

How does spatial heterogeneity influence resilience to climatic changes? Ecological dynamics in southeast Madagascar

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Abstract. Conceptual models suggest a link between spatial heterogeneity, diversity, and resilience, but few empirical studies exist to demonstrate such an ecological relationship. In this study, we investigated the nature of spatial heterogeneity and resilience of two forest fragments from Madagascar's highly endangered littoral forest, and two nearby sites in the surrounding ericoid grassland. This ecosystem has been subjected to a number of large environmental disturbances over the last 6000 years, including a late Holocene sea-level rise of 1–3 m above the present level, pronounced drought events, and natural and anthropogenic fires. The aims were to determine the driving mechanisms for heterogeneity and to compare the impact of large environmental disturbances among the four sites.

Overall, our results indicate that, contrary to previous assumptions of continuous forest cover, the ecosystem was already spatially heterogeneous prior to the arrival of humans. Differences in groundwater, nutrients, and fires maintained a natural mosaic of forest and open vegetation giving rise to high floristic diversity. The four sites differed significantly in their resilience to climatic disturbances, as measured by compositional turnover and by the timing and extent of biotic recovery. The highly diverse littoral forest reverted more quickly to forest than the surrounding vegetation, which was composed of open *Uapaca* woodland (a no-analogue community) prior to the formation of the ericoid grassland. Further, species and populations from sites with low nutrients and nitrogen-fixing species as dominants were able to persist despite climatic perturbations, whereas there was higher turnover in the other sites. Overall, minimal extinction occurred in the ecosystem despite widespread landscape transformations. It is suggested that spatial heterogeneity and diversity in southeastern Madagascar may have enhanced species survival during climatic perturbations.

Key words: alternative stable states; drought; edaphic; extinction; heterogeneity; Madagascar; no-analogue; nutrient; recovery; refugia; turnover; water.

INTRODUCTION

A number of ecological models have suggested that a diverse and heterogeneous ecosystem is more ecologically resilient to environmental stress as it has an increased ability to absorb disturbance without dramatic change to ecosystem properties and processes. Also, such ecosystems may recover more quickly (Holling 1973, Gunderson 2000). For example, it is predicted that spatial heterogeneity will enhance species survival during rapid climatic changes (Thuiller et al. 2005). One explanatory model suggests that heterogeneous landscapes, where species are generally patchily distributed with sub- or metapopulations, are more likely to experience different microenvironmental conditions to the same climatic perturbations and therefore fluctuate asynchronously (Yachi and Loreau 1999, Loreau et al. 2003). As a consequence, species with subpopulations in

heterogeneous landscapes are less likely to go regionally extinct.

Diversity may also contribute to resilience. It is predicted that the large regional species pool in heterogeneous sites may maintain the assembly and functioning of an ecosystem by increasing the probability of recruiting key species, which will maintain ecological processes during periods of environmental stresses (Tilman 1999, Loreau et al. 2001). This "insurance" hypothesis also postulates that even if high diversity is not critical for maintaining ecosystem processes under benign environmental conditions, nevertheless, during periods of environmental fluctuations, high diversity provides insurance or a buffer because the large number of species present responds differentially (Yachi and Loreau 1999, Loreau et al. 2001, 2003).

Both spatial heterogeneity and diversity, then, have the potential to increase ecological and engineering resilience. These theoretical models have, however, rarely been tested in real ecosystems. One of the difficulties of studying heterogeneity and diversity is

Manuscript received 14 July 2008; revised 26 November 2008; accepted 17 February 2009. Corresponding Editor: C. C. Labandeira.

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that they are scale dependent; therefore, data are needed both in time and space. Paleocological studies in multiple sites provide the means of testing ideas about heterogeneity by being both spatially constrained and temporally explicit. Further, resilience of ecosystems to perturbations can also be measured in the fossil records by measuring the time required for a system to return to an equilibrium following a disturbance (defined as engineering resilience; e.g., Holling 1973, Gunderson 2000). Compositional turnover in the paleocological record can indicate the amount of disturbance that a system can absorb without a drastic change in its internal properties (defined as ecological resilience; e.g., Holling 1973, Gunderson 2000).

In this study, we investigated the nature of spatial heterogeneity and resilience in Madagascar's smallest and most endangered ecosystem, the littoral forest (Dumetz 1999, Ganzhorn et al. 2001, Cadotte et al. 2002, de Gouvenain and Silander 2003). The fragmented littoral forest, interspersed by sharp boundaries of ericoid grassland, provided an ideal landscape system to test ideas of the relation between resilience, heterogeneity, and diversity. Biotic responses to environmental stresses that included climatic desiccation, high sea-level rise, and fire episodes were contrasted among the four sites. The vegetation in the four sites is: a short-canopy littoral forest (M15), tall-canopy littoral forest (S9), and their matrix vegetation (defined as the vegetation types that embed the forest fragments), and ericoid grassland (MM and SM) (Fig. 1; Table 1). Specifically, we addressed the following questions: (1) How do the four sites compare in functional groups and vegetation composition through time and what factors (edaphic, climatic, fire, human impacts) contribute to spatial and biotic heterogeneity? (2) How did the four sites respond to environmental fluctuations (sea-level rise, aridity, and fire) and what are the interactions and feedback loops among biotic and abiotic components? (3) How does resilience (using compositional turnover and time required to return to former diversity and composition as determinants) differ at the local scale? (4) Is there a link between heterogeneity, resilience, and persistence?

STUDY SITE

Madagascar's littoral forest has been identified nationally as the 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). It has also been classified as one of the world's hottest hotspots because it is critically endangered (Ganzhorn et al. 2001), threatened by a large mining project to extract ilmenite, anthropogenic degradation, and anticipated future sea-level rise. The littoral forest is currently distributed as small forest fragments along the eastern coast from the northeast coast in Vohemar to its southern point at Petriky (Du Puy and Moat 2003).

Previous work on the littoral forest has hypothesized that the fragmented nature of this ecosystem is as a result of previous anthropogenic activity (Ganzhorn et al. 2001, de Gouvenain and Silander 2003, Consiglio et al. 2006). It also is hypothesized that the littoral forest would have been contiguous with the lowland evergreen forest that occupies the adjacent eastern mountain slopes (de Gouvenain and Silander 2003) and would have been continuous along the whole of the eastern coast, of which 90% has been lost and transformed into an ericoid grassland (Consiglio et al. 2006).

Alternative scenarios for change are also possible. Recently, it has been shown that the littoral forest of Mandena has been subjected to intense environmental fluctuation, which included late Holocene highest sea-level rise of 2–3 m above the present level between 1800 and 800 cal yr BP (calibrated years before present; Battistini et al. 1976, Camoin et al. 1997, 2004), four pronounced drought events which occurred around 5800, 4500, 3200, and 950 cal yr BP, and episodes of local and regional fires (Virah-Sawmy et al. 2009).

In this study, we focused on the littoral forest of Mandena and Ste-Luce along the southeast coast. The two littoral forest fragments share many endemic plant species and are dominated by *Asteropeia* (Asteropeiaceae), *Bembicia* and *Homalium* (Flacourtiaceae), *Cynometra* (Fabaceae), *Syzygium* (Myrtaceae), *Pandanus* (Pandanaceae), *Tripselium* (Moraceae), and *Uapaca* (Euphorbiaceae), but there are important differences in terms of structure and composition. For example, the tall canopy littoral forest (S9) has different emergent trees from the short-canopy littoral forest (M15). They also differ in the range and types of local endemics present. These floristic differences are attributed to physiographic differences, including a rainfall gradient running from north to south, a marine influence attributable to littoral forest located at varying distances from the coast, and to edaphic variations in nutrients (Dumetz 1999).

The ericoid grassland of Mandena and Ste-Luce also are similar to each other and composed of *Erica* (Ericaceae), *Myrica* (*Morella*) (Myricaceae), *Helichrysum* spp. and *Veronica nudicaulis* (Asteraceae), and the dominant grass, *Aristida similis*. Again, there are some important floristic differences between the two sites. The ericoid grassland in Mandena is homogeneously distributed whereas at Ste-Luce, the ericoid grassland is a more diverse community composed of tiny patches of littoral forest species, carnivorous plants such as *Nepenthes madagascariensis* (Nepenthaceae), sedges (Cyperaceae), and grasses (Poaceae).

METHODS

Sedimentary sequences were retrieved from small and closed peat basins of no more than 15 m radius, with the aim of gaining temporal records reflecting vegetation records in the immediate to local (100–300 m) vicinity of the basin (Bradshaw 1981, Heide and Bradshaw 1982,

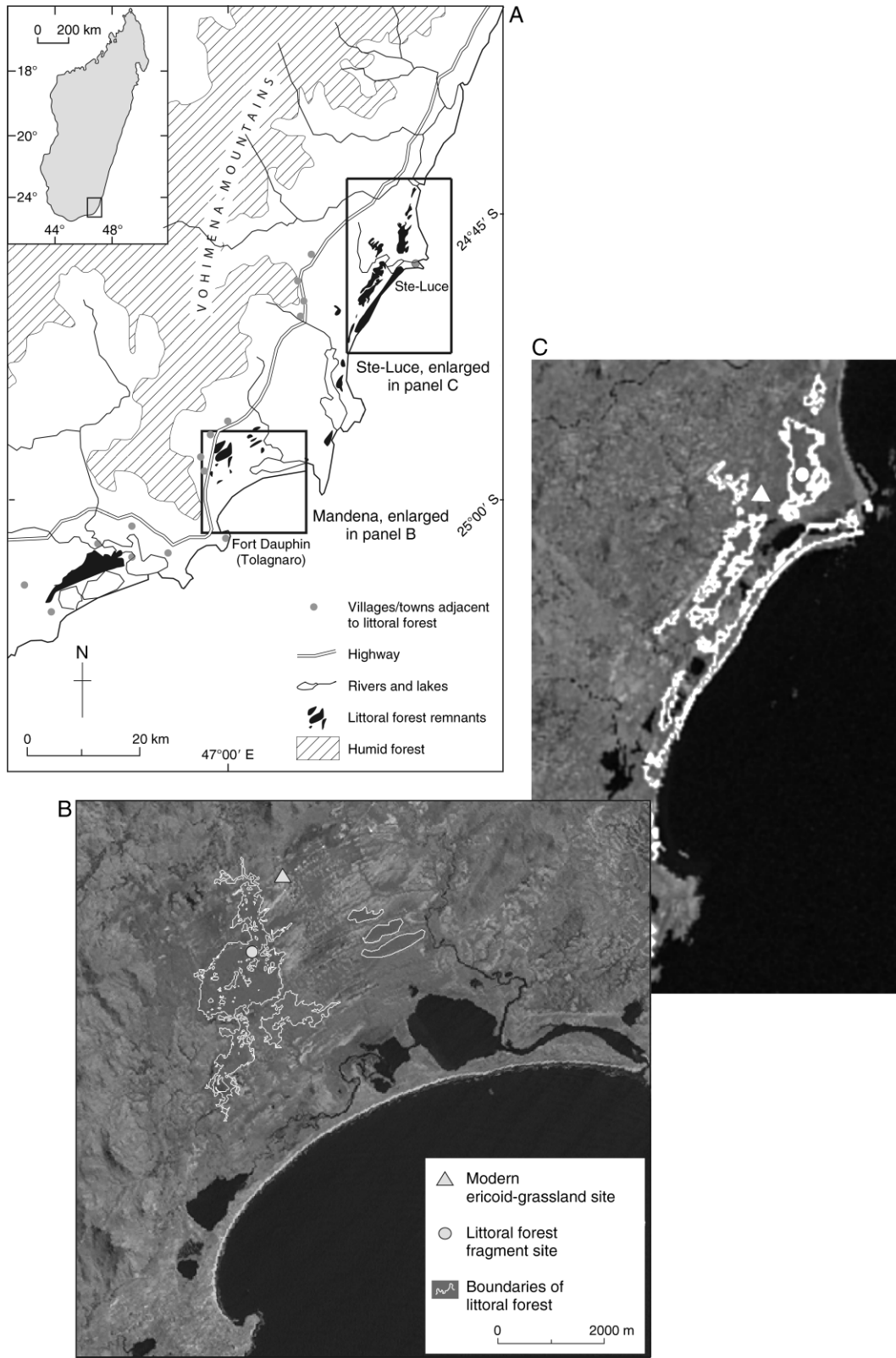


FIG. 1. Distribution of the littoral forest in southeast Madagascar (adapted from Virah-Sawmy et al. [2009]) in relation to sedimentary sequences collected from ericoid grassland and littoral forest (shown in panels B and C).

TABLE 1. Physiographic and compositional features of the four sites (two from the littoral forest and two from the surrounding ericoid grassland) in southeastern Madagascar.

Characteristics	Mandena matrix (MM) surrounding M15 fragment	Mandena forest fragment (M15)
Location of basin cored	24°56'4.956" S, 47°0'11.7" E	24°57'3.095" S, 47°0'2.952" E
Nature of substrate of surrounding vegetation	dry sandy soil of marine/aeolian origin	moist pseudo podzols with alluvial deposits above sandy substrate
Proximity to the sea (km)	5	5
Elevation (m)	13	12
Size of fragment (ha)		230
Rainfall per year (mm)	~1800	~1800
Common species	ericoid grassland: Asteraceae (<i>Helichrysum</i> spp. and <i>Vernonia nudicaulis</i>), <i>Erica</i> sp., <i>Canthium</i> sp., <i>Indigofera</i> sp., <i>Psorospermum</i> , and grasses	short-canopy littoral forest: <i>Asteropeia</i> , <i>Bembicia</i> , <i>Cynometra</i> , <i>Dracaena</i> , <i>Eugenia</i> , <i>Homalium</i> , <i>Intsia</i> , <i>Melaleuca</i> , <i>Syzygium</i> , <i>Pandanus</i> , <i>Tripselium</i> , <i>Uapaca</i>
Turnover (SD) over the last 3000 years	2.039	1.826
Inertia (variance) over the last 3000 years	1.086	1.059
Mean taxonomic richness (no. taxa)		
1) Post sea-level rise	33	52
2) Prior to sea-level rise	49	59
Pollen composition		
1) Post sea-level rise (post 800 cal yr BP)	Asteraceae, <i>Erica</i> , <i>Macaranga</i> type 1, <i>Myrica</i> , <i>Vaccinium</i> , and grasses	Asteraceae, <i>Erica</i> , <i>Macaranga</i> type 1, <i>Melaleuca</i> , <i>Myrica</i> , <i>Pandanus</i> , <i>Syzygium</i> , <i>Vaccinium</i> , and grasses
2) Prior to sea-level rise (prior to 1800 cal yr BP)	<i>Allophylus</i> , <i>Macaranga</i> type 2, <i>Pandanus</i> , <i>Syzygium</i> , <i>Uapaca</i> , Solanaceae, and Scrophulariaceae/Brassicaceae	<i>Cynometra</i> , <i>Faurea</i> , cf <i>Elaeocarpus</i> , <i>Dypsis</i> type 1, <i>Faurea</i> , <i>Homalium</i> , <i>Macaranga</i> type 2, <i>Pandanus</i> , <i>Syzygium</i> , <i>Symphonia</i>
Fossil extinction among abundant taxa >1% of total sum (date last observed in fossil record)	Fabaceae type (950 cal yr BP), Solanaceae type 2 (850 cal yr BP)	<i>Uncaria</i> (1150 cal yr BP), Solanaceae type 2 (1026 cal yr BP), Solanaceae type 3 (976 cal yr BP), <i>Symphonia</i> (950 cal yr BP)

Note: SD is standard deviation.

Jackson 1994, Sugita 1994; Table 1). The peat basins form part of an extensive but disconnected wetland system. These wetlands are fed mainly by groundwater and are highly sensitive to droughts (QIT Madagascar Minerals, unpublished report).

Two sites each of littoral forest and ericoid grassland were sampled. At Mandena, littoral forest fragment (hereafter referred to as M15; 24°57'3.095" S, 47°0'2.952" E) and its matrix, (hereafter referred to as MM; 24°56'4.956" S, 47°0'11.7" E), and at Ste-Luce, littoral forest fragment (hereafter referred to as S9; 24°46'37.307" S, 47°10'23.807" E) and its matrix, (hereafter referred to as SM; 24°46'41.123" S, 47°9'36.971" E) were sampled (Table 1; Fig. 1). M15 and S9 are the names given to the littoral forest fragments in regional conservation zoning and are therefore used here for consistency. The two sites in Mandena and two at Ste-Luce are ~1 km apart, respectively, and the two regions are ~50 km apart. The region of Ste-Luce receives slightly higher annual rainfall than Mandena (Lowry and Faber-Langendoen 1991; Table 1). S9 is a larger fragment and is situated relatively closer to the coast than M15 (Table 1).

Sample preparation for pollen analysis was carried out following standard protocols (Bennett and Willis 2001). Identification of pollen grains involved comparison of fossil pollen to reference material held at the

Oxford Long-term Ecology Laboratory and reference publications (Straka and Simon 1967, Straka et al. 1967, Lobreau-Callen et al. 1975, Rasoarimalala et al. 1982, Lienau et al. 1986, Burney 1988). A minimum of 300 terrestrial pollen (excluding Cyperaceae) was counted per sample in order to ensure a statistically significant sample size (Bennett and Willis 2001).

Edaphic variation was assessed in three sites using ICP-AES (inductively coupled plasma atomic emission spectroscopy) analyses of the sedimentary sequences. Previous studies indicated that changes in the geochemical elements in sedimentary sequences can provide a good record of changes occurring in soils surrounding the basins (Engstrom and Wright 1984). Previously published soil maps also were used to determine the organic content and the ground soil water budgets in the four sites and the processes of soil formation (QIT Madagascar Minerals, unpublished report). ICP-AES analyses on 11 elements were conducted on three sequences (those from MM, M15, and S9). In particular, we focused on concentrations of phosphorus deposited in the sedimentary sequence as it is the most limiting nutrient to plant growth in the tropics (Vitousek and Sanford 1986), it is not easily leached from the soil, and it is not very mobile in the water column of sedimentary sequences (Engstrom and Wright 1984). In addition, we also compared the concentrations of potassium and

TABLE 1. Extended.

Ste-Luce forest fragment (S9)	Ste-Luce matrix (SM) surrounding S9 fragment
24°46'37.307" S, 47°10'23.807" E moist pseudo podzols above sandy substrate	24°46'41.123" S, 47°9'36.971" E moist sandy soil of marine/aeolian origin
2.5	4
19	14
377	
~2000	~2000
tall-canopy littoral forest: <i>Anthocleista</i> , <i>Asteropeia</i> , <i>Bembicia</i> , <i>Canarium</i> , <i>Dracaena</i> , <i>Dyopsis</i> , <i>Homalium</i> , <i>Macphersonia</i> , <i>Myrica</i> , <i>Symphonia</i> , <i>Uapaca</i>	ericoid grassland: Asteraceae, <i>Erica</i> , <i>Hibbertia</i> , <i>Myrica</i> , and grasses (<i>Aristida similes</i> , <i>Imperata</i> sp.) and cultivated plants, e.g., <i>Ananas comosus</i>
1.670	0.550
0.910	0.470
61	55
66	59
Araliaceae, <i>Dyopsis</i> type 2, <i>Myrica</i> , <i>Macaranga</i> type 1, <i>Psychotria</i> , <i>Syzygium</i> , <i>Symphonia</i> , <i>Uapaca</i>	Asteraceae, <i>Erica</i> , <i>Hibbertia</i> , <i>Myrica</i> , <i>Macaranga</i> type 1, <i>Pandanus</i> , <i>Rapanea</i> , <i>Symphonia</i> , <i>Vaccinium</i>
Araliaceae, <i>Dyopsis</i> type 1, <i>Homalium</i> , <i>Myrica</i> , <i>Macaranga</i> type 2, Meliaceae, <i>Psychotria</i> , <i>Syzygium</i> , <i>Symphonia</i> , <i>Uapaca</i>	Asteraceae, <i>Erica</i> , <i>Hibbertia</i> , <i>Myrica</i> , <i>Macaranga</i> type 1, <i>Pandanus</i> , <i>Rapanea</i> , <i>Symphonia</i> , <i>Vaccinium</i>
Fabaceae type (966 cal yr BP), Euphorbiaceae type 110 (635 cal yr BP), Solanaceae type 2 (403 cal yr BP)	none

magnesium because they are the nutrients most likely to limit primary production and other ecosystem functions in the tropics (Vitousek and Sanford 1986).

We reconstructed local fire history through time in the four sites using analyses of macrofossil charcoal in the sedimentary sequences. Macrocharcoal (charcoal pieces larger than 120 μm) gives a strong signal of local fire history (Clark 1988, Carcaillet et al. 2001, Duffin et al. 2008). Macrocharcoal was extracted from 1-cm³ sub-samples using standard extraction charcoal methods (Whitlock and Larsen 2001) and counted using a light microscope.

Chronology and resolution

The chronologies of the sedimentary sequences were established based on a total of 15 calibrated accelerator mass spectrometry ¹⁴C dates (Appendix A). Calibration of radiocarbon dates was performed using BCAL software, an internet-based Bayesian radiocarbon calibration service (*available online*).⁵ The calibrated chronologies were also supported by up to five ²¹⁰Pb datings for the sequences in Mandena.

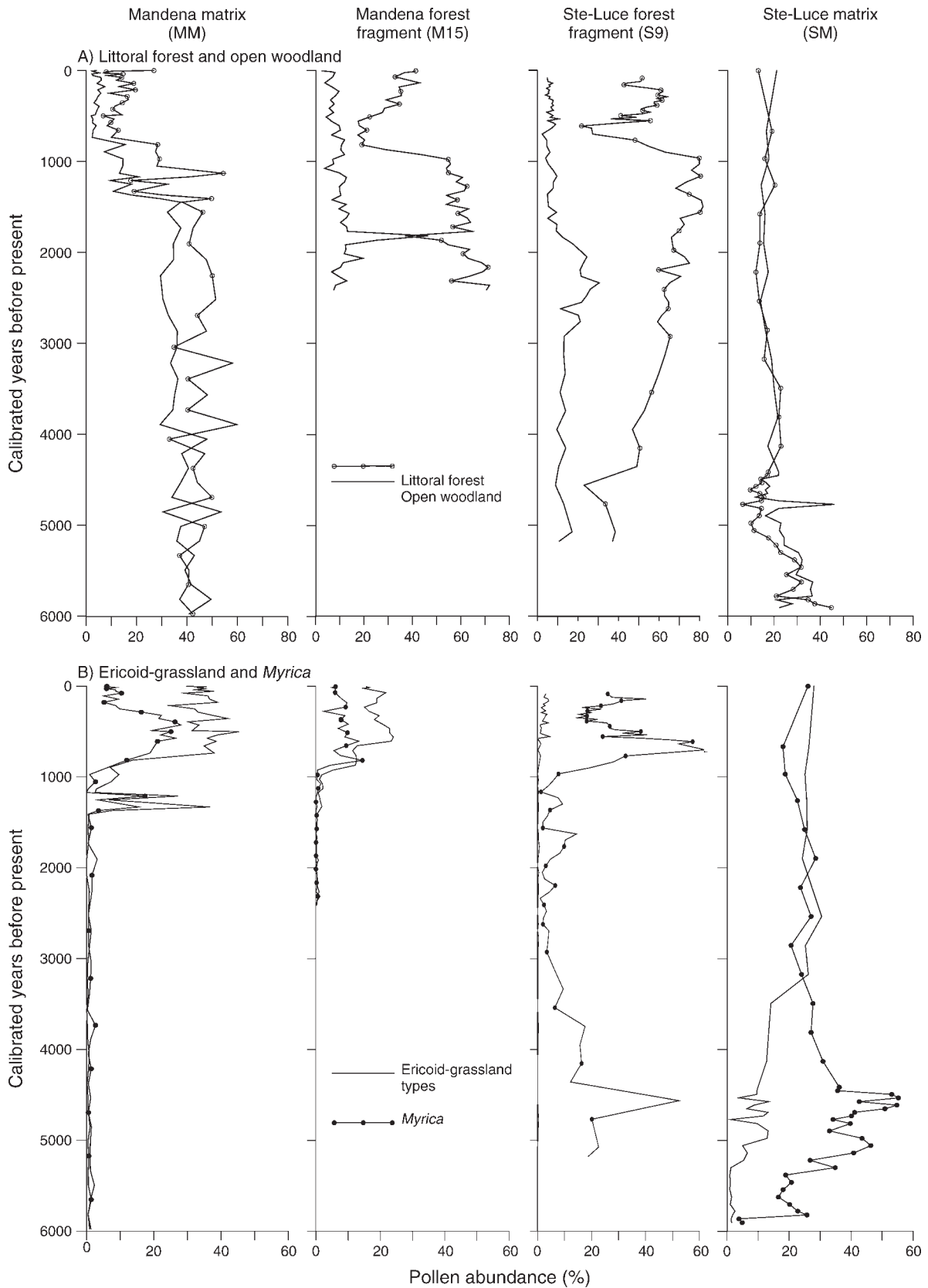
Pollen and charcoal analyses were conducted on the sediments at a fine resolution. For the Mandena sequences, samples were counted at an interval of 4 cm; 66 and 51 samples were counted for MM and M15,

respectively. The sequences from Ste-Luce were analyzed at a sample resolution of every 2 cm; the total number of pollen samples analyzed were 72 and 40 samples for S9 and SM, respectively. Geochemical analysis was conducted at the same interval as that used for the pollen analysis except for the S9 sequence, which was analyzed at a resolution of every 4 cm.

Numerical analyses

The pollen data were converted to pollen percentage data by expressing the value for each pollen type counted in a sample as a percentage of the sum of all the terrestrial pollen. The pollen types were classified into four main functional groups defined by traits that are potentially relevant to ecological processes: closed littoral forest, open woodland (including light-demanding shrubs and herbs), taxa of poor nutrient soil and disturbance (including *Erica*, *Vaccinium*, and Asteraceae such as *Helichrysum*, and graminoids, that is, grasses and sedges), and taxa of poor nutrient soils with nitrogen-fixing potential (*Myrica*) (Miguel and Rodrigues-Barrueco 1974, Morris et al. 1974, Mian et al. 1976, Tjepkema et al. 1986, Vitousek and Walker 1989). These groups differ in characteristics that may influence ecological processes such as biomass, decomposition, nitrogen fixation, rooting depth, root-to-shoot ratio, size, and flammable foliage. We plotted these functional groups on similar timescales to compare how each site

⁵ (<http://bcal.shef.ac.uk/>)



responded to environmental fluctuations. We also plotted macrocharcoal (particles/cm³) and geochemical data (weight percentage) against calibrated age.

Statistical analysis

We compared taxonomic (palynological) richness using rarefaction analysis of the lowest sample size (300) in the four sites. Rarefaction analysis removes any bias in richness estimates caused by different pollen count sizes (Birks and Line 1992). The software PSIMPOLL 4.25 was used for analyses of rarefaction (Bennett 2005).

Principal components analysis (PCA) in CANOCO 4.5 was used to perform an indirect gradient analysis to observe variation in pollen composition among the four sites (ter Braak 1986). PCA was the preferred analysis because the length of the compositional gradient was less than 2.0 standard deviations, and the data were relatively homogenous (Lepš and Šmilauer 2003). We first classified the data for each site as three main time sequences: pre-high sea-level rise (prior to 1800 cal yr BP), high sea-level rise (between 1800 and 800 cal yr BP), and post-sea-level rise (between 800 cal yr BP to present time). The percentage pollen data were square-root transformed before performing a PCA and rare taxa were not downweighted. The taxa were centered to eliminate any bias caused by certain taxa with wind-dispersed pollen, which tend to be overrepresented in paleoecological reconstructions due to high pollen productivity. Ordination biplots were used to display the results of the PCA.

In addition, redundancy analysis (RDA) was used to identify the relationships between pollen taxa and environmental variables (11 soil variables and charcoal concentrations). Constrained ordination is a powerful tool to determine whether the variability in species composition can be explained by the measured environmental variables. In order to decide which variables to include in the ordination model, Monte Carlo permutation tests of 999 time-series restricted permutations were used (Lepš and Šmilauer 2003). Only the variables that had a significant relationship with the pollen data significantly higher than what could have occurred by chance were included in the model. RDA was undertaken on data from all sites together, in addition to a site-to-site basis analysis.

Detrended canonical correspondence analysis (DCCA) was used to estimate compositional turnover (Hill and Gauch 1980, Birks 2007, Birks and Birks 2008) over the last 3000 years, as this period is covered by all the sedimentary sequences. The sole constraint used was sample age. Compositional turnover was estimated by

measuring the gradient length of the temporally constrained first DCCA axis for each site (Birks 2007, Birks and Birks 2008). One of the main advantages of estimating turnover with DCCA is that the results are scaled in standard deviation units of compositional turnover (Birks 2007, Birks and Birks 2008). The overall turnover at each site was estimated as the gradient length for the last 3000 years (Birks 2007, Birks and Birks 2008). A site with high turnover will have completely different species compositions at opposite ends of the temporal sequence (Hill and Gauch 1980, Birks and Birks 2008) indicating significant changes in the properties of the system and thus, lower ecological resilience. As with the other ordinations, percentages were square-root transformed to stabilize variances and rare taxa were not downweighted. In addition, detrending by segments and nonlinear scaling was applied to the DCCA.

RESULTS

Age models

The resulting calibrated ¹⁴C and ²¹⁰Pb dates were used to estimate extrapolated ages for the rest of the sequence using an age–depth model (Blaauw and Heegaard 2001). ¹⁴C dates indicate that organic materials had accumulated in the basins from: 6455 cal yr BP at MM, 2410 cal yr BP at M15, 5128 cal yr BP at S9, and 5905 cal yr BP at SM. In all of the sequences, we obtained reliable age–depth models by linear interpolation using the software PSIMPOLL 4.25 with no evidence of hiatus or mixing (Appendices A and B).

Linear interpolation indicated that pollen, charcoal, and geochemistry analyses were conducted on the sediments at a high temporal resolution: an interval of between 50 to 100 years for all sequences except for the geochemical records of S9, which was undertaken at every 140 years, and pollen analysis of SM sequence covered every 50 years between 5905 and 3962 yr BP and every ~260 years for the period following 3962 yr BP.

Functional groups

Functional groups here are interpreted as a subset of species with similar ecological traits, although other definitions exist (Díaz and Cabido 2001). Four broad functional groups were identified in this ecosystem over the last 6000 years: littoral forest (closed canopy) types, open woodland types, ericoid grassland types, and *Myrica* bushland.

Functional groupings of pollen taxa revealed little compositional change in three of the four sites (M15, S9, and MM) until ~950 cal yr BP (Fig. 2A, B). During this stable period, littoral forest taxa predominated M15 and

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FIG. 2. Changes in pollen abundances for different functional groups in southeast Madagascar: taxa typical of (A) closed littoral forest and open woodland types; and (B) ericoid-grassland and *Myrica* bushland types. Note the rapid biotic changes in three of the sites at 950 cal yr BP.

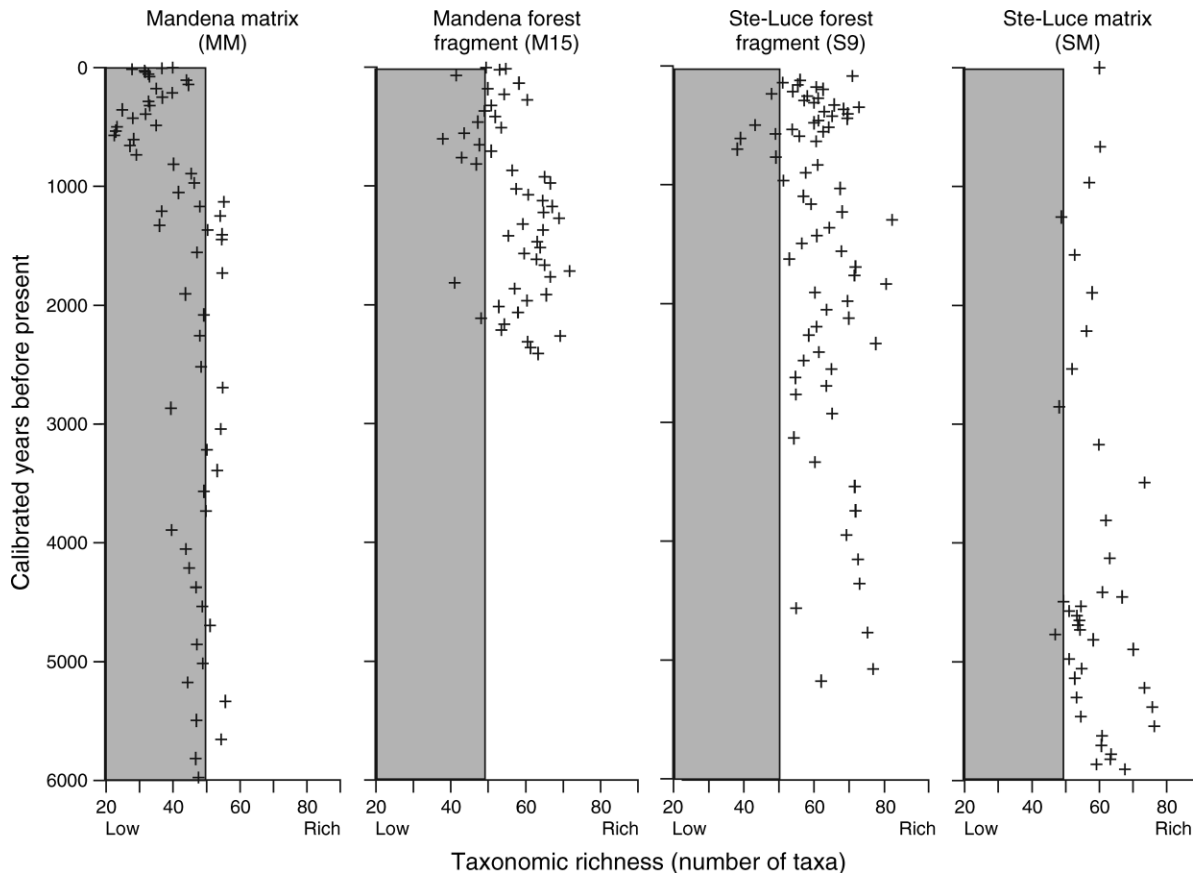


FIG. 3. Changes in taxonomic richness in the littoral forests and adjoining sites. Note the rapid decline in taxonomic richness in three sites at 950 cal yr BP.

S9 fragments, whereas open (*Uapaca*) woodland taxa dominated MM. SM is the only site that experienced compositional changes during this period with paleoecological evidence to suggest a switch from open (*Uapaca*) woodland to ericoid grassland between 5800 and 5000 cal yr BP (Fig. 2A, B). It is important to note here that the open (*Uapaca*) woodland is a no-analogue community, that is, this past vegetation does not have a modern equivalent.

All sites shifted synchronously to ericoid grassland or *Myrica* bushland (also a no-analogue community) at 950 cal yr BP except for SM, where ericoid grassland was already prevalent (Fig. 2A, B). There were small variations in response among the different sites.

Myrica and *Erica* increased abruptly as dominants from near zero abundance in M15 and MM at Mandena following the 950 cal yr BP event, but in the Ste-Luce sites at S9 and SM, *Myrica* had already been an important biotic component (Fig. 2B). *Erica* remained mostly absent from fragment S9. There, *Myrica* gained even greater dominance following the 950 cal yr BP event. A precursor but temporary increase in *Erica*, *Myrica*, and graminoid had already occurred in the open *Uapaca* woodland of MM at 1400 cal yr BP, but this

shift was short-lived and the vegetation returned to open woodland after ~200 years.

A switch back to littoral forest is observed at M15 and S9 between 600 and 400 cal yr BP (Fig. 2B). This change occurred rapidly in S9 between 600 and 500 cal yr BP, but in M15 the transition to forest was more gradual, lagging behind by a century. This switch was not observed in the matrix sites of MM and SM.

Diversity

Results from the rarefaction analysis revealed that M15, S9, and SM were comparable in taxonomic richness (mean ranging from 58 to 66 taxa) until ~950 cal yr BP (Fig. 3). MM, by comparison, was less taxonomically rich (mean ~ 48 taxa) during the same period. Rarefaction indicated a synchronous decline in taxonomic richness at 950 cal yr BP in all sites except for SM, which has remained taxonomically rich over the last 6000 years (Fig. 3).

An increase in taxonomic richness is observed from ~500 cal yr BP in S9, M15, and MM. However, it appears that the sites in Mandena have not fully returned to their former richness.

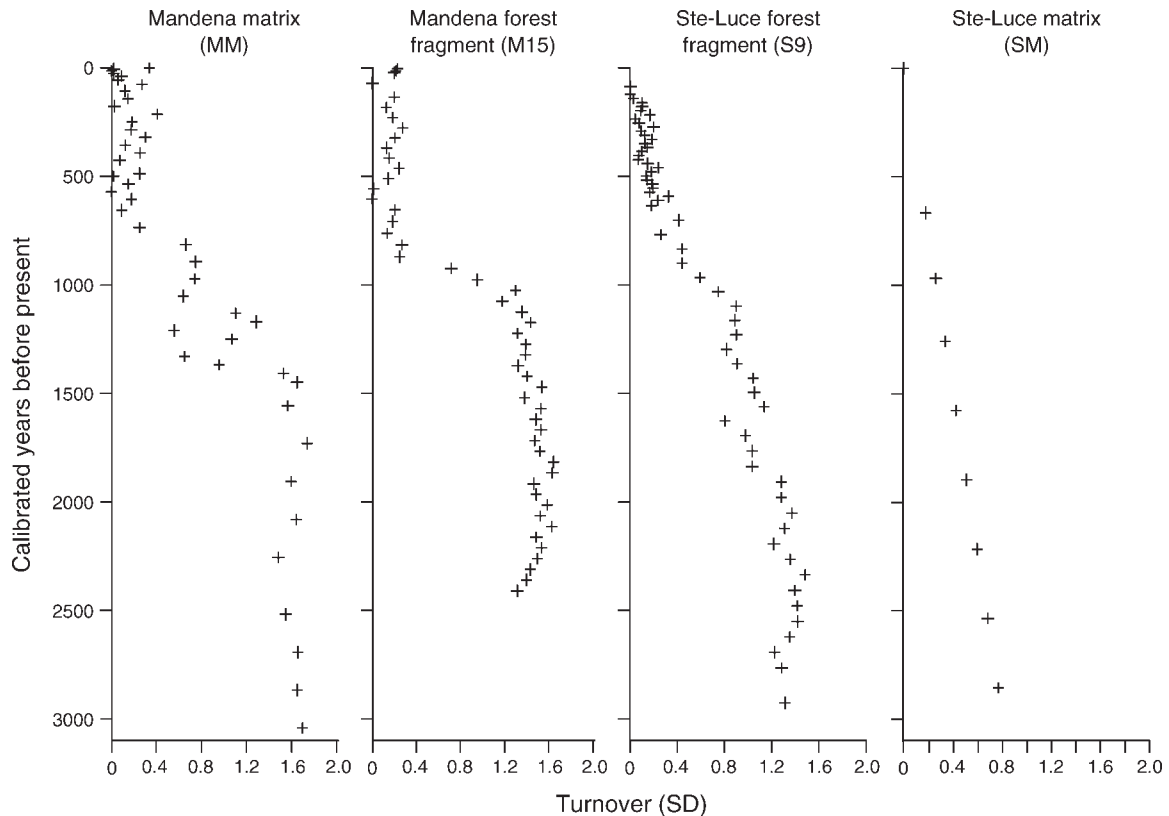


FIG. 4. Compositional turnover in the littoral forests and adjoining sites over the last 3000 years using DCCA (detrended canonical correspondence analysis). Note that the first DCCA axis (turnover) is scaled to standard deviation units. There were high compositional changes in three sites at 950 cal yr BP.

Of the 100 taxonomic pollen types classified from common to uncommon (but not rare) in the time sequence (>1% of total pollen sum), only a few went locally extinct in M15, MM, and S9 (Table 1). These local extinctions occurred between 1200 to 400 cal yr BP (Table 1). At SM, there is no documented fossil extinction.

Compositional turnover

DCCA was used to quantitatively estimate compositional turnover (Birks 2007, Birks and Birks 2008) through time.

Among the four sites, turnover over the last 3000 years was highest at MM, followed by M15, and there was least compositional turnover at the sites S9 and SM in Ste-Luce (turnover was 2.039, 1.826, 1.670, and 0.550, respectively; Table 1).

Through time, there are high compositional changes around the 950 cal yr event associated with the transition from littoral forest or open woodland to ericoid grassland or *Myrica* bushland at MM, M15, and S9 (Fig. 4).

Geochemical results

A comparison of the geochemical trace elements in the three sequences indicates variability in availability of

nutrients in the soils around the basins through space and time. M15 was extremely nutrient-rich between 950 and 2500 cal yr BP, with elevated concentrations of P, K, Mg (Fig. 5), and other micronutrients (Fe, Zn, Mn). In contrast, MM and S9 were both nutrient-deficient throughout the time sequence.

The geochemical concentrations remained relatively unchanged in S9 throughout the sequence, but in MM there were declines between 1400 and 1100 and again between 950 and 850 cal yr BP (Fig. 5). In this sequence, there was then a return to previous nutrient concentrations in less than a century. In the M15 sequence, nutrient concentrations similarly declined between 950 and 850 cal yr BP (Fig. 5). However, in M15 nutrient concentrations never returned to former levels following this decline.

Charcoal

Signals of local fires, reflected by the incidence of macrocharcoal particles in the four sites, demonstrate that fire peaks became continuous at Mandena from 1400 cal yr BP at MM and 950 cal yr BP at M15 (Fig. 6). At Ste-Luce, fires were rare at S9 but occurred sporadically throughout the reconstructed fire history of SM (Fig. 6).

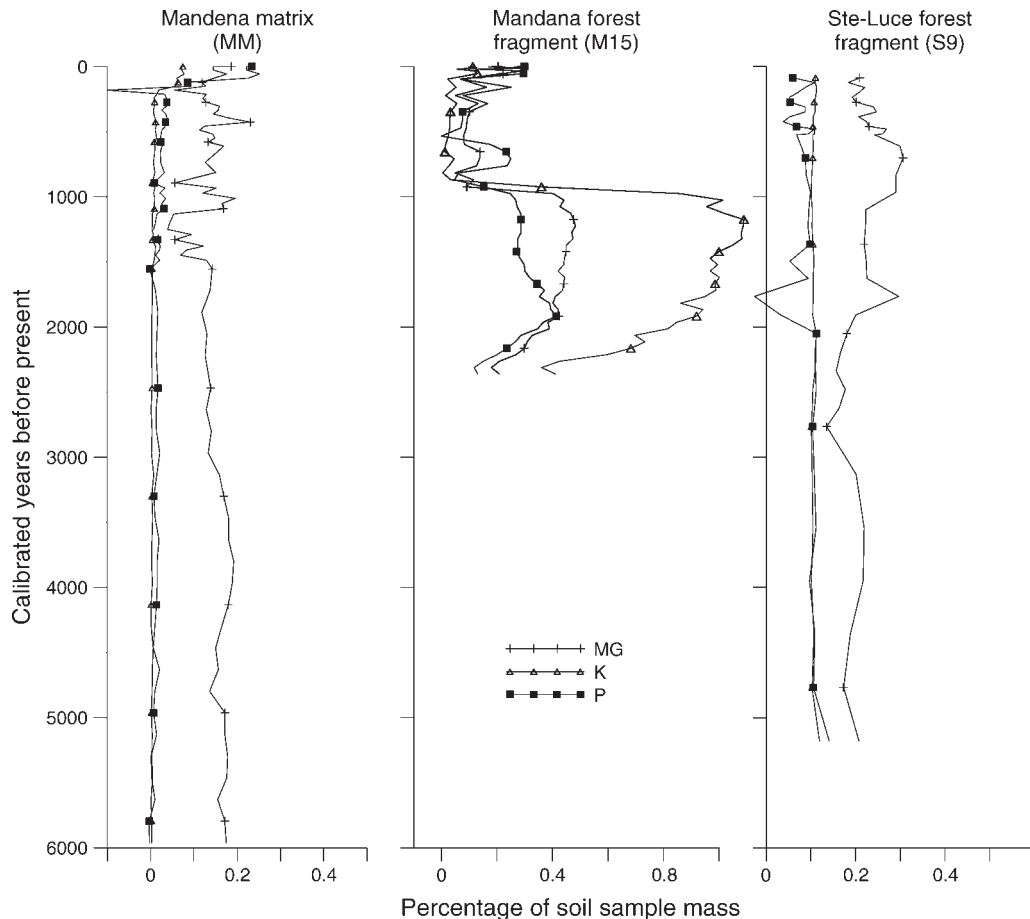


FIG. 5. Changes in three selected nutrients in the littoral forests and adjoining sites: magnesium (Mg), potassium (K), and phosphorus (P). These geochemical elements were measured as the percentage of the mass in the inorganic soil sample. Note that the scale for M15 differs from MM and S9. There are large nutrient losses at 950 cal yr BP in M15 and smaller losses in MM between 1400 and 1100 and again between 950 and 850 cal yr BP. S9 soils have remained relatively unchanged.

Large fire peaks in the records are observed around 1000 and between 400 and 200 cal yr BP at MM, between 500 and 250 cal yr BP at M15, sporadically at SM, but no large fires are ever recorded at S9. Higher concentrations of macrofossil charcoal were observed in both of the Mandena sites with concentrations of at least 500 macrofossil charcoal particles/cm³ of sediment during peaks of burning, in comparison to Ste-Luce, where concentrations never reached >120 macrofossil charcoal particles/cm³ in SM and as few as 10 macrofossil charcoal particles/cm³ in S9.

Multivariate analyses

Principal components analysis (PCA).—Results from the PCA indicate that the four sites have distinct pollen assemblages and that a clear difference occurs between Mandena and Ste-Luce (Fig. 7A). In response to environmental perturbations, the matrix sites become more homogenous in composition, as *Erica* and *Myrica* assume dominance, whereas the forest fragments (M15 and S9) have diverged in composition (Fig. 7A). The

PCA also indicates that the trajectory from one compositional state to another along the ordination axes was gradual at the Ste-Luce sites whereas at Mandena, both sites appeared to have undergone rapid and threshold response from one state to another.

All four sites share a common species pool (e.g., dominants are *Uapaca* type 1 and 2, *Syzygium*, *Macaranga* type 1 and 2, and *Pandanus*), although a number of taxa provided distinct signatures of each site prior to the 950 cal yr BP event. Prior to rapid compositional changes, M15 was distinct from the rest of the sites with species of *Cynometra*, Apocynaceae, and *Faurea* (Proteaceae) as dominants, suggesting a swamp and paludal forest (Fig. 7B). During the same period, MM was distinctive to the dominance of herbs and shrubs including several Solanaceae, Scrophulariaceae–Brassicaceae, *Canthium* (Rubiaceae), and *Allophylus* (Sapindaceae), indicative of a more open woodland. Another key difference among the sites was the presence of the rain forest taxa, *Symphonia* (Clusiaceae), in all sites except for MM. S9 was, and

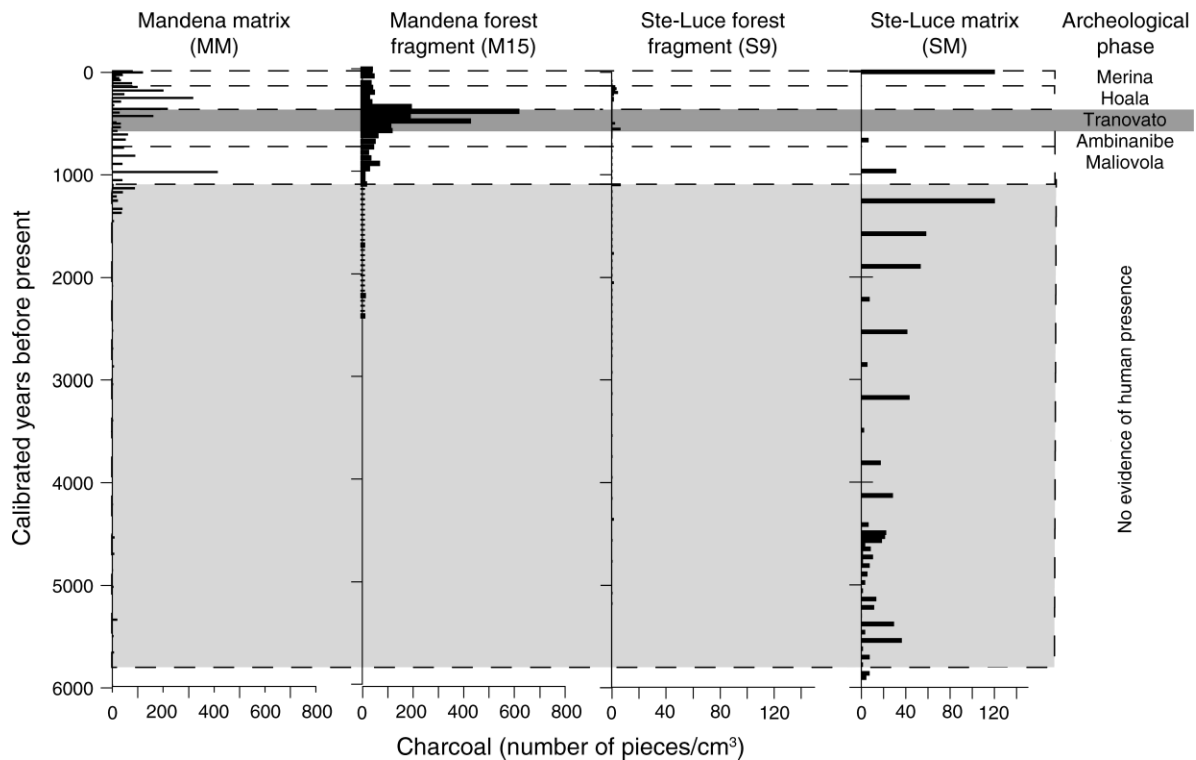


FIG. 6. Fire history in relation to human settlement. Note that the scales for Mandena and Ste-Luce sites differ. Fires are associated with emerging fire-prone ericoid vegetation, long before human arrival on the island. Large charcoal peaks may signal anthropogenic fires (e.g., during Tranovato phase; from Rakotoarisoa [1997]) showing settlement pattern during the five archeological phases: Maliovola (1150–750 cal yr BP), fishing and rudimental agriculture, small settlement; Ambinanibe (750–450 cal yr BP), fishing, cattle herding, and agriculture; Tranovato (450–350 cal yr BP), irrigated rice farming, cattle herding, large settlement; Hoala/Merina (350 cal yr BP–present time), irrigated rice farming, cattle herding, decrease in village size.

still is, different than the other sites with species of Meliaceae, Araliaceae, and *Psychotria* (Rubiaceae) as dominant components of the forest pollen assemblage. Prior to 5000 cal yr BP, SM was represented by a subset of the taxa from the Ste-Luce forest fragment but with less evenness among taxa because *Myrica* and *Uapaca* type 1 were strong dominants.

Redundancy analysis (RDA).—RDA, using environmental and pollen data from all the sites, indicated that zircon, which is strongly correlated with most other geochemical elements except for phosphorus and sodium, is a significant variable, explaining 13% of pollen variability (Fig. 7B; Table 2). Taxa that occurred only in Mandena are closely associated with high levels of zircon and associated elements. In contrast, *Myrica* and *Hibbertia* (Dilleniaceae), which are abundant in Ste-Luce, are associated with low levels of zircon and associated elements.

Other significant variables are sodium and phosphorus, explaining 7% of the variance in the pollen data. Taxa confined to S9 (Meliaceae, *Psychotria*, and Araliaceae) appear to be associated with low levels of phosphorus and sodium (Fig. 6B; Table 2). Charcoal is also a significant factor, although explaining <7% of the variability in the overall data. Charcoal is positively

associated with ericoid grassland. In contrast, the most sensitive taxa to fires appear to be species of *Uapaca*, *Symphonia*, and *Pandanus*. A site-to-site analysis revealed that geochemical variables explained a larger proportion of the compositional variability than charcoal concentrations for all three sites for which there were geochemical data (Table 2).

DISCUSSION

Spatial heterogeneity in southeast Madagascar

Madagascar's mosaic landscape is a puzzling feature of the island. Extensive grasslands, interspersed with a variety of forest types, occur both in the arid zones and in humid regions that can climatically support evergreen rain forests (Du Puy and Moat 2003, Bond et al. 2008, Willis et al. 2008). Forest fragmentation and predominance of secondary forests and wooded grasslands have been attributed to the influence of human activities (Perrier de la Bathie 1921, Humbert 1927, Lowry et al. 1997). However, in the southeast region of Madagascar, this multisite paleoecological reconstruction demonstrates that the mosaic landscape is a natural plant formation that predates the accepted date for human arrival around 2000 years ago (Burney et al. 2004).

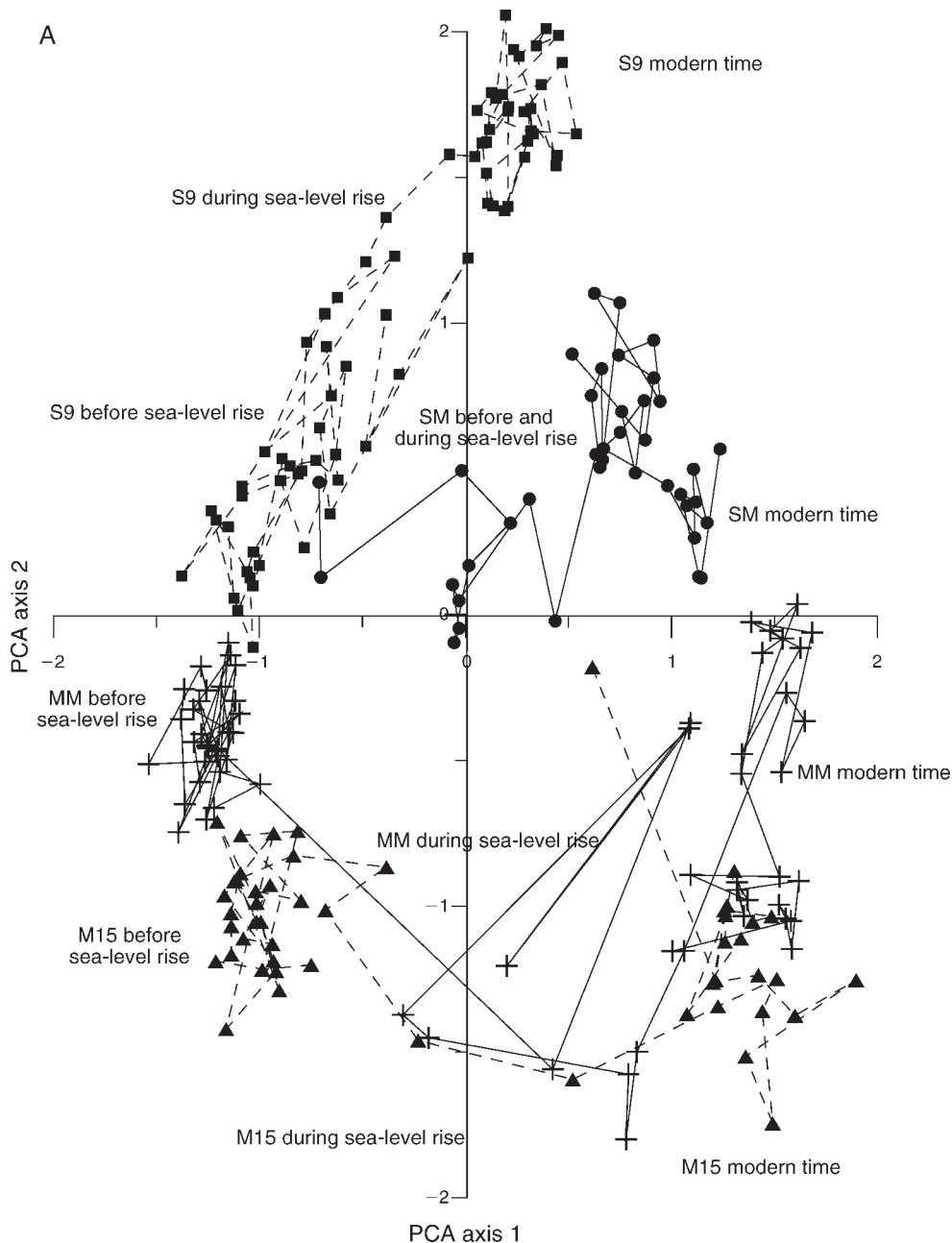


FIG. 7. (A) Trajectories of the four sites in three time sequences: prior to sea-level rise (6000–1800 cal yr BP), high sea-level rise (1800–800 cal yr BP), and modern time (800 cal yr BP–present) using PCA. PCA results for S9 are shown as squares, SM as circles, MM as crosses, and M15 as triangles. Note that over the last 6000 years, compositions of the fragments have diverged from each other in response to environmental disturbances, but compositions in the matrix sites have become more similar. Note also the more gradual transitions in Ste-Luce sites in response to climate change in contrast to threshold responses in Mandena. Also note that the MM vegetation prior to high sea-level rise (a no-analogue community) appears to be a transition between the composition of S9 and M15 littoral forest fragments also prior to sea-level rise. (B) Distribution of taxa from the four sites along known environmental gradients using RDA (redundancy analysis). Note the geochemical variables; e.g., zircon explains 13% of the pollen data ($F = 33.1$, $P = 0.01$) whereas charcoal explains less than 7% ($F = 16.3$, $P = 0.01$).

In both Mandena and Ste-Luce regions, it is apparent from functional groupings of species (Fig. 2A, B) that the two forest fragments remained forested by littoral forest except for a short period between 950 to 600 years ago. The ericoid grassland adjacent to the

littoral forest has not always been covered with the present fire-prone vegetation but neither was it ever covered by littoral forest. In the past, the matrix site at Mandena was composed of open *Uapaca* woodland whereas at Ste-Luce, the matrix was open *Uapaca*–

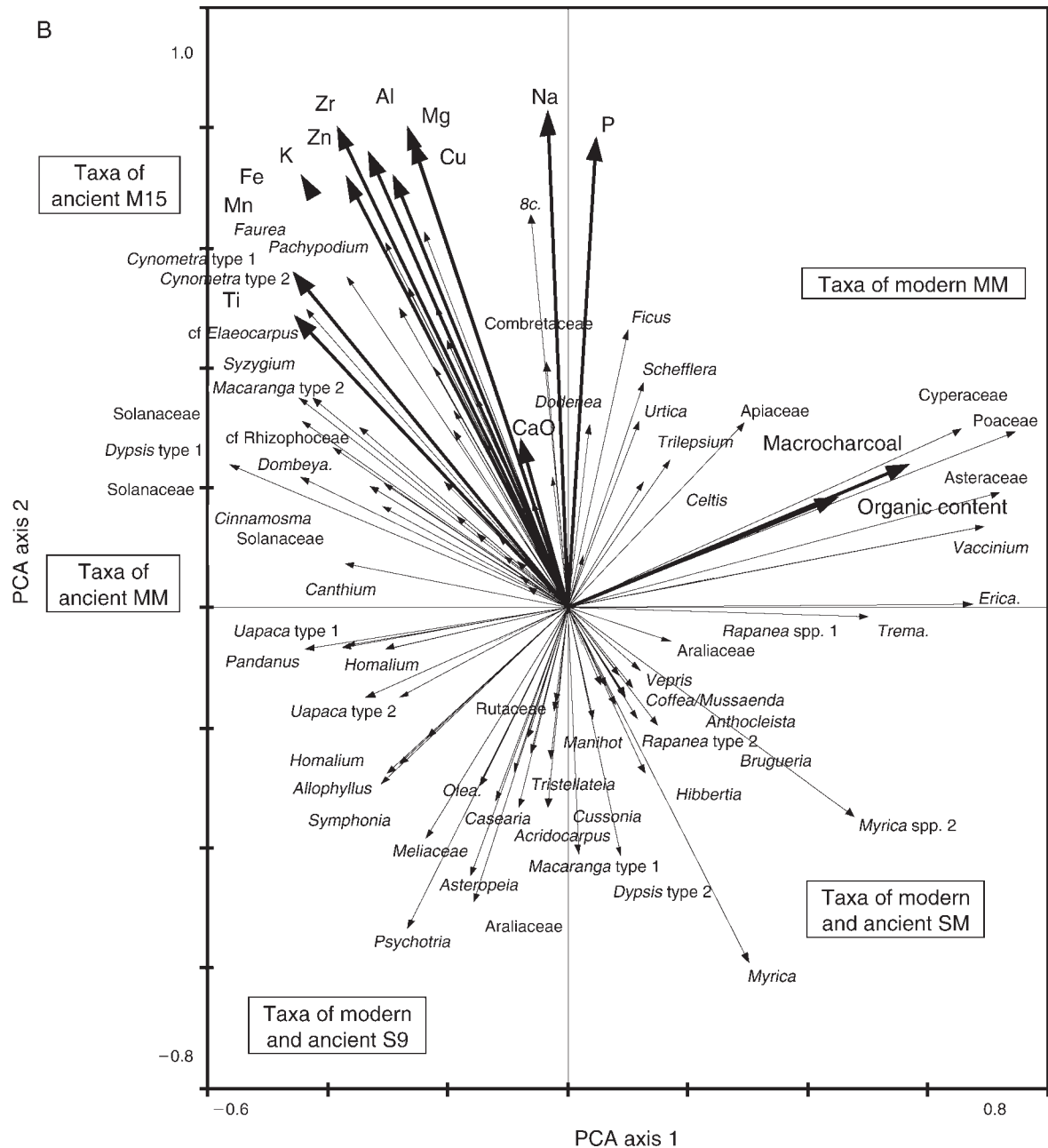


FIG. 7. Continued.

Myrica woodland. Fire-sensitive open *Uapaca* or *Uapaca-Myrica* woodlands that were once abundant in the southeast are no-analogue communities, that is, communities that are compositionally unlike any found today.

The most striking result from this study, therefore, is the evidence that the spatial heterogeneity of this landscape is a constant feature and not the result of differential anthropogenic pressures resulting in some areas becoming degraded anthropogenic landscapes. Three abiotic parameters to consider for these spatial

differences include differential precipitation regimes, groundwater availability, and edaphic variation.

1. *Differential precipitation regimes.*—Rainfall gradient has previously been suggested as a factor that influences floristic composition (Lowry and Faber-Langendoen 1991). Rainfall is known to diminish progressively from north to south, with annual precipitation ranging around 1800 and 2000 mm at Mandena and Ste-Luce, respectively (Lowry and Faber-Langendoen 1991). However, despite the differences in rainfall between the two regions, results from this study indicate

TABLE 2. The amount of variability in the pollen data explained by environmental variables based on a spatial/temporal analysis (all sites together) and temporal analysis (site-by-site) using RDA (redundancy analysis).

Explanatory variable	Eigenvalue	<i>F</i>	<i>P</i>
All sites (<i>n</i> = 228)			
Zircon	0.13	33.1	<0.01
Sum of canonical axes 1 and 2	0.35		
Charcoal	0.07	16.3	<0.01
Sum of canonical axes 1 and 2	0.39		
Total variance in pollen data	1		
MM-Mandena matrix (<i>n</i> = 65)			
Zircon	0.32	30.7	0.24
Sum of canonical axes 1 and 2	0.37		
Charcoal	0.14	10.2	0.13
Sum of canonical axes 1 and 2	0.545		
Total variance in pollen data	1		
M15-Mandena forest fragment (<i>n</i> = 52)			
Zinc	0.52	53.2	0.02
Sum of canonical axes 1 and 2	0.59		
Charcoal	0.13	7.1	0.07
Sum of canonical axes 1 and 2	0.59		
Total variance in pollen data	1		
S9-Ste-Luce forest fragment (<i>n</i> = 72)			
Titanium	0.1	7.6	0.12
Sum of canonical axes 1 and 2	0.51		
Charcoal	0.012	0.9	0.9
Sum of canonical axes 1 and 2	0.60		
Total variance in pollen data	1		
SM-Ste-Luce matrix (<i>n</i> = 40)			
Charcoal	0.234	11.3	0.09
Sum of canonical axes 1 and 2	0.38		
Total variance in pollen data	1		

Note: The eigenvalue of each variable (e.g., charcoal) is compared to the eigenvalue of the canonical axes 1 and 2 for a given ordination.

that there is still clear spatial heterogeneity within both landscapes, suggesting that more local factors such as groundwater availability and edaphic variation are probably more important factors driving vegetation heterogeneity.

2. *Groundwater availability.*—The interface between littoral forest and the current ericoid grassland (ancient open woodland) may be as a result of disconnected drainage patterns, which create a patchy distribution of groundwater resources. Soil hydrological maps of this system confirm that groundwater is as high as 4 m below the surface of forest fragments but drops as deep as 10 m in the matrix sites (QIT Madagascar Minerals, unpublished report). Results from this study suggest that littoral forest dominates the fragments and not the surrounding matrix principally because they are constrained by groundwater availability.

3. *Edaphic variation.*—Analysis of geochemical elements in this study demonstrates pronounced variability in key soil nutrients ranging from nutrient-rich soils in M15, to those that are moderately poor at MM and nutrient-poor at S9. Redundancy analysis clearly demonstrates that edaphic variation contributes to biotic heterogeneity (Fig. 7B).

Overall results from this study therefore suggest that forest fragment boundaries are defined by local groundwater resources rather than anthropogenic exploitation as had been previously hypothesized (Ganzhorn et al. 2001, de Gouvenain and Silander 2003, Consiglio et al. 2006). Further, floristic diversity may have been promoted by edaphic variation and the rainfall gradient.

Response to environmental change

When considering the impacts of the late Holocene environmental changes upon the littoral forest and its surrounding vegetation there are three key driving mechanisms that need to be considered: (1) sea-level rise, (2) climate changes, and (3) human (prehistoric and historic) impacts (Virah-Sawmy et al. 2009). Previous evidence indicates a high sea-level rise of 2–3 m above the present level occurred between 1800 and 800 cal yr BP (Battistini et al. 1976, Camoin et al. 1997, 2004, Virah-Sawmy et al. 2009). In addition, climate change in the form of intervals of aridity occurred periodically over the past 6000 years: between 5900 and 5600 (lowest water levels at 5800), 4900 and 4500 (lowest water levels at 4600), 3400 and 3000 (lowest water levels at 3200), and 1200 and 700 (lowest water levels at 950) cal yr BP in the southeast (Virah-Sawmy et al. 2009).

Evidence for human impact in Madagascar is more patchy. Although people arrived on the island possibly around 2300 years ago, the archaeological records from the southeast detect the first human presence in the region around 1150 cal yr BP (Rakotoarisoa 1997; Fig. 6). The first settlers were nomads and fisherman equipped with simple tools. This phase lasted until the period of cultural transformation dated to 450 cal yr BP when rice began to be cultivated and settlement expanded (Rakotoarisoa 1997). The macrofossil charcoal records from two sites (M15, MM) indicate large fires around 450 cal yr BP, coinciding with the period of cultural transformation. However, fires are not necessarily human signals, as at the site SM, burning has been constant and regular throughout the sequence (dating back to 5900 cal yr BP). At site MM, there is also another large peak in macrofossil charcoal ~1000 cal yr BP, but this occurs during an interval of aridity and is likely to be a natural event in an emerging fire-prone ericoid grassland (Fig. 6).

How did these intervals of sea-level rise, aridity, and later human presence influence the four sites? To first summarize the vegetation changes apparent at the four sites, there is evidence that the two fragments have remained continuously forested by littoral forest except for a period of rapid compositional change around 950 cal yr BP. During this period, widespread forest decline resulted in the dominance of ericoid grassland at M15 and *Myrica* bushland only at S9. These fragments then began reverting to littoral forest again between 600 and 400 cal yr BP. The open *Uapaca* woodland at MM and SM also transformed into ericoid grassland but the timing of these transitions was not synchronous. Open

woodland at MM in Mandena switched rapidly into ericoid grassland at ~950 cal yr BP, thus at approximately the same time as the two littoral forest fragments. By contrast, at SM this transition occurred much earlier between 5800 and 5000 cal yr BP but it was a more gradual transition (Fig. 2A, B).

The gradual transition in SM from open (*Uapaca*) woodland to ericoid grassland preceded the currently accepted date of 2000 cal yr BP for human arrival on the island by several millennia and coincided with a moderate drought event 5800 cal yr BP (Virah-Sawmy et al. 2009). It suggests that this transition may have been driven by climate change and also implies that the open woodland at Ste-Luce is extremely sensitive to drying events. It is interesting to note here that the vegetation at SM has remained ericoid grassland for 5000 years in the absence of human influences for nearly three millennia despite return of moister climatic conditions. It appears, therefore, that this formation forms a persistent and self-sustaining system maintained by natural fires. Further, despite regular low-burning fires, as evidenced in the charcoal record from this sequence (Fig. 6), SM has remained consistently species rich with no documented fossil pollen extinction (Fig. 3; Table 1). High taxonomic richness at SM may reflect its current and possibly consistent open mosaic nature composed of ericoid grassland with tiny littoral forest patches. Open landscapes in Madagascar are generally perceived as anthropogenically derived and degraded formations because they are less biodiverse than forest sites (Lowry et al. 1997). In the case of this ecosystem, long-term ecological evidence indicates that they are natural phases of ecosystem variability.

But what occurred at 950 cal yr BP to cause such rapid and synchronous ecological transformations in the other sites? This study, substantiated from previous work, also indicates that Madagascar's littoral forest was extremely sensitive to the coupling impacts of seawater influx and climatic desiccation occurring at ~950 cal yr BP (Virah-Sawmy et al. 2009). All sites except for SM, which already had switched to stable ericoid grassland, experienced rapid forest declines as evidenced by a reduction in tree pollen from ~60% to as low as 20% in less than a century. These significant declines accompanied losses in alpha biodiversity (measured by taxonomic richness) with high compositional changes. These declines, which occurred in the absence of large fires except for MM (Fig. 6), can be attributed to physical stresses caused by the combined impacts of marine surges and groundwater withdrawals (Virah-Sawmy et al. 2009). Redundancy analysis certainly indicates that geochemical changes in soils (possibly as a result of complex geoclimatic feedbacks) explained more of the variability in the vegetation than charcoal at all sites (Table 2). Therefore in this ecosystem, fire (whether natural or anthropogenic) was not the primary driver for the transition to alternate compositional states.

Since 950 cal yr BP, the matrix sites have remained stable ericoid grassland. In contrast, the forest fragments appear to be recovering into new "hybrid" communities in which littoral forest species are abundant alongside species of ericoid grassland. These hybrid communities reflect ecological time lags, but their presence may also be mediated by anthropogenic impacts such as fires and grazing, which may also maintain the matrix sites into stable ericoid grassland. It also is possible that small nutrient and charcoal peaks, together with small forest declines over the last few hundred years especially at Mandena (Figs. 2A, 5, 6), are a result of human influence. For example, during the Travanoto phase of cultural transformation dated between 450 and 350 cal yr BP (Rakotoarisoa 1997), the M15 fragment at Mandena appears to have been burned intensively, possibly by people. However, the evidence presented in this study suggests that in a hierarchical framework, human legacy is relatively small on this landscape and superimposed on climatic changes.

Resilience to environmental changes

What makes an ecosystem resilient? Spatial heterogeneity or species diversity? Responses of the four sites to environmental stress in this study provide interesting observations toward understanding the mechanism of resilience. When comparing resilience using compositional turnover, and the time required to return to original functional state and diversity, it becomes apparent from our study that resilience differed among the four sites.

First, it appears that the four sites have different tolerances to climatic perturbation. For example, the resilience of the open woodland at SM had been exceeded in response to a drought. Ericoid grassland became established as an alternate stable state, replacing the former open (*Uapaca*) woodland (Fig. 2A, B).

Second, the forest fragments were more resilient to climatic changes (aridity and marine surges) and reverted to their approximate former forest extent as hybrid communities, in contrast to the matrix sites (Fig. 2A).

Third, the two forest fragments differed both in ecological and engineering resilience. The forest fragment at Ste-Luce recovered more quickly both in terms of return to original forest abundance and diversity, and together with its matrix, experienced the least turnover to environmental disturbance (Figs. 2A, 4; Table 1). So what has contributed to the differential resilience?

1. *Spatial heterogeneity and resilience.*—It is currently believed that the multiple states of the littoral forest and the surrounding ericoid grassland are a result of differential anthropogenic effects. There is some evidence of differential anthropogenic effects with regard to recent charcoal peaks in Mandena. However, evidence presented here suggests that spatial heterogeneity, created by abiotic conditions, had a stronger

influence in these multiple states giving rise to differential resilience. For example, groundwater dynamics that constrain the distribution of littoral forest, may also have contributed to more rapid growth of forest species at the fragments following collapse, in contrast to the drier soils of the matrix sites. However, although both fragments tended to revert to a previous functional state, there was some reassembly of taxa over the whole landscape. Previously abundant forest species such as *Dyopsis* type 1 and *Macaranga* type 2 have experienced differential recovery to other species such as *Syzygium* and *Macaranga* type 1 in both fragments (Table 1).

Edaphic variation, which promotes floristic diversity in the ecosystem, may have also contributed to the differential resilience. The low-nutrient soils of Ste-Luce sites may have necessitated nitrogen-fixing plants as keystone species as evidenced in the pollen record with the presence of *Myrica*. Facilitation by *Myrica* may have maintained ecological functions and community stability during climate change. By contrast, the large decline of nutrients in Mandena together with soil desiccation, especially at M15, may have exceeded the tolerance range of formerly abundant forest species, leading to significant community reassembly there with high turnover (Table 1).

2. *Diversity, floristic composition, and resilience.*—Species diversity is believed to increase resilience as it maintains the assembly and functioning of a system and provides buffering during perturbations. Evidence from this study supports this suggestion in that the most diverse sites within this ecosystem experienced the least turnover (compositional change) to environmental perturbations except for a small reversal in S9 and SM, confirming that diversity may contribute to species persistence (Table 1).

In addition, floristic composition of the forest fragments may have influenced differential resilience because species differ in their traits, which drive ecological processes (Vitousek et al. 1987, Vitousek and Walker 1989, Tilman 1999). It appears that S9 may have maintained compositional stability because it was able to resist the colonization of *Erica* and therefore did not experience intensive fires that burned sites dominated by this flammable vegetation (e.g., M15, MM, and SM). It is known that the structural property of tissue flammability in *Erica*, when compared to other taxa, allows for the promotion and maintenance of fire within its habitat (van Wilgen et al. 1990). For example, continuous fires are associated with the colonization of ericoid vegetation, 1400 cal yr BP in the Mandena matrix and 950 cal yr BP in the Mandena fragment. The abundance of *Erica* throughout the 6000-yr reconstructed history of SM also explains why it is the only habitat to have burned regularly.

This absence of *Erica* begs the question of why it did not colonize and expand in S9 during the period of abrupt forest decline, when it did so in the other sites including the Ste-Luce matrix? It is possible that the

absence of *Erica* in S9 may be due to feedback interactions between biotic and abiotic factors that advantaged *Myrica*, (which are apparent in this sequence), and thus, outcompeted *Erica*. Different population models such as coexistence, exclusion, and facilitation models have been applied to the data to explore these dynamics (Virah-Sawmy et al. 2009). Overall, it is concluded that the absence of *Erica* and fires explains the apparent intactness of Ste-Luce fragments over the period of recovery in comparison to forest fragments at Mandena.

CONCLUSION

This study suggests that the landscape in southeastern Madagascar, composed of littoral forest interspersed with ericoid grassland, is ancient, dynamic, and a naturally heterogeneous landscape. There is also evidence that this ecosystem reorganized itself drastically over the past 6000 years in response to environmental changes including intervals of sea-level rise and aridity.

Evidence from this study suggests that processes that maintain spatial heterogeneity within this landscape are abiotic in nature, forming patchy vegetation (subsystems). These subsystems either experienced different microconditions, or feedback loops between abiotic and biotic factors created a range of responses to climate change, thus the sites exhibited differential resilience. As a consequence, most taxa did not go regionally extinct.

Current mining for ilmenite may destroy much of the southeast littoral forest because it is assumed that, as they are remnant forests through human impacts, it is acceptable for the region to undergo further degradation. This study contradicts this view as well as the assumption that the littoral forest once extended as a homogenous and uninterrupted band along the eastern coast (Consiglio et al. 2006). Instead, it suggests that the littoral forest has always been distributed as small isolated fragments embedded in a naturally occurring mosaic of open (*Uapaca*) woodland and/or ericoid grassland.

The paleoecological evidence suggests that the high concentrations of local endemic plants currently observed in the littoral forest (at least 25% only occur in this habitat [Consiglio et al. 2006]) have been naturally constrained in their distribution for millennia. These rare endemics must have persisted in low numbers for a few centuries (during the transition to ericoid grassland and *Myrica* bushland) in the marginal fragments. It therefore suggests that climatically disturbed littoral forest can maintain hotspots of diversity under both benign and stressful environmental conditions. There is mounting evidence that heterogeneous and dynamic refugial ecosystems, such as the littoral forest, are key adaptive components for diversity and persistence in variable environments. It is therefore imperative to consider the temporal perspective presented here, which strongly indicates that more littoral forest should be set aside for conservation under global change.

ACKNOWLEDGMENTS

M. Virah-Sawmy thanks the Oxford University Centre for the Environment, the Wingate Foundation, Rufford Small Grant, Environment Change Institute, and Jesus College for funding this research. Many thanks to John Birks for discussions about numerical methods and to NERC Radiocarbon Laboratory for the provision of radiocarbon dates through grant allocation 1217-0407. We are grateful for permission and assistance in the field from the Ministère de l'Énergie et des Mines, the University of Antananarivo, Missouri Botanical Garden, and QIT Madagascar Minerals (QMM). We also thank the Daubeny Herbarium of the University of Oxford and the Royal Botanical Gardens, Kew, for providing reference materials. Finally, many thanks to three reviewers for extremely useful comments.

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APPENDIX A

Radiocarbon dates for the sedimentary sequences (*Ecological Archives* M079-019-A1).

APPENDIX B

Age–depth model for the sedimentary sequences (*Ecological Archives* M079-019-A2).