothesized that it occupied much of the eastern coastal fringe (up to 90%) before being considerably reduced in extent, principally as a result of human impacts. However, given that Madagascar's littoral ecosystem currently occurs along the eastern coast at a low elevation, there is a high probability that late Holocene sea-level rise would have had an important influence on the landscape and its diverse communities. It is known from previous estimates of Holocene sea-level rise in Madagascar, based on fossil coral sequences, that these were up to 1–3 m above the present level between 3000 and 800 cal. yr BP before falling to its present level (Battistini *et al.*, 1976; Camoin *et al.*, 1997, 2004); such rises and associated marine surges would have inundated many areas of the littoral forest. So far, the impacts of sea-level rise have not been subjected to scrutiny because of the underlying assumption in Madagascar that most ecological changes are human-driven.

The overall aim of this study was therefore to determine the relative influence of past sea-level change and aridity on the composition and extent of the littoral forest of Madagascar. To do this we reconstructed historical vegetation dynamics over the past 6500 years at two sites (the littoral forest fragment and its surrounding *Erica*-matrix) using fossil pollen sequences. Alongside these records we reconstructed past marine transgressions from the same sedimentary sequences using geochemical analyses, and a drought index through analysis of fossil diatoms. We also assessed past burning regimes through macrofossil charcoal analyses. Using these records in conjunction with previously published palaeoclimatic records and archaeological records detailing human occupation (Battistini *et al.*, 1976; Camoin *et al.*, 1997, 2004; Rakotoarisoa, 1997), we addressed the

following four questions. (1) What impact did past intervals of sea-level rise and drought have upon the composition and distribution of the littoral forest? (2) What impact did human activity (prehistoric and historic) have? (3) Is the current fragmentation of the littoral forest a human or natural legacy? (4) How resilient is the littoral forest to human impacts and climate change?

MATERIALS AND METHODS

Study site

The study site is located in the region of Mandena along the south-east coast of Madagascar (Fig. 1). Within Mandena, the vegetation consists of small littoral forest fragments embedded in an *Erica*-grassland matrix, where the latter is generally assumed to be anthropogenic in origin (Lowry & Faber-Langendoen, 1991).

Sedimentary sequences suitable for palaeoecological analyses were collected using a Russian piston corer from two small basins in the Mandena region, one located in the *Erica*-matrix and the other in the littoral forest fragment. The first sedimentary sequence in the *Erica*-matrix was taken from a small circular closed basin (diameter *c.* 10 m) (S 24.93471, E 047.0032) at an elevation of approximately 13 m a.s.l. (Fig. 1). This basin forms a small freshwater wetland within the dune system and is dominated by marshland-adapted trees such as *Pandanus* spp, *Melaleuca quinquenervia* and *Ravenala madagascariensis*. The vegetation around the basin is dominated by species-poor open grassland and *Erica*-heath. Other abundant shrubby species in the *Erica*-matrix are *Psorospermum revolutum*, *Canthium* sp, *Vernonia nudicaulis* and *Indigofera* sp.

The second sequence in the littoral forest fragment was taken less than 1 km from the first site in a small freshwater basin (diameter *c.* 10 m) that bisects a 230-ha littoral forest fragment M15 (S 24.95086, E 047.00082) at an elevation of approximately 12 m a.s.l. (Fig. 1). This basin forms a freshwater wetland and is also dominated by *Pandanus* spp, *M. quinquenervia* and *R. madagascariensis*. In contrast to the first site, however, the vegetation around this basin is a closed forest canopy. The most abundant trees are *Anthocleista longifolia*, *Asteropeia micraster*, *Dracaena* spp, *Homalium* spp, and *Uapaca louvelii* among many others. Both basins are less than 5 km from the coastline and are supplied with fresh water from the dune aquifer.

Laboratory analyses

Chronology and resolution

The chronology of the first sedimentary sequence was established based on four calibrated accelerator mass spectrometry (AMS) ¹⁴C dates (see Appendix S1 in Supporting Information). For the sequence from the littoral forest, it was based on three AMS ¹⁴C dates (see Appendix S1). In addition, the chronologies were supplemented by two or three ²¹⁰Pb dates each (see Appendix S1).

Calibration of radiocarbon dates was performed using BCal software, an internet-based Bayesian radiocarbon calibration

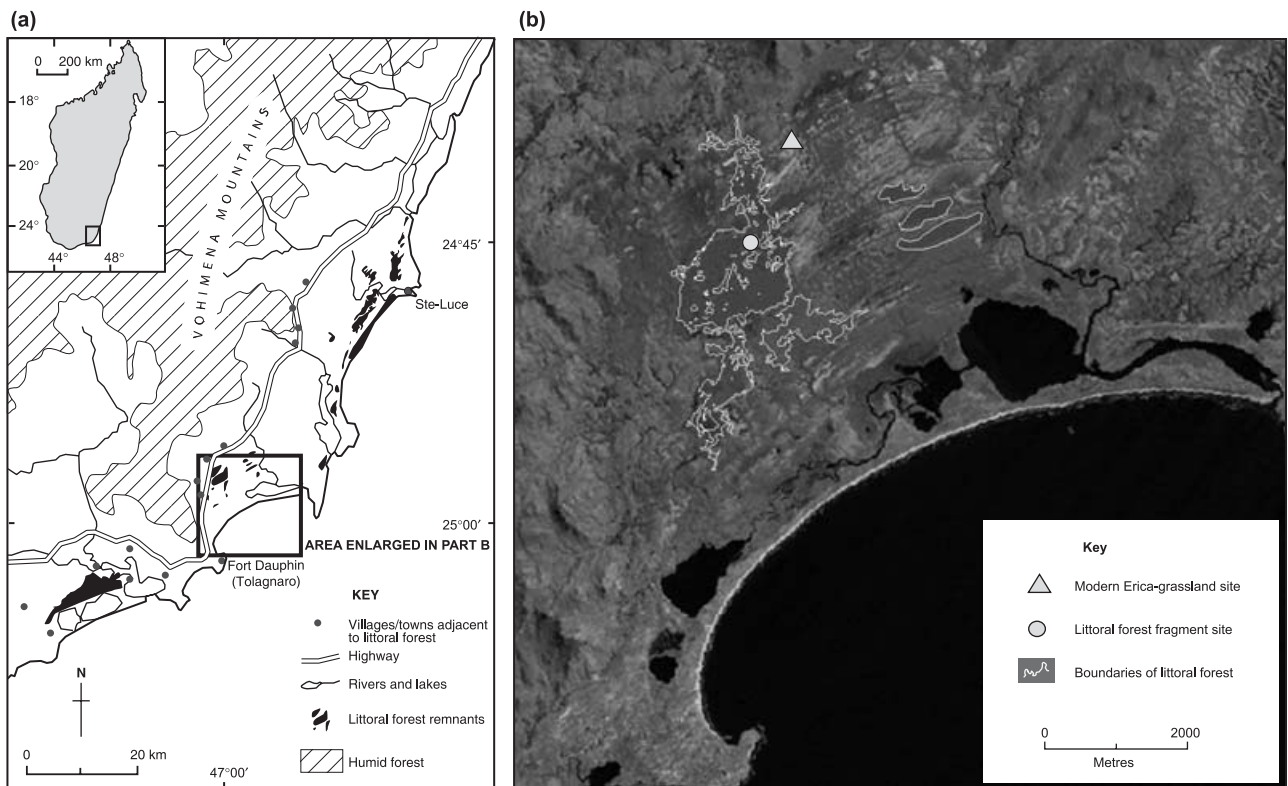


Figure 1 Location of south-east littoral forest fragments along the eastern coast of Madagascar. (a) Subtypes of the south-east littoral forest fragments modified from Watson *et al.* (2004). (b) Close-up satellite image of Mandena showing the sites analysed: littoral forest fragment (all forest fragments in Mandena delineated with white lines) and *Erica*-matrix.

service (<http://bcal.shef.ac.uk/info/>). We used the Southern Hemisphere calibration curve to calibrate our radiocarbon dates to actual calendar dates. The resulting calibrated dates were used to estimate extrapolated ages for the rest of the sequence using an age–depth model calculated from linear interpolation (Bennett & Heegaard, in press).

Pollen, charcoal and geochemistry analyses were conducted on the sediments at a fine resolution. For the first sequence (*Erica*-matrix), we analysed 66 samples (sample interval of 4 cm). In addition, we analysed the sedimentary sequence at the even higher resolution of every 2 cm during periods of vegetation transition. In the second sequence (littoral forest) 51 samples were analysed (sample resolution of every 4 cm). Diatom analysis was conducted at a sample interval of 8 cm. During periods of marine transgression, we analysed the diatoms at a higher resolution of 2 cm.

Geochemistry

Detailed geochemical analysis of the two sequences was undertaken on 31 elements using inductively coupled plasma-atomic emission spectrometry (ICP-AES) of 0.2 g of dry sediment (Perkin Elmer Optima 3300RL ICP-AES, operated by the Department of Geology, Royal Holloway, University of London) at the same sample interval as that used for the pollen analysis.

Diatoms

Diatom analysis was undertaken on the *Erica*-matrix sedimentary sequence because the basin there was larger, more exposed and with older sediment, therefore representing a better site for obtaining a clear diatom signal over a longer time period. For diatom analysis, each sediment sample was treated with HCl to remove carbonates, and oxidized with H₂O₂ to remove organic matter. A minimum of 300 frustules were counted for samples with abundant diatom concentrations and 100 frustules in samples with low concentrations. Identification was carried out mainly with reference to several key publications (Cleve-Euler, 1951; Krammer & Lange-Bertalot, 1991a,b,c,d; Hasle & Syversten, 1996). Diatom species were grouped in relation to salinity tolerances and life-forms using existing literature on their ecology (Dam *et al.*, 1994; Spaulding & Kocielek, 2003).

A diatom water depth index (DWDI) was also developed to infer broad temporal patterns of precipitation and aridity (Stager *et al.*, 1997, 2003; Barker *et al.*, 1998). The species were grouped into benthic (substrate dwelling) and planktonic (water-column dwelling), and then the relative abundances for the two categories were summed at each level.

Pollen

Sample preparation for pollen analysis was carried out following standard protocols (Bennett & Willis, 2001). Identification of

pollen grains involved comparison of fossil pollen with reference material held at the Oxford Long-term Ecology Laboratory and reference publications. A minimum of 300–400 terrestrial pollen grains (excluding Cyperaceae) were counted per sample in order to ensure a statistically significant sample size (Bennett & Willis, 2001).

Charcoal

Local fire history from the two sites was reconstructed through the measurement of macrocharcoal. Macrocharcoal (> 150 µm) was extracted from 1-cm³ subsamples using standard charcoal extraction methods from the organic non-pollen material and counted using a light microscope (Whitlock & Larsen, 2001).

Numerical analyses

The diatom and pollen data were converted to percentage data by expressing the value for each diatom/pollen type counted in a sample as a percentage of the sum of all the diatom or terrestrial pollen excluding aquatics and Cyperaceae. The percentage data were then plotted in a pollen diagram against age using the plotting program *PSIMPOLL*. Sedges (Cyperaceae) and ferns (Pteridophytes) were plotted as a percentage of the total sum of pollen and spores. We used the same program to plot macrofossil charcoal concentrations (particles cm⁻³) and geochemistry concentrations (weight percentage) against age.

We compared the rate of ecosystem changes in the two sites using chord distance dissimilarity between pairs of samples for which we have pollen and geochemical data (Bennett & Humphry, 1995). In addition, rarefaction analysis was used to measure how taxonomic richness changed through time (Birks & Line, 1992; Birks *et al.*, in press). The software *PSIMPOLL* was used for analyses of rate of change and rarefaction.

Results

Chronology and resolution

Results from the dating of the two sequences indicate that sedimentary record from the *Erica*-matrix site extends back to 6455 cal. yr BP and the littoral forest fragment to 2410 cal. yr BP. Modelling indicated that a linear interpolation provides a good representation of the relationship between age and depth (see Appendices S2 & S3 in Supporting Information). The age models for both sequences revealed consistent deposition with no evidence of mixing (see Appendices S2 & S3). The models indicated that vegetation was reconstructed at a resolution of about every 165 years per 4 cm for the *Erica*-matrix sequence (or every 82 years during periods of vegetation transition) between 6455 and 1500 cal. yr BP and a resolution of 50 years per 4 cm between 1500 cal. yr BP and the present time. For the littoral forest sequence, the model indicated that vegetation was reconstructed at a resolution of every 50 years per 4 cm for the whole period.

Geochemical analyses

Previous work has indicated that geochemical analyses of sedimentary records can provide an indication of past marine transgressions based on a number of indicators including Sr/Ca ratios and calcium influx (Shen *et al.*, 2005). Because seawater is enriched with Sr in contrast to fresh water, high Sr/Ca ratios indicate periods of seawater influx (Shen *et al.*, 2005). Similarly, calcium influx can be indicative of marine influences because seawater is enriched in this element. It is also possible to determine whether the influx is due to above- or below-ground influx through analysis of the sedimentology of the sequence (Donnelly & Woodruff, 2007); high-energy above-ground surges are associated with sand translocation and movement. In contrast, below-ground seawater influx should result in salinity peaks with no sand deposition into the coastal basins.

Results from the *Erica*-matrix sedimentary sequence indicate significant peaks in the Sr/Ca ratio occurring at approximately 2200, 1700, 1400, 1200 and 950 cal. yr BP (Fig. 2). The highest peak occurred at c. 1400 cal. yr BP. At 1400 cal. yr BP, most trace elements (Al, Mg, Ti, Fe, Mn, Zr, Co and others) except for calcium also declined abruptly, indicating significant soil disturbances (Fig. 2). Calcium peaked at 1400 cal. yr BP and 100 years later.

Previous work has indicated that sand in this region is rich in titanium, manganese and zircon (QIT Madagascar Minerals, 2001). Deposition of these elements into the *Erica*-heath basin is observed around 5800, 4600 and 3000 cal. yr BP (Fig. 2). Overall, chord distance analysis indicate that peaks in the rate of change of geochemical elements occurred between 1400 and 1200 and at 950, 550 and 100 cal. yr BP (Fig. 3a).

In the sedimentary sequence from the littoral forest, the geochemical analysis indicates a stable period prior to 950 cal. yr BP. The highest peak in Sr/Ca ratio occurs at 950 cal. yr BP and coincides with a steep decline in most elements indicating both seawater influx and soil disturbances (see Appendix S4). High rates of change in geochemical elements are recorded at 950 and 650 cal. yr BP (Fig. 3b).

Diatoms

Results from the analysis of the diatom assemblages from the *Erica*-matrix basin reveal relatively little change between 6455 and 1400 cal. yr BP. At 1400 cal. yr BP, however, a brief transition of less than a century occurred from freshwater, e.g. *Aulacoseira italica*, to salt-tolerant diatom species, such as *Cyclotella meneghiniana*, *Campylodiscus bicostatus*, *Campylodiscus clypeus*, *Nitzschia compressa*, *Nitzschia granulata*, *Rhopalodia acuminata*, *Lyrella* spp. and *Thalassiosira visurgis* (Fig. 2). *Cyclotella meneghiniana* is known to have wide tolerance for salinity. The other diatoms present at this level, namely *C. bicostatus*, *C. clypeus*, *N. compressa*, *N. granulata*, *R. acuminata*, *Lyrella* spp., and *T. visurgis*, have also been described as marine species with high salinity tolerances (Dam *et al.*, 1994; Hasle & Syversten, 1996; Spaulding & Kocielek, 2003).

Results from the construction of the diatom water-depth index using planktonic/benthic ratios indicates periods of lower water levels, probably indicating droughts of at least century-scale

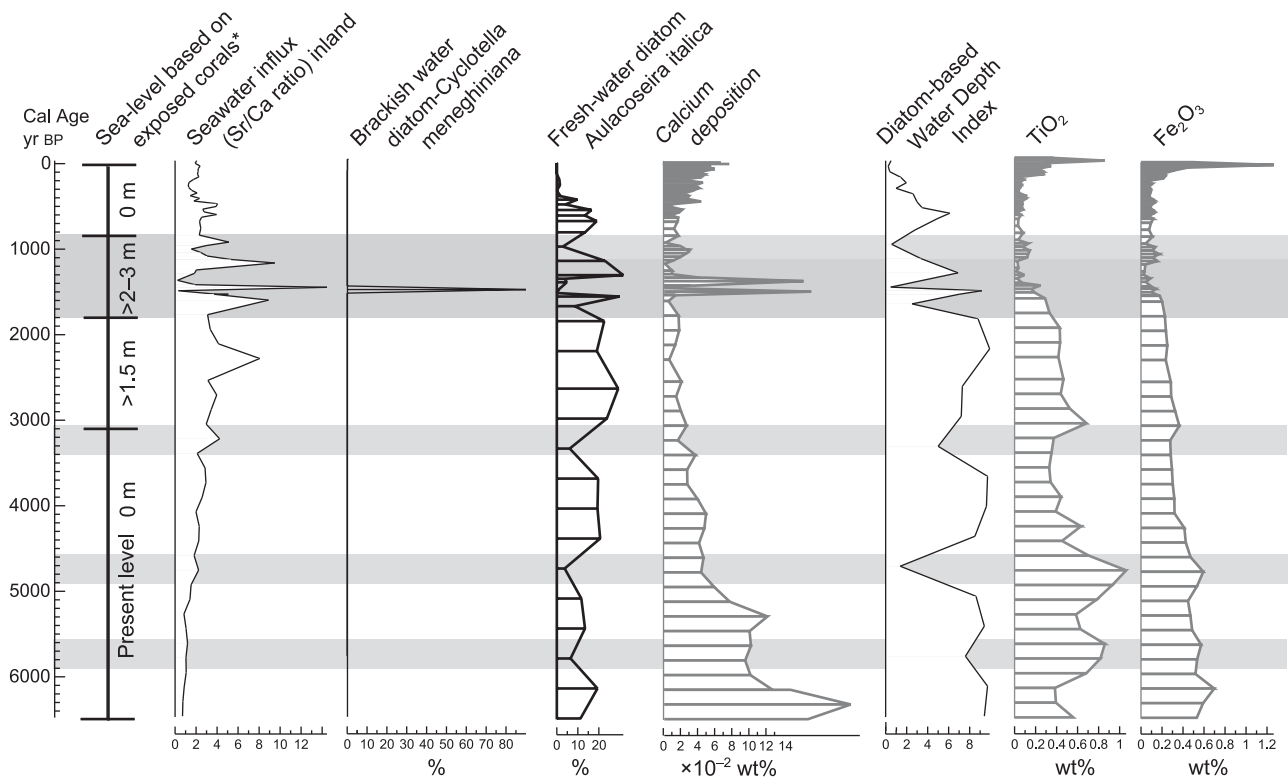


Figure 2 Selected geochemical elements and diatom species together with diatom water-depth level over the last 6500 years from the *Erica*-heath matrix (Mandena) in relation to reconstructed sea level using exposed coral units. Asterisk indicates sea level reconstructed from Battistini *et al.* (1976). Light grey bands are intervals of aridity based on diatom-water depth index (note that arid intervals are associated with peaks in Ti). Dark grey bands are periods of marine surges based on Sr/Ca ratios (the highest surge at 1400 cal. yr BP coincides with Ca deposition and the last surge at 950 cal. yr BP coincides with an arid interval). All Sr/Ca peaks occur within the period of high sea level (between 3000 and 800 cal. yr BP).

duration. Pronounced arid intervals occurred around 4600, 3000 and 950 cal. yr BP and a moderate arid interval around 5800 cal. yr BP (Fig. 2). The driest event occurred at 4600 and 950 cal. yr BP. Short arid intervals occurred at 1600, 1300 and 250 cal. yr BP (Fig. 2). We found strong and significant relationships between the diatom water-depth index and two other proxies of aridity, e.g. charcoal and Cyperaceae (Spearman correlation $r = -0.738, -0.483$, respectively, $P < 0.01$, $n = 33$) supporting the validity of the diatom proxy as a water-depth indicator. Additionally, we observed that the drying of the coastal basin during the pronounced droughts of 5800, 4600 and 3200 cal. yr BP is strongly associated with increased inorganic material (Ti, Zr and Mn) interpreted as mineralized sand infilling (Spearman correlation of diatom water-depth index and Ti concentration $r = 0.524$, $P < 0.01$, $n = 33$) (Fig. 2).

Pollen

Erica-heath matrix

Analysis of fossil pollen from the sedimentary sequence collected in the modern *Erica*-matrix in Mandena reveals that this site was forested between 6455 and 1400 cal. yr BP (Fig. 3a). Intriguingly, the forest species composition during this period at the *Erica*-matrix was different from that of the extant littoral forest fragments; the fossil plant assemblage suggests a species-rich

community of open *Uapaca* woodland with abundant shrubs and herbs, which are restricted to this open forest, e.g. *Canthium*, *Allophylus*, cf. *Schrophulariaceae* types and several *Solanum* types. Also growing abundantly in the site were generalist tree species that are typical of the littoral forest fragment, e.g. *Macaranga*, *Syzygium* and *Pandanus*. This past community assemblage appears to lack a comparable modern equivalent.

Around 1400 cal. yr BP at this site, the vegetation changed abruptly characterized by a rapid transition from a *Uapaca* woodland to an *Erica*-dominated system, and pollen of forest species declined abruptly from 80% to 35% in less than a century (Fig. 3a). In addition to *Erica*, *Myrica*, grass and sedges became abundant, suggesting a more open landscape. Biotic recovery was equally rapid; forest pioneers such as *Macaranga* and *Pandanus* rose from 35% to 70% of the total pollen in the following two centuries until another decline in forest pollen (to 40% of total pollen) at 1200 cal. yr BP (Fig. 3a). Analysis of the rate of change in this sequence revealed the highest rate of vegetation changes between 1400 and 1200 cal. yr BP (Fig. 3a).

A third decline in forest pollen (to 20% of total pollen) occurred between 950 and 850 cal. yr BP. The *Uapaca* woodland (*Canthium*, *Allophylus*, cf. *Schrophulariaceae* types, *Solanum* types) disappeared, shifting to an *Erica/Myrica*-heath/grassland. This decline coincides with the most significant decline in taxonomic richness between 950 and 500 cal. yr BP (Fig. 3a). Further, two

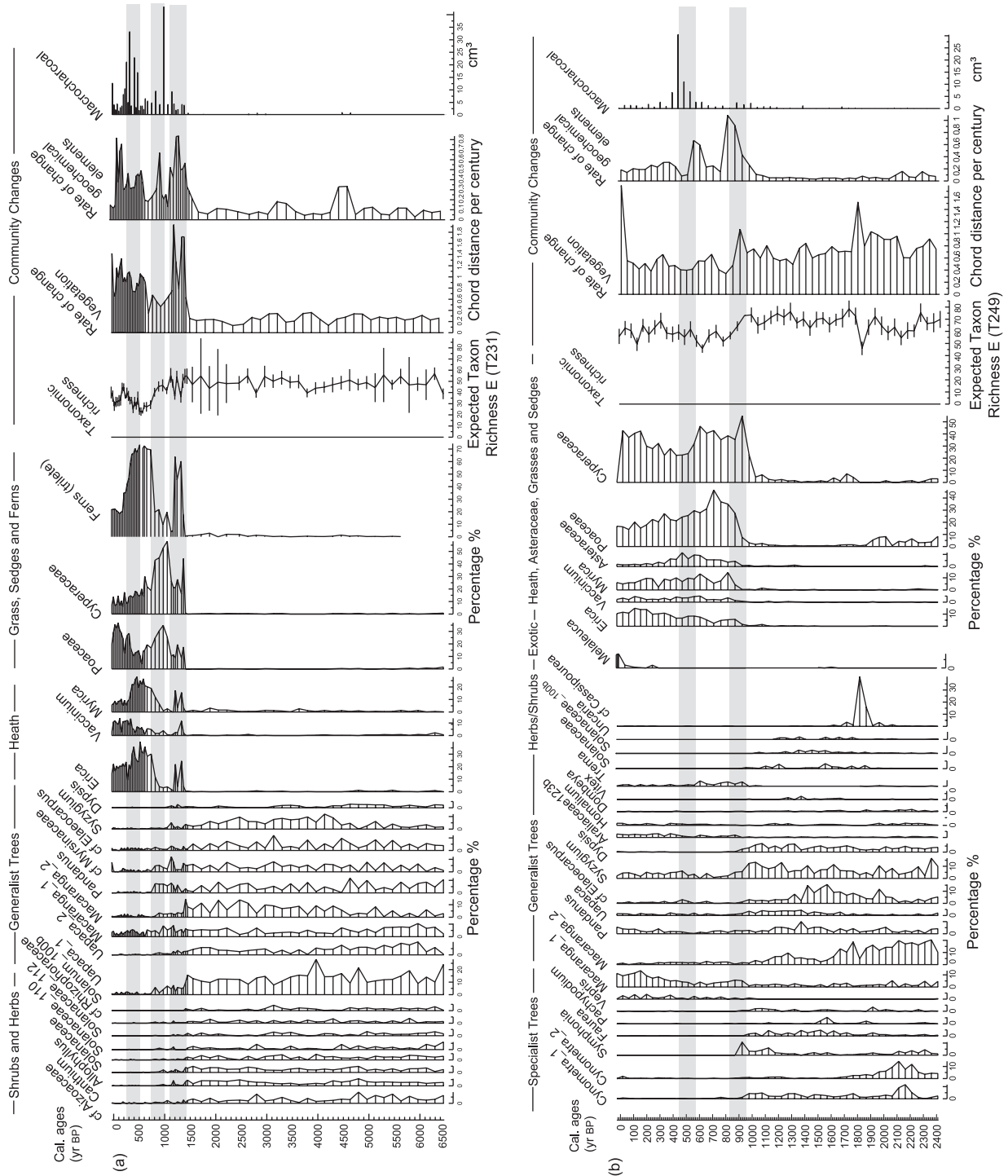


Figure 3 Changes in selected taxa together with the rate of change of vegetation and geochemical elements, and charcoal concentrations at the two habitat types. Grey bands are periods of biotic changes corresponding to vegetation shifts. Note the difference in species composition between the two sites: (a) *Erica*-heath matrix (ancient open *Uapaca* woodland); (b) littoral forest fragment.

taxa, a Fabaceae type and Solanaceae type 2, are last recorded in the fossil record around 950 and 850 cal. yr BP, respectively. Thereafter, it appears that *Erica/Myrica*-heath/grassland matrix formed a stable alternative ecological state with an increasing predominance of grassland to *Erica*-heath over the past 500 years (Fig. 3a).

Littoral forest

Analysis of the fossil pollen from the littoral forest sequence reveals that this site was extensively forested from 2410 to 950 cal. yr BP by rain forest specialists, e.g. *Symphonia*, *Faurea* and *Cynometra* (Fig. 3b). These species indicate humid and cool microclimatic conditions. Pollen evidence suggests that the first synchronous ecological transformation of this habitat occurred at around 950 cal. yr BP when the littoral forest fragment became greatly reduced and a decline of forest pollen from 77% to 35% is observed (Fig. 3b). The forest fragment lost its distinct identity in less than 50 years with the decline of forest specialists including *Symphonia*, *Faurea* and *Cynometra* (Fig. 3b). These forest specialists were replaced by open heath species, e.g. *Erica*, *Myrica*, Asteraceae types, and forest pioneers, e.g. *Trema* and *Macaranga* (two species of *Macaranga* occur in this ecosystem – the one which became abundant post-950 cal. yr BP is possibly *Macaranga obovata*, a weedy shrub where as the other *Macaranga*, possibly *Macaranga perrieri* a forest pioneer, was only abundant prior to 950 cal. yr BP) (Fig. 3b). During this period of vegetation transition, three previously abundant species, namely *Symphonia*, *Uncaria* and a *Solanum* type, disappeared from this region and there is no fossil record of their presence since this time (Fig. 3b).

Between 950 and 550 cal. yr BP, open habitat species and forest pioneers continued to be dominant components of the vegetation. Recovery of most forest species does not occur until c. 550 cal. yr BP at which time generalist forest trees adapted to some disturbances, e.g. *Macaranga*, *Pandanus*, *Syzygium* and Araliaceae became dominant (Fig. 3b).

The compositional changes apparent in the fossil record are synchronous with changes in taxonomic richness, which declined between 950 and 600 cal. yr BP and then increased again from c. 550 cal. yr BP (Fig. 3b). Rates of change analysis indicate that the highest rate of vegetation change at this site occurred at 1700 and 950 cal. yr BP, and in last 50 years. The high rate of change over the last 50 years can possibly be attributed to colonization and expansion of some introduced species such as *Melaleuca* in the site.

The present-day littoral forest at this site therefore appears to have become established from c. 550 cal. yr BP following recovery from an open *Erica*-heath landscape.

Charcoal

The charcoal records indicate sporadic fires at the *Erica*-matrix between 6455 and 1400 cal. yr BP (Fig. 3a). During this period, small localized fires occurred between 5600 and 4500 cal. yr BP and again between 3500 and 2500 cal. yr BP. Small fires became continuous from 1400 cal. yr BP until the present time. Large fire peaks are observed in the *Erica*-matrix at 950 cal. yr BP and between 250 and 500 cal. yr BP.

At the littoral forest, continuous charcoal peaks are not recorded until c. 1200 cal. yr BP (Fig. 3b). Large peaks in the charcoal record are also observed between 450 and 500 cal. yr BP (Fig. 3b). This period has been documented for its rapid population increases as a result of cultural transformation in the south-east region.

Chronological summary of the multi-proxy data

Overall, the vegetation from both sites remained stable and charcoal concentrations low during the period from 6455 to 1400 cal. yr BP despite evidence of: (1) several arid intervals around 5800, 4600 and 3200 cal. yr BP as attested by the diatom water-depth index, and (2) marine surges based on Sr/Ca ratios at 2200 and 1700 cal. yr BP during higher sea levels as observed in marine records. Severe biotic changes occurred from 1400 cal. yr BP. At the *Erica*-matrix, there is a short-lived decline in forest species and an increase in *Erica*, *Myrica*, grasses, ferns and sedges at 1400 cal. yr BP. At this particular point, we identified the highest peak of the Sr/Ca ratio, a peak of Ca, a decrease in freshwater diatoms, a steep increase in a brackish diatom and a small charcoal peak (that latter is thereafter continuous). In addition, there is the highest peak in the rate of change of pollen and geochemical elements. There is another decline in forest pollen at 1200 cal. yr BP, which coincides with another peak in the Sr/Ca ratio at the *Erica*-heath matrix. These geochemical and vegetation changes at 1400 and 1200 cal. yr BP are not observed at the littoral forest fragment site. However, at 950 cal. yr BP, forest species from both sites declined synchronously, shifting to open vegetation made up of *Erica*, *Myrica* and grasses, ferns and sedges. This is the period with the most significant decline in taxonomic richness and the highest peak in the rate of change of geochemical elements at both sites. In addition, it is the period of highest rate of change in vegetation at the littoral forest site. These biotic changes coincided with an arid interval, a peak in Sr/Ca ratios at both sites and a charcoal peak at the *Erica*-matrix. Around 550 cal. yr BP, forest species at the littoral forest fragment site began to recover and taxonomic richness increased. This period coincided with another significant peak in the rate of change of the geochemical elements and charcoal peaks at both sites. At the *Erica*-heath matrix, there is no apparent change in forest abundance, but the vegetation shifted towards more abundant grassland around 500 cal. yr BP with an increase in taxonomic richness. Over the last 300 years, rates of vegetation changes remained high at the *Erica*-matrix, but less so at the littoral forest, except for a peak over the last 50 years, which coincided with the invasion of the exotic forestry tree *Melaleuca*.

DISCUSSION

Evidence from the various proxies reconstructed in this study indicates that the coastal ecosystems of south-eastern Madagascar have been highly dynamic over the past 6500 years with significant biotic and abiotic changes occurring (Figs 3a,b & 4). When considering the impacts of past environmental change upon the littoral forests of south-eastern Madagascar there are three key driving mechanisms that need to be considered: (1) climate

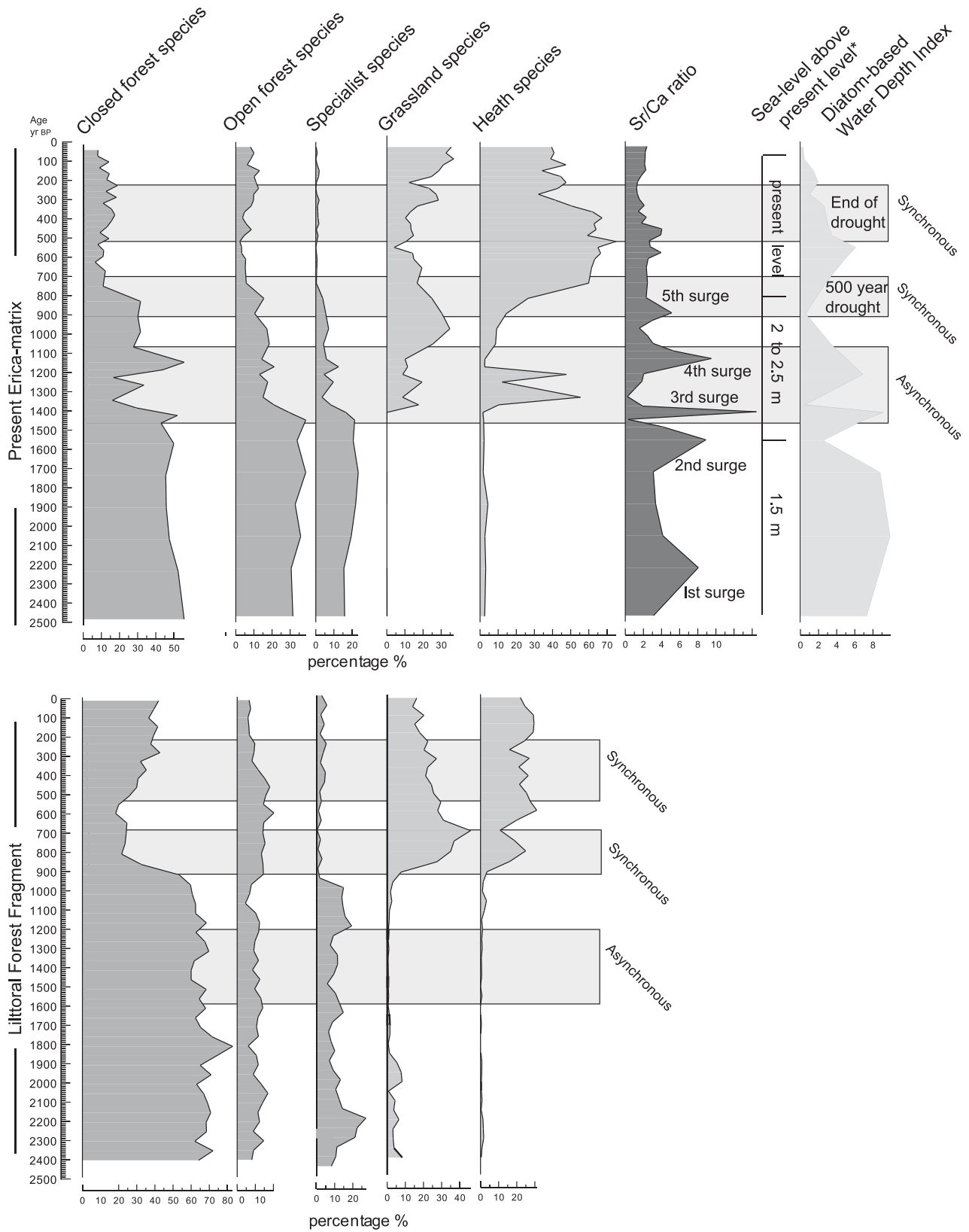


Figure 4 Summary diagram of biotic changes in the two habitats. Grey bands represent asynchronous and synchronous vegetation shifts.

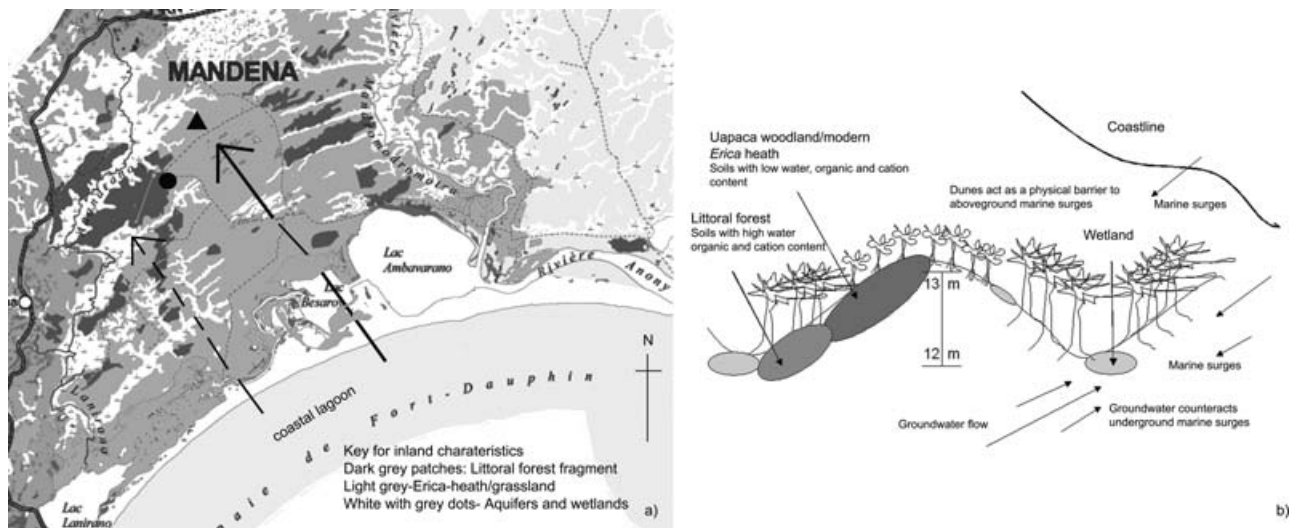


Figure 5 Schematic model of sea-level dynamics in Madagascar's littoral ecosystem in relation to landscape features. (a) Presence of wetlands around littoral forest fragments (modified from QIT Madagascar Minerals, 2001). (b) Importance of groundwater and dunes in counteracting under- and above-ground marine surges, respectively. Note that differences between the two habitats in terms of (1) topographical location on the dune system, (2) soils, and (3) the presence of wetlands and aquifers may influence the type of vegetation and resilience to environmental changes (marine surges and aridity). Sediment sequences retrieved from *Erica*-matrix (triangle symbol) and littoral forest fragment (circle symbol).

change, (2) sea-level rise, and (3) human (pre-historic and historic) signals. We will briefly discuss the evidence for these driving mechanisms in the region followed by a consideration of their impact upon the littoral forest vegetation and a comparison of the resilience of the two plant communities under investigation.

Climate change

Continuous climatic records independent of the pollen records are scarce in Madagascar. Only one diatom record exists for the Holocene period (Gasse & Van Campo, 1998) which provides a proxy climatic record from central highland Madagascar. This indicates that the warmest and driest period of the Holocene occurred around 4500 cal. yr BP (Gasse & Van Campo, 1998). Further, this record, together with other pollen sequences from Madagascar, suggests that another interval of drought and warmer climatic conditions occurred 1000 cal. yr BP (Matsumoto & Burney, 1994; Gasse & Van Campo, 1998). This climatic shift is also observed in most of East Africa.

These palaeorecords (Matsumoto & Burney, 1994; Gasse & Van Campo, 1998) are consistent with both our diatom and geochemical results, which indicates the most severe droughts around 4600 and 1000 cal. yr BP. The more moderate droughts at 5800 and 3200 cal. yr BP observed in our records are not apparent in the central highland palaeoclimate (Gasse & Van Campo, 1998). However, a decline in precipitation at approximately 3000 cal. yr BP has been suggested as the driving mechanism for change in vegetation apparent in a pollen sequence from the south-west of Madagascar (Burney, 1993).

In terms of shorter arid intervals, the two short drought events apparent at 1300 and 1600 cal. yr BP are not observed in other records. In these cases, the lower water depth index from the diatom record may be a reflection of other influences e.g. marine as

attested by a peak of the Sr/Ca ratio, which would have changed the abundance of marine diatoms mimicking a drought signal. However, the short arid interval of 250 years observed in our record is supported by a similar event recorded in a 400-year record of rainfall reconstruction based on annual layers of stalagmites from north-west Madagascar (Brook *et al.*, 1999).

Sea-level change

Published palaeoclimatic records indicate sea-level highstands of 1–3 m above present levels between c. 3000 and 800 cal. yr BP on the east coast of Madagascar (Camoin *et al.*, 1997; Camoin *et al.*, 2004). In addition, a detailed published record on the timing and height of sea level in the south-eastern Madagascan lagoons demonstrates a highest sea level of 2–3 m above the present level between c. 1800 and 800 cal. yr BP (Battistini *et al.*, 1976). This record is based on the dating of emerged coral units in coastal Madagascar (Battistini *et al.*, 1976). These published results are consistent with our geochemical and diatom records which suggest a series of marine influences on the Madagascan littoral forest at 2200, 1700, 1400, 1200 and 950 cal. yr BP with a high point at around 1400 cal. yr BP (Fig. 4).

Evidence from Sr/Ca ratio (Fig. 4) suggests that seawater influx in the littoral forest occurred in pulses, possibly indicating infrequent high-energy events such as ocean surges during storm events. In both sedimentary sequences there is no evidence from the geochemical evidence to suggest that these salinity peaks were associated with sand translocation and deposition. This therefore suggests seawater influx caused by underground infiltration, whereby the sand dunes may have protected the terrestrial systems from above-ground ocean surges of ocean water, a scenario observed in Sri Lanka during the tsunami of 2004 (Liu *et al.*, 2005) (Fig. 5).

Human signals

Archaeological evidence, including records from dated bones, pollen indicative of introduced plants and charcoal, points to a human presence in Madagascar from as early as 2000 cal. yr BP (Burney *et al.*, 2003). The evidence for the early human settlement on the island is patchy, however, and in the south-east, archaeological evidence indicates first human settlement nearly a millennium later around 1150 cal. yr BP (Rakotoarisoa, 1997). In the south-east, the first settlements were small and communities were most likely involved in rudimentary agricultural farming and frequent movement in search of food (Rakotoarisoa, 1997). Archaeological records also indicate that the most eventful period of cultural transformation in south-east Madagascar centred around 450 cal. yr BP; the Fort Dauphin region experienced a transformation known as the 'Tranovato Phase' with larger settlements, irrigated rice farming, cattle herding, fortification and prosperity by the Zafiraminia and their allies (Rakotoarisoa, 1997).

Differentiating between natural and anthropogenic fires in the palaeorecords to infer human presence remains problematic and can only be attempted in conjunction with archaeological and climatic records. Fossil charcoal from our two sequences indicates continuous low-burning fires from 1400 and 950 cal. yr BP in the *Erica*-matrix and forest fragment site, respectively, indicating possible human impacts. However, the synchronous emergence of fires and a fire-prone Ericoid vegetation rather suggests natural fires, which responded to compositional changes.

Large infrequent fires, which are above the background rate, are a more apparent signal of anthropogenic burning (Whitlock & Larsen, 2001). These are recorded at 1000 cal. yr BP in the *Erica*-matrix, but this peak also coincides with a pronounced drought. Other large charcoal records are observed between 250 and 500 cal. yr BP in both sites during the period of cultural transformations and they are very likely to be anthropogenically induced.

Drivers of vegetation changes

In summary, evidence from previous studies in combination with the two new records presented in this study indicate that significant changes were occurring in the region in terms of sea-level change (marine surges), climate change (intervals of drought) and human impact (agriculture and burning) over the past 6500 years. So what impact did these events have upon the composition and distribution of vegetation? What is clear from the pollen record is that both sites (the current littoral forest fragment and the *Erica*-heathland matrix) were formerly forested. The *Erica*-heath site was covered in open *Uapaca* woodland until approximately 1400 cal. yr BP. The littoral forest fragment was a closed forest until 950 cal. yr BP, became an open landscape dominated by Ericaceous plants and reverted to a closed forest again (but with a different composition from the former closed forest type) approximately 550 years ago.

Interestingly, evidence from both sedimentary sequences indicates that these forest types were remarkably resilient to

marine surges when they occurred in the absence of droughts. For example, the surges of 2200 and 1700 cal. yr BP occurred without noticeable change to the composition of the littoral or open *Uapaca* forest (Fig. 4). Similarly, it would appear that the intervals of drought (5800, 4600 and 3200 cal. yr BP) in the absence of seawater surges had little discernible impact on the vegetation in both habitats. However, when intervals of drought and marine surges occurred together, as evidenced at 950 cal. yr BP, a threshold was passed where the vegetation rapidly change (within 100 years) from open *Uapaca* woodland to *Erica*-*Myrica* heath and from littoral forest fragment also to *Erica*-*Myrica* heath (Fig. 4). Evidence from this study therefore suggests that that it is a combination of marine surges as a consequence of high sea level coupled with rainfall deficit that triggers a threshold event in the ecosystem, leading to a drastic ecosystem switch from forest to contrasting open *Erica*-*Myrica* heath assemblages. Thus it appears to be a nonlinear response whereby a combination of drought and salt-water stress triggers an ecological threshold event.

Another result to emerge from this study is that the closed littoral forest appears to have been much more resilient to marine surges than the open *Uapaca* woodland (Fig. 4) (where resilience refers to 'the magnitude of disturbance that can be absorbed before the system redefines its structure') (Walker, 1981; Gunderson, 2000). For example, the littoral forest maintained its composition during the high-impact surge of 1400 cal. yr BP whereas the matrix fluctuated temporarily from an open woodland to an *Erica*-heath. In contrast, there is no evidence of either marine inundation, soil or vegetation disturbances at the littoral forest fragment site during this period. We hypothesize three possible ways in which the denser and moister littoral forest fragments would have been more resilient: first, the effects of seawater influxes could have been counteracted by the coastal aquifers and wetlands located around the forest fragments, which maintained a high soil moisture (Fig. 5); second, deep water intake by roots of rain forest species, as observed in other rain forests (Oliveira *et al.*, 2005), could have provided a moist soil microclimate especially during times of sub-optimal water budgets. Thirdly, the dunes would have buffered the littoral forest fragments (which are situated at the base of the dune) from marine surges.

The littoral forest also appears to have been more resilient in its capacity to recover from water and salt stresses. Despite a community shift from a closed forest to an open *Erica*-heath community, the forest fragment is recovering to near former forest extent over the last 500 years. In contrast the open *Uapaca* forest never recovered from the 950 cal. yr BP event.

There is little evidence from our records to indicate severe human impact upon this environment. The charcoal record indicates low levels of background fires, probably occurring naturally, from 1400 cal. yr BP and onwards, and large fires between 500 and 250 cal. yr BP. Interestingly, the onset of forest recovery and contraction of *Erica*-heath from 500 cal. yr BP coincides with the largest fires and the most eventful period of cultural transformation in south-east Madagascar (Figs 3a,b & 4). Our results therefore support the archaeological evidence for this region (Rakotoarisoa, 1997) that suggest that anthropogenic activities were probably small-scale and did not have a major impact on

the prevailing vegetation. There is certainly no evidence for human activities resulting in the transition to the *Erica*-heathland matrix, although human-induced fires may have maintained the *Erica*-*Myrica* heath and contributed to the shift towards a more grass-dominated matrix through the use of fire.

CONCLUSION

In summary this study indicates that the vegetation of Madagascar's south-eastern littoral ecosystem is heterogeneous not only over time but also in space. In contrast to prevailing assumptions, our data suggest that the littoral forest fragments did not form a homogeneous and uninterrupted band along the south-east coast. The forest fragment was embedded in a matrix of open *Uapaca* woodland that was transformed by the climatic changes to an *Erica*-grassland matrix. Thus, the current heterogeneity and fragmentation observed in Mandena is a direct result of landscape attributes and climatic influences.

While climate change-integrated conservation strategies address the effects of climate change on species distribution and dispersal, our work suggests that more attention should be paid to the impacts of interactive climatic variables on ecosystem thresholds. This study emphasizes that species and communities within an ecosystem responded individually, maintaining ecosystem stability during sea-level rise; however, a threshold was crossed by the compounded effects of sea-level rise coupled with aridity, causing rapid ecological transformations. This research suggests that conservation efforts should focus on identifying thresholds of concern and maintaining ecosystem resilience.

Our work contradicts current prevailing narratives in Madagascar that landscape transformation is necessarily anthropogenically induced. Throughout the eastern coast of Madagascar, the dense littoral fragments are no more than a few kilometres wide. From our studies, we speculate that these fragments survived or recovered from severe climatic perturbations. Currently, these forest fragments have been devalued and categorized as degraded landscapes that have been transformed by human activities. Instead, the littoral forest fragments should be viewed as critical refugia for the survival of biodiversity in the extremes of climatic variability that have occurred in the past, and are likely to occur again in the future. With expected increases in the rate of sea-level rise, coupled with increasing drought frequency, Madagascar's littoral forest is likely to play an ongoing key role in maintaining biodiversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Radiocarbon dates from the two sequences.

Appendix S2 Age–depth model of *Erica*-matrix sequence using calibrated radiocarbon and ^{210}Pb dates.

Appendix S3 Age–depth model of littoral forest fragment using calibrated radiocarbon and ^{210}Pb dates.

Appendix S4 Changes in selected geochemical element at the littoral forest fragment site.

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