UNIVERSITY OF AMSTERDAM

Mauritius Since the Last Ice Age. Paleoecology and Climate of an Oceanic Island
E.J. de Boer

Summary

8.1 Thesis aims (chapter 1)

Colonized by the Dutch in AD 1638, Mauritius was one of the last places on Earth to be inhabited by humans (Burney and Flannery, 2005). It took the Dutch, the French, and the British less than four centuries to almost completely deforest the island. As a consequence, our knowledge of the natural vegetation distribution relies on historical records from early ship logs and small remnants of degraded natural vegetation. The general aim of this thesis is to reconstruct the distribution of main vegetation types and the natural vegetation dynamics since the last glacial maximum (21,000 years ago) from terrestrial sediment cores. Palynological and macrofossil analysis provide information on vegetation composition and vegetation change, whereas local environmental and regional conditions are derived from pollen and diatom assemblages, ostracod-based isotope analysis, and granulometric and geochemical analyses. These vegetation and climate reconstructions provide an understanding of the long-term ecosystem dynamics of the forests and climate of Mauritius.

Islands are considered stable environments (MacArthur and Wilson, 1967; Heaney, 2007). Persistence on islands, or in other words lower extinction rates, are hypothesized to be derived from a lower species diversity, less interspecific competition and lower immigration rates compared to the continent (Cronq, 1997), and stable environments due to the buffering effect of the surrounding oceanic waters (Whittaker and Fernandez-Palacios, 2007). However, only few studies so far have sufficient resolution and pollen preservation, without interfering human activity, to identify ecological processes driving/controlling composition changes to investigate the paradigm of island stability.

The first high-resolution paleoecological records from Mauritius offer great potential to study the stability of an oceanic island. To understand the long-term ecological processes in the Mauritian forests, the nature of local environmental dynamics and regional climate change are determined. Local environmental dynamics are reflected in terms of the hydrology of the wetland, and soil properties and topography of the field site; climate change is reflected in terms of glacial/interglacial dynamics, precession-driven monsoon precipitation variability, and decadal- to centennial-scale climate anomalies. The oceanic island setting of Mauritius allows for an unprecedented integration of terrestrial and marine climate records, as island ecosystems are predominantly affected by external oceanic dynamics with little effect of the hinterland.

8.2 Mauritius during the last glacial – steady states and rapid succession (chapter 2 and 3)

The 36,500 year long Kanaka Crater pollen record shows a continuous presence of montane forest, suggesting that precipitation levels during the last glacial were comparable to the present-day (Van der Plas et al., 2012). Although many paleorecords across the length of Africa show orbitally-driven monsoon changes (e.g. Partridge et al., 1997; Verschuren et al., 2009; Rampelbergh et al., 2013), the Mauritian uplands record little influence of this 23-ky periodicity. Instead, long-term high precipitation levels are facilitated by the orographic setting of the crater (Vaughan and Wiehe, 1937), warm water masses in the Indian Ocean (Prell et al., 1980; Barrows and Juggins, 2005), and the Indian Ocean Dipole (Saji et al., 1999; Marchant et al., 2006).

Long-term stable composition of montane forest in the Eastern Arc Mountains in Tanzania and Kenya were facilitated by the low amplitude of temperature and precipitation change across glacial to interglacial time periods (Mumbi et al., 2008; Finch et al., 2009). The Kanaka Crater record, however, shows a clear contrast between the glacial and Holocene forest composition: the glacial forest (36,500 – 11,500 cal yr BP) is an open, wet, unstratified montane forest dominated by trees of *Nuxia verticillata*, *Weinmannia*, *Syzygium*, *Tambourissa*, Cycadaceae and *Securinega durissima*, and *Cyathea* tree ferns; the Holocene forest (7600 – 2300 cal yr BP) is a closed, relatively drier, stratified montane forest dominated by sapotaceous canopy trees, understorey trees *Securinega durissima*, *Allophyllus* and *Molinaea*, interspersed with *Dracaena* palm-like growth forms and emergent *Latania* palms.

A high-resolution vegetation reconstruction (up to 20-yr between samples) reveals a rapid succession of different plant associations starting at the onset of the Holocene (De Boer et al., 2013a). An apparent critical threshold was crossed at 11,500 cal yr BP, after which the montane forest system was propelled into an unstable period lasting for 4000 years. This regime shift from a stable glacial to a stable Holocene forest associations is expressed by four abrupt species turnover events. The initial change occurred at the Lateglacial to Holocene transition at 11,500 cal yr BP suggesting that a shift to Holocene global climatic conditions, such as high atmospheric levels of greenhouse gasses or the evolution of the meridional overturning circulation, pushed the Mauritian montane forest biome into instability. The subsequent events of species turnover do not coincide with climate events of global, African, or SW Indian Ocean significance. Therefore, the cascade of discrete plant associations are likely to be driven by intrinsic forest dynamics (Williams et al., 2011).

The re-assortment in taxonomic composition of montane forests is suggested to act as an alternative response mechanism to glacial-interglacial climate change on remote islands, opposed to a displacement of forest types to new altitudinal intervals as recorded on the continent, and gives better understanding how in a small island a high level of diversity in conserved across glacial – interglacial timescales.

8.3 The lost vegetation of Mauritius – human impact in the uplands (chapter 4)

No evidence was found in the pollen records of natural plant extinction or extirpation. We assume that taxa being replaced by others would be able to reside elsewhere, using gallery forests as biodiversity reservoir and migration corridor (Mayle et al., 2007; Chapter 3). In the Kanaka Crater for example, glacial forest taxa *Nuxia*, *Weinmannia*, *Syzygium* and *Eugenia* increase after 2300 cal yr BP, being (almost) absent for several thousands of years. Other taxa, such as *Erica* and Cycadaceae, disappear from the Kanaka Crater, but remain present in other records such as Pétrin and Grand Basin Crater until the recent past.

The suite of fossil pollen taxa of which the parent plants are currently – in the absence of paleoecological studies - not considered native to the Mauritian flora most likely went extinct rapidly after colonization in AD 1638. Already large areas of forest were destroyed before the first reliable botanical surveys took place in the 1800s (Cheke and Hume, 2008). The fact that new species are still being discovered (e.g. Florens and Biader, 2006; Le Péchon et al., 2011; Baider et al., 2012, 2013; Baider and Florens, 2013) shows there are significant gaps in the current knowledge of the native status and distribution of the Mauritian flora.

To get a better understanding of the human impact on the upland environment, we compared the natural settings before and after human arrival in the flat uplands around Le Pétrin (De Boer et al., 2013b). Granulometric analysis of the record shows that the shallow sediments in these flat uplands are mainly derived from weathering of basaltic rocks, and are accumulated over long periods of time. However, small pools of stagnant water provide local reservoirs where organic material can be accumulated. The 1000-yr long pollen record from Pétrin showed a mosaic display of marsh, ericaceous heathland and stunted forest, with changes driven by local hydrological and edaphic characters that over millennial time-scales. *Pandanus*- and fern-dominanted marshes grew in waterlogged areas, and ericaceous heathland grew on better drained surfaces, while wet forest taxa grew inside the heathlands as stunted forest and on the surrounding slopes. Although ericaceous heathland and wetland forest share many species, this study disagrees with the conclusion of Vaughan and Wiehe (1941) that ericaceous heath represents the initial stage in the development of 'climax' forest (montane forest). *Erica* heath is currently restricted to an area less than 0,5 km^2, but occurred much larger areas before colonization (Chapters 2, 3 and 4; De Boer & Sandoval et al., *in preparation*); these areas are now occupied by pine plantations and secondary stunted forest (De Boer, 2010-2014, *pers. obs.*). Ericaceaous heath is adapted to xeric conditions from bare lava slabs and immature and highly laterized soils (Vaughan and Wiehe, 1937). While individual montane forest taxa can be found inside the heathlands as stunted trees, a fully developed 'climax' forest would only develop on more sloped parts of the uplands. The destruction of natural landscape after colonization is documented by a sudden appearance of exotic species, deforestation, fire evidenced by charcoal particles, and increasing abundance of grassy vegetation reflecting degraded vegetation.

8.4 Holocene climate of the Mauritian lowlands (chapter 5)

The lowlands are much more sensitive to changes in precipitation compared to the uplands because the mean annual evapotranspiration is similar or higher than the mean annual precipitation, in particular during the dry season in the austral winter (Senapathi et al., 2010). This sensitivity was used to reconstruct in detail the Holocene climate of Mauritius from the Tatos wetland in the northeastern coastal lowlands. Hydrological analyses showed that these coastal wetlands receive a surplus of water from surrounding higher grounds. During drier periods, decreased inflow of fresh groundwater and increasing evapotranspiration rates raises the fresh-salt groundwater interface. Therefore, changing precipitation can be deduced from changes in salinity. Salinity and environmental reconstructions based on diatoms, ostracods, stable isotopes, and sediment compositions were performed to disentangle and assess the different influences over time of rising sea levels and precipitation change. In addition, the abundance of semi-dry forest and palm woodland reconstructed from the pollen record provides an independent proxy of regional climate (De Boer et al., 2014).

The reconstructed millennial-scale precipitation changes (8000 – 6800 cal yr BP, wet; 6800 – 1200 cal yr BP, dry; 1200 cal yr BP – present, wet) reflect northern hemisphere monsoon activity. Although Mauritius receives most precipitation during the northeast monsoon (opposite to the Indian Summer Monsoon), the northern hemisphere monsoon is more prominent in the record than the southern hemisphere monsoons. This northern hemisphere monsoon signal may have overwritten the southern hemisphere monsoon, as the Asian landmass experiences larger climate variability than the Indian Ocean water surface on the southern hemisphere. Secondly, modern observations show that the southern equatorial Indian Ocean is the dominant source of moisture for the Asian boreal summer monsoons, indicating that Mauritius shares a common moisture source with Indian Summer Monsoon (ISM) and Asian Summer Monsoon (ASM) rainfall (Rohling et al., 2009; Clemens et al., 2010).

During the middle Holocene, a distinct contrast between western and eastern Indian Ocean climate is present, as Mauritian climate became drier while the Austral-Indonesian summer monsoon was enhanced (Partin et al., 2007; Griffiths et al., 2010; Denniston et al., 2013). The relative dry conditions in Mauritius correspond with decreasing strength of ISM (Gupta et al., 2005; Fleitmann et al., 2007) and decreasing ASM rainfall (Wang et al., 2005), and distinct lower temperatures in the Kilimanjaro record (Thompson et al., 2002). We propose that these middle Holocene rainfall patterns demonstrate a prolonged negative Indian Ocean Dipole (IOD)-like configuration of the Indian Ocean (De Boer et al., 2014).

Climate conditions in the Mauritian lowlands were relatively stable between 4000 and 2650 cal yr BP, while humidity remained relatively low. Reduced precipitation in both the eastern and western equatorial Indian Ocean has been associated with weakening of AISM rainfall after 4200 cal yr BP (Partin et al., 2007; Griffiths et al., 2010; Denniston et al., 2013). Increased climate variations linked to El Niño Southern Oscillation (ENSO)-variability have been revealed in the Caribbean Sea (Donnely and Woodruff, 2007), Peru (Moy et al., 2002), the Eastern Pacific (Toth et al., 2012), the Galápagos islands (Conroy et al., 2008), the Indonesian shelf (Gagan et al., 2004) and Australia (Donders et al., 2008). These studies show that ENSO frequency and intensity increased between 5000 and 4000 cal yr BP and became the dominant forcing of late Holocene climate variability in tropical and subtropical regions (Moy et al., 2002; Gagan et al., 2004; Donders et al., 2007, 2008; Conroy et al., 2008; Toth et al., 2012).

Increased input of biogenic $CaCO_3$ in the Tatos basin after 2650 cal yr BP reveals an increase in droughts and storm activity. Mauritian storm events correspond with weakening of the boreal summer monsoons (Wang et al., 2005; Fleitmann et al., 2007) and an abrupt reduction of upwelling in the Arabian Sea (Gupta et al., 2005). The droughts and increased storm activity after 2650 cal yr BP are also linked with El Niño – Southern Oscillation (ENSO) events in lake Pallcacocha in Peru (Moy et al., 2002) and extreme ENSO events in the eastern Pacific (Conroy et al., 2008; Toth et al., 2012), as well as lowest AISM rainfall between 1500 and 1200 cal yr BP in western tropical Australia (Denniston et al., 2013). Conroy et al. (2008) relate the shift at 2600 cal yr BP to the decoupling of ENSO from the Atlantic intertropical convergence zone (ITCZ). Without the southward migrations of the Atlantic ITCZ into South America during which climate variability was enhanced in the Cariaco Basin between 4000 and 2600 cal yr BP (Haug et al., 2001), ENSO events developed that also affected climate events in the SW Indian Ocean (De Boer et al., 2014).

The onset of increased ENSO-activity after 4000 cal yr BP was preceded by the driest conditions in the Mauritian lowlands recorded around 4300 cal yr BP. These driest conditions correspond to a global-scale period of monsoon weakening, which is considered as the driver of civilization collapses in Pakistan, Mesopotamia and eastern Africa (Cullen et al., 2000; Thompson et al., 2002; Staubwasser et al., 2003; Wang et al., 2005; MacDonald, 2011). This 'megadrought' coincides with wettest conditions in tropical western Australia (Denniston et al., 2013), and may therefore represent an anomalously strong negative IOD event.

8.5 A deadly cocktail (chapter 6)

Standing freshwater in the lowlands is rare due to rocky basaltic soils with poor water retention capacity and high evapotranspiration rates (Rijsdijk et al., 2009). Shallow lakes in the dry coastal lowlands, such as Tatos and Mare aux Songes, resembled oases for the Mauritian fauna. Abundant coprophilous fungi, growing on dung of larger vertebrates, indicate that animals were attracted to these wetlands in large concentrations.

In 2005, a rich fossil bed was discovered at Mare aux Songes (MAS), a wetland in the southeast coastal lowlands (Rijsdijk et al., 2009). The fossil depository constitutes a *Lagerstätten* with more than 250 bone fragments/m^2 from a diverse spectrum of plants and animals, including the dodo (*Raphus cucullatus*) and giant tortoises (*Cylindraspis* spp.). Radiocarbon dating of vertebrate bones, wood and seeds indicate that fossils accumulated between 4235 and 4100 cal yr BP, suggesting that more than half a million vertebrate individuals died within a time frame of less than 150 years (Rijsdijk et al., 2011).

Analysis of pollen, diatoms, pigments and hydrological measurements provide a unique window in how a very rich fossil bone bed developed at MAS 4200 years ago (De Boer et al., *subm.*). A reconstruction of regional vegetation change and local wetland development under influence of sea-level rise and inferred climate change between 4400 and 4100 cal yr BP was compared to the climate reconstruction at Tatos (Chapter 5). A prolonged drought in Mauritius and around the Indian Ocean is recorded between 4330 and 4130 cal yr BP. This abrupt increased aridity induced fires on Mauritius and at MAS, and caused in the MAS-site lower water levels. The lake shrank resulting in a further concentration of animals in the wetland. Upconing of the saline wedge underlying the fresh water hole induced progressive salinization. The excrements of the animals, indicated by the presence of coprophilous fungi and N-tolerant diatoms, led to hypertrophic conditions. These polluted conditions combined with salinization and high temperatures were suitable for cyanobacteria blooms of which traces of pigments have been found. Ultimately these factors led to a deadly cocktail of salinification, eutrophication and regional fire, which resulted in the death of 100,000s of vertebrates by intoxication, dehydration, trampling and miring.

Even though at MAS preferential taphonomic conditions led to a unique conservation of fossils, the 4200 cal yr BP aridity event must have induced similar bottlenecks elsewhere around the Indian Ocean. The '4.2 ka megadrought' was a phenomenon of global impact (Davis and Thompson, 2006) and is considered as the driver of civilization collapses in Pakistan, Mesopotamia and eastern

Africa (Cullen et al., 2000; Thompson et al., 2002; Staubwasser et al., 2003; Wang et al., 2005; MacDonald, 2011). Therefore, the uniqueness of the MAS fossil layer lies in the fact that it reflects the direct consequence of a natural catastrophe in an insular ecosystem, and challenges the stability paradigm of climatologically inert islands.

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