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DOI

[10.1016/j.palaeo.2013.04.025](https://doi.org/10.1016/j.palaeo.2013.04.025)

Publication date

2013

Document Version

Final published version

Published in

Palaeogeography, Palaeoclimatology, Palaeoecology

[Link to publication](#)

Citation for published version (APA):

de Boer, E. J., Slaikowska, M., Hooghiemstra, H., Rijdsdijk, K. F., Vélez, M. I., Prins, M., Baider, C., & Florens, F. B. V. (2013). Multi-Proxy reconstruction of environmental dynamics and colonization impacts in the Mauritian uplands. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 383-384, 42-51. <https://doi.org/10.1016/j.palaeo.2013.04.025>

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Multi-proxy reconstruction of environmental dynamics and colonization impacts in the Mauritian uplands

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ARTICLE INFO

Article history:

Received 27 November 2012

Received in revised form 25 April 2013

Accepted 28 April 2013

Available online 6 May 2013

Keywords:

Oceanic island
Mauritian uplands
Ericaceous heathland
Pandanus marsh
Human impact
Invasive species
Late Holocene

ABSTRACT

A 115 cm long sediment core retrieved from the exposed uplands of Mauritius, a small oceanic island in the Indian Ocean, shows environmental change from the uninhabited era into post-colonization times. Well-preserved fossil pollen and diatoms in the uppermost 30 cm of the core reflect environmental conditions during the last 1000 years. Granulometric analysis along the core shows that the sediments below 30 cm consist of weathered material and that the record may contain hiatuses. This is also illustrated by a ¹⁴C date at 96 cm depth of 35,000 calibrated years before AD 1950 (35.0 cal ka). The pollen record shows that pristine vegetation at 650 m elevation consisted of ericaceous heathland and *Pandanus* marsh. Around 0.9 cal ka wet montane forest and fern-rich marsh replaced heathland vegetation, indicating higher moisture availability. Natural changes in upland vegetation associations are mainly driven by changes in sediment accumulation causing changes in soil properties and drainage conditions. The historically well-dated start of colonization (AD 1638) is reflected by the sudden arrival of exotic plant taxa *Camellia sinensis* (tea), *Pinus* spp. (pine), *Casuarina equisetifolia* (coastal she-oak), *Psidium cattleianum* (strawberry guava), *Homalanthus* (Queensland poplar) and *Saccharum officinarum* (sugar cane), as well as an increase in charcoal, indicating deforestation.

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1. Introduction

Human impact on the environment already began, in places, in pre-Holocene times and is often well documented by paleoecological and archeological records (Roberts, 1998; Mackay et al., 2003; Oldfield and Dearing, 2003; Hughes, 2005; Ruddiman, 2005). Only few places maintained their pristine environments up to a few centuries ago, amongst which a small number of oceanic islands (Whittaker and Fernández-Palacios, 2007). These islands experienced rapid and distinctive transformations after human arrival (Burney and Burney, 2007; Van Leeuwen et al., 2008; Florens et al., 2012; Restrepo et al., 2012; Van der Knaap et al., 2012) resulting in biodiversity loss and extinction of many endemic species (Burney, 1997; Biber, 2002; Whittaker and Fernández-Palacios, 2007; Caujapé-Castells et al., 2010).

A comparison between the natural settings before and after human arrival indicates the full magnitude of biodiversity loss and ecological transformation that resulted from human impact (Burney and Burney,

2007). Paleocology plays an important role in documenting these changes, as it provides insight into the natural ecosystem dynamics and vegetation composition prior to human arrival, the so-called 'baseline' environmental setting (Willis and Birks, 2006; Willis et al., 2007; Figueroa-Rangel et al., 2008). It can furthermore show the scales, rates and processes of human impact after colonization (Willis et al., 2007). Examples of paleoecological baseline studies were performed in the Galápagos Islands (Van Leeuwen et al., 2008; Restrepo et al., 2012), Tenerife (de Nascimento et al., 2009), and in the Azores (Connor et al., 2012) where, after colonization, dramatic changes were documented in vegetation cover and composition. A better understanding of the difference between natural and human induced ecological changes is essential to assess major current and future threats for island species (Diamond, 1989; Caujapé-Castells et al., 2010) and to provide scientific justifications for conservation efforts (Burney and Burney, 2007).

The small tropical island of Mauritius is one of the most recently colonized areas of the world (Cheke and Hume, 2008). After colonization by the Dutch in AD 1638, Mauritius rapidly became deforested (Vaughan and Wiehe, 1937) and several endemic species, such as the enigmatic dodo, went extinct (Cheke and Hume, 2008). Today, native vegetation suffers from many introduced invasive alien plants (Lorence and Sussman, 1986; Safford, 1997; Florens, 2008; Caujapé-Castells et al.,

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2010; Baider and Florens, 2011). The number of introduced plants (1675 species; Kueffer and Mauremootoo, 2004) far outnumbers the number of native species (691 species of which 39.5% are endemics; Bosser et al., 1976–onwards; Baider et al., 2010). Despite the small size of the island (ca. 40 × 55 km) and the long history of botanical inventories, species new to the Mauritian flora, including endemics, are still being discovered (Florens and Baider, 2006; Le Péchon et al., 2011; Baider et al., 2012; Baider and Florens, 2013). Due to the rapid deforestation of Mauritius, little is known about natural ecosystem dynamics, whereas the ongoing discovery of new species stresses the gaps in the current botanical knowledge and underlines the uncertainties as to which part of the present flora can be considered native.

This paper presents a study of vegetational and environmental changes from a site at 650 m elevation in the uplands of Mauritius. The objective is to reconstruct the biotic and abiotic environments from the pristine recent past (pre-AD 1638) into the current era of human disturbance. We infer vegetation change from a pollen record, hydrological changes from a diatom record, and changes in sediment transport from a record of grain size distributions. The combined results provide a reconstruction of the previously unknown pre-human baseline history and post-colonization environmental development of the Mauritian uplands.

2. Setting

2.1. Geology and geography

The island of Mauritius is situated in the southwest Indian Ocean approximately 830 km east of Madagascar (Fig. 1). Together with the islands of Réunion and Rodrigues it comprises the Mascarene Islands. Mauritius was formed between 7.8 and 6.8 million years ago (McDougall and Chamalaun, 1969) from a hotspot that is currently situated off the southeast coast of Réunion. Volcanic activity in Mauritius lasted until 25 thousand years ago (Saddul, 2002). The soils of the island are largely formed in basaltic lava (Craig, 1934). The highest peak in Mauritius reaches 828 m elevation. The studied heathland of Le Pétrin, part of Black River Gorges National Park, is situated in the southern uplands at 650 m elevation. The site is characterized by a flat area, with small ~0.5 m deep waterlogged depressions formed in tropically weathered basaltic rocks. Duricrust formation in the soils, i.e. tropical iron pan formation, is common in the study area. The soils are weathered and range from humic ferruginous latosols on hilly and convex slopes to ground water laterites in the plains and depressions where the water table is permanently high (Saddul, 2002).

2.2. Climate

Mean annual temperature in Mauritius at sea level is 22 °C and mean annual precipitation (MAP) is 2100 mm. Depending on relief and the orientation of the slopes to the prevailing wind direction, MAP varies from 800 mm in the western coastal lowlands, to more than 4000 mm in the uplands including the study area. Precipitation is seasonal, with a dry season from May to October under influence of the cool and dry easterly trade winds, and a wetter and warmer season from November to April when the inter-tropical convergence zone (ITCZ) has its southernmost position (Senapathi et al., 2010).

2.3. Vegetation

About 95% of Mauritius has been deforested and an outline of the natural vegetation distribution must therefore rely on early historical records and small remnants of degraded natural vegetation. The pristine island of Mauritius was fringed by a variety of coastal communities such as mangroves, coastal marshes and vegetation types associated with basaltic cliffs and coralline sand dunes (Cheke and Hume, 2008). Dry palm-rich woodland occurred on the driest leeward side of the island. A larger area of semi-dry evergreen forest occurred inland

Fig. 1. (a) Map showing the location of the Mascarene Islands in the Indian Ocean, the southernmost position of the Intertropical Convergence Zone (ITCZ) and the South Equatorial Current (in blue arrows); (b) Elevation map of Mauritius showing the location of pollen sites Le Pétrin and Kanaka Crater; (c) Map showing sites Le Pétrin and Kanaka Crater in a partially deforested landscape with pine plantations and crop fields. The border of the current heathland vegetation is shown in green; plantations are shown in red. Map courtesy: Google Maps.

(Vaughan and Wiehe, 1937; Cheke and Hume, 2008). Wet forest covered about 50% of the island and grew on slopes and on higher and wetter grounds. Azonal vegetation included heath formations or stunted thickets on shallow rocky soils, and marshes with screw pine (*Pandanus*) in wet areas on poorly drained soils (Vaughan and Wiehe, 1937; Cheke and Hume, 2008). Dense, stunted vegetation grew on exposed mountainous ridges with sparse herbaceous and scrubby vegetation occurring on the steeper cliffs. The distribution of many plant taxa is poorly altitudinally constrained (De Boer et al., 2013), resulting in a mosaic-pattern vegetation cover rather than a zonal pattern.

In this paper, we focus on the upland vegetation in the southern uplands where MAP exceeds 2500 mm. This flat and exposed area is covered by heath and thicket vegetation on well drained soils, while stagnant water leads to the formation of marshy vegetation (Fig. 2). The heath and marshy areas in Le Pétrin form a mosaic depending

Fig. 2. Left: photograph of Le Pétrin heathland vegetation with pine plantations in the background. The red circle indicates the location of the coring site; a: *Pinus* spp. (non-native); b: *Ravenala madagascariensis* (non-native); c: *Gleichenia* (native); d: various native sedges. Right: heathland vegetation near the coring site. Photographs courtesy: EjdB, 2010.

on edaphic conditions. Pine and tea plantations occur within 0.1 and 4 km radius of the coring site, respectively.

3. Materials and methods

The coring site is located at 20°40'S/57°47'E at 650 m elevation. We collected a continuous sediment profile in increments of 50 cm length with a 50 mm diameter Russian corer. Sediments could be collected up to 115 cm where the corer hits the volcanic rock. Eight accelerator mass spectrometry (AMS) radiocarbon dates were obtained from bulk material to provide a chronological framework of the sediment sequence. Calibration of radiocarbon ages was carried out using the CALIB 6.0 software (Stuiver and Reimer, 1993). Calibration was done using the southern hemisphere calibration curve (McCormac et al., 2004) for ages younger than 11 ka; older ages were calibrated using the IntCal09 curve (Reimer et al., 2009).

Details on pollen sample preparation are described in Van der Plas et al. (2012). For pollen analysis, a minimum of 400 pollen grains were counted for the pollen sum. Identification, where possible, was based on pollen morphological literature from East Africa (Caratini and Guinet, 1974; Bonnefille and Rioulet, 1980) and in particular the pollen morphological documentation published by H. Straka and coworkers between 1964 and 1989 in the series 'Palynologia Madagassica et Mascarenica' (listed in Hooghiemstra and Van Geel, 1998). The African Pollen Database (<http://medias3.mediasfrance.org/apd/accueil.htm>) was also used for identification and several African pollen experts helped with determinations. All pollen taxa,

except undeterminable pollen grains, were included in the pollen sum; fern spores, fungal spores, and non-pollen palynomorphs were excluded. Identified pollen taxa were categorized into meaningful ecological groups. Unidentified pollen and spore types were documented and numbered. Microscopic charcoal was identified into two size classes: particles from 15 to 50 μm and particles $>50 \mu\text{m}$. Pollen diagrams were plotted with TILIA 1.5.12 (Grimm, 1993, 2004) software. Zonation was based on CONISS analysis as included in the TILIA program.

Samples for grain size analysis were prepared according to the method described by Konert and Vandenberghe (1997). About 1–2 g of bulk sediment was pre-treated with H_2O_2 and HCl to remove organic matter and carbonates, respectively. In case of a violent reaction, additional aliquots of H_2O_2 and/or HCl solution were added to ensure complete removal of organic matter and/or carbonates. The purified samples were then measured with a Helium–Neon Laser Optical System (Helos KR) (Sympatec Inc., Clausthal-Zellerfeld, Germany) laser particle sizer at the Vrije Universiteit Amsterdam (VUA), which resulted in a grain size distribution with 57 size classes in the size range 0.15 to 2000 μm . For practical purposes, we report our results in three grain-size classes: clay ($<8 \mu\text{m}$), silt (8–63 μm) and sand (63–2000 μm).

For diatom analysis, samples of 0.8 cm^3 were immersed in 30 ml of H_2O_2 (30%) for 30 min at room temperature, after which a few drops of KMnO_4 were added. Subsequently, 10 ml of HCl was added. Samples were then washed with distilled water and permanent slides were mounted in Naphrax and analyzed with an

Table 1
List of radiocarbon dates, obtained from bulk material, and sample specific data.

Depth (cm)	Lab. no.	^{14}C yr BP (BP)	% C	Activity (%)	Cal yr BP (2 σ)	Area ^a (%)	Age in graph
3	GrA-54996	Recent $\pm$ 30	36.2	109.4			
10	GrA-52819	355 $\pm$ 30	29.8	95.7	308–463 ^b	100	386
16	GrA-54997	975 $\pm$ 30	37.5	88.6	773–918 ^b	100	846
21	GrA-54998	1210 $\pm$ 30	12.2	86.0	976–1149 ^b	94	1163
26	GrA-54999	1070 $\pm$ 30	25.9	87.5	903–973 ^b	89	938
30	GrA-49944	1085 $\pm$ 35	29.4	87.4	904–1005 ^b	89	955
41	GrA-52820	1155 $\pm$ 30	24.6	86.6	955–1065 ^b	99	1010
96	GrA-50010	30040 $\pm$ 170	60.4	2.4	34494–35046 ^c	100	34,770

^a Area (%) under probability distribution.

^b After McCormac et al. (2004).

^c After Reimer et al. (2009).

Fig. 3. Graph showing the lithological column and the location of calibrated AMS ¹⁴C dates of Le Pétrin core. The left graph shows all dates of the sediment core Le Pétrin-1. The right graph zooms in on the upper 50 cm of the record. The dotted red line shows the established depth vs. age relationship.

Olympus microscope at 1000 $\times$. A minimum of 400 valves was counted per slide. For diatom taxonomy and ecology we used Evans (1958), Gaiser and Johansen (2000), Krammer and Lange-Bertalot (1997), Patrick and Reimer (1966), Sala et al. (2002) and Gasse (1986).

4. Results

4.1. Lithology, grain size and chronology

The chronology of Le Pétrin sediment record is based on eight radiocarbon dates (Table 1). Ages in the upper 41 cm of the record range between 1.1 calibrated years before AD 1950 (cal ka) up to recent times. The ages are gradually younger towards the top of the record, except for the date at 21 cm depth (Fig. 3). This date is considered to be less reliable because of the low carbon content of this bulk sample. The deepest part of the core dates back to more than 35 cal ka. The old age suggests the presence of one or more hiatuses below 41 cm core depth. We calculated zone boundary ages using linear accumulation rates between the dated samples from the upper 41 cm.

The lithology of the core shows a basal unit (115–30 cm core depth) composed of indurated silty clay (80%) and sand (20%). Maximum fractions of silt and sand were identified at 93 and 85 cm core depth. The fractions of silt and sand decrease from 65 to 30 cm core depth. Organic material was not recovered in the basal unit and pollen grains were not preserved. From 30 to 12 cm core depth sediments are composed of organic rich clay (70%) with minor variations in the fraction of silt and sand (30%). Several samples contain laterized particles of duricrust formation (>1 mm in size) after the preparation for grain size analysis, which might have influenced the result. The uppermost 12 cm of the core is composed of dark clay rich in organic matter.

4.2. Pollen diagrams and pollen zones

Temporal vegetation changes are shown by the records of the most important individual taxa (Fig. 4) and the records of meaningful ecological groups (Fig. 5). CONISS recognized three pollen zones (PET-1, PET-2 and PET-3), which closely reflect the lithological changes in the record. Six species indicative of human impact were found: *Camellia sinensis* type (tea), *Casuarina equisetifolia* type (coastal she-oak), *Pinus* spp. (pine), *Psidium cattleianum* (strawberry guava), *Homalanthus*

populifolius type (Queensland poplar) and *Saccharum officinarum* (sugar cane). No known non-pollen palynomorphs (NPPs) were encountered.

4.2.1. Pollen zone PET-1 (113–31.5 cm; 12 samples)

No identifiable pollen grains were found between 113 and 89 cm core depth, apart from a few NPPs without known ecological constraints. Samples between 81 and 32 cm core depth provided a pollen sum not exceeding 110 grains. These samples contained pollen grains of *Erica*, *Dracaena* type, *Securinega* type, *Potamogeton* type and *Pandanus*. Most *Pandanus* species endemic to Mauritius have an anemophilous pollination syndrome and therefore may be over-represented in the pollen record. Fern spores and NPPs (especially T.mau-A and T.mau-B) are also present in most of the samples of PET-1. Few samples contained charcoal (Fig. 5).

4.2.2. Pollen zone PET-2 (31.5–12.5 cm; 18 samples)

Heath vegetation dominates with percentages of *Erica* starting at 50% and gradually decreasing over time. At the end of the zone wet forest increases due to increasing abundances of *Syzygium*, *Securinega* type, *Aphloia theiformis* type, *Nuxia verticillata*, *Weinmannia*, *Eugenia*, *Molinia* and *Melastomataceae*. *Dracaena* type and marsh taxa *Pandanus*, *Potamogeton* type, *Stillingia* type and *Cyperaceae* are stable. The wet forest element *Dracaena* is a stable part of the forest, but this record may also point to *Dracaena reflexa*, which is characteristic of shallow soils; this species is present in today's vegetation of Le Pétrin. The presence of *Stillingia* may be indicative of marshy vegetation, in association with ferns (Vaughan and Wiehe, 1937), but it can also contribute to thicket vegetation. Ferns gradually increase, with highest percentages at 16 cm core depth. Charcoal is rare zone PET-2.

4.2.3. Pollen zone PET-3 (12.5 cm–1 cm; 12 samples)

The proportions of heath and marsh taxa are stable. Poaceae starts its record and reaches almost 10%. The proportion of wet montane forest remains high, with a stable abundance of *Dracaena*, *Securinega* type, *Syzygium*, *Aphloia theiformis* type, *Weinmannia*, *Eugenia* and *Melastomataceae*. *Nuxia verticillata* increases, while *Molinia* disappears from the record. *Labourdonnaisia* type and *Tambourissa* type are wet montane forest elements that appear during PET-3. Taxa indicative of human impact are well represented, with *Homalanthus* type being most abundant and continuously present. Other human indicators are *Camellia sinensis* type, *Casuarina equisetifolia* type, *Saccharum officinarum*, *Pinus* spp. and *Psidium cattleianum*. Most fern taxa decrease in abundance. The unidentified type T.mau-O dominates the NPP spectra. Charcoal is present in all samples. Both charcoal size categories register a peak at 9 cm core depth.

4.3. Diatom analysis

Sediments from 115 to 13 cm core depth did not contain diatoms. Although cluster analysis identified five diatom zones (Fig. 6), we combined zones 2–5 into a single zone and we considered the spectra of the uppermost 3 samples as distinctly different from the underlying samples. Zone-‘2–5’ coincides with the period of first human impact as seen in the pollen record.

4.3.1. Diatom zones ‘2–5’ (11–4 cm; 8 samples)

Frustulia rhomboides, *Anomoeoneis serians*, and *Anomoeoneis serians* var. *brachysira* show combined abundances of 70–80%. The spectra contain several species of *Eunotia*. A minor increase in *Eunotia bilunaris* v. *mucophila* occurs at 7–8 cm.

4.3.2. Diatom zone 1 (3–1 cm; 3 samples)

This zone differs from zones 2–5 showing an increase of *Navicula* aff. *subtilissima*, *Cymbella naviculiformis*, and *Cymbella* sp.

5. Environmental reconstruction

In the following section we integrate the information from the pollen, diatom, charcoal, lithology, and grain-size distribution records in order to reconstruct the environmental history of the Mauritian uplands. We discuss the environmental developments using the periods identified in the pollen record, as most other proxies mirror the changes seen in the palynological record.

5.1. Period 1: ca. 35,000 cal ka to ca. 960 cal a (113–31.5 cm; pollen zone PET-1; grain size zones A and B)

The grain size distributions suggest that this part of the record reflects a weathered paleosol or a weathered sedimentary deposit (e.g. slope wash) and it includes one or many hiatuses (Fig. 5). Therefore, we do not assume a linear sediment accumulation between the radiocarbon ages for this part of the record. The sediments consist of indurated clay where organic material is poorly preserved. Few charcoal particles, mostly smaller than 50 μm , suggest the influx of windblown particles from fires elsewhere on the island. The few pollen grains present are preserved relatively well compared to the weathered conditions in which the clayey sediments were deposited. We assume that these pollen grains have been transported downwards, e.g. by penetrating roots. These anachronous pollen grains were mainly grains of *Erica* and *Pandanus*, indicating the presence of *Erica* heath and *Pandanus* swamp. At present, *Erica* heathland occurs in the uplands on immature and highly laterized soils, which reflect substrate bound xeric conditions (Vaughan and Wiehe, 1937). Most *Pandanus* species

of the Mauritian flora occur in waterlogged areas or near slowly flowing water, much like the marshy depressions in the study area. However, the full ecological range is broader as some *Pandanus* species occur on well-drained montane forest soils, and one species even occurs on well-drained dry soils.

Maximum sand-fractions below 65 cm core depth probably represent granular relicts of in situ weathered soils or washed-in residual grains from surrounding slopes, including sand-sized iron nodules. Lower fractions of sand in the top 65 cm of the record suggest input of washed-in clays with organic material from the surrounding slopes.

5.2. Period 2: ca. 960 to 580 cal a (31–12.5 cm; pollen zone PET-2; grain size zone C)

The sediment contains a higher content of organic material: from 25 cm core depth upward the color becomes grayer and rootlets are present. Similar as in the previous period, charcoal is rare and therefore there is no signal of increased fire frequency. Relatively high fractions of clay and sand and lowest fractions of silt indicate marshy conditions where sand-sized particles are easily retained in wet vegetation (Vriend et al., 2012). Local marshy conditions, an increase in organic matter in the sediments, a better preservation of the pollen grains, and the absence of evidence of fire all point to increasing humidity.

Erica heath and *Pandanus* marsh dominated the uplands between ca. 960 and 900 cal a. Ericaceous heath vegetation declined after ca. 900 cal a. Increasing presence of *Securinega* type, *Syzygium*, *Eugenia* and *Nuxia verticillata* shows that wet montane forest became more

Fig. 5. Pollen percentage diagram of sediment core Le Pétrin (650 m elevation, Mauritius) showing from left to right: age, depth, lithology, downcore changes in grain size distributions, abundance of charcoal particles, pollen concentration, representation (%) of plants reflecting main ecological groups, pollen zones, pollen sum values, and the CONISS cluster dendrogram. Sediments below 83 cm core depth are devoid of microfossils.

abundant. Higher proportions of fern spores at the end of this period indicate the local development of a fern-rich marsh. Increasing wet montane forest and fern-rich marsh with *Pandanus* and *Stillingia* both suggest that precipitation increased and/or the dry season shortened.

5.3. Period 3: ca. 500 cal a to recent (12–1 cm core interval; pollen zone PET-3; diatom zones 5–1; grain size zone D)

The sediment contains a high proportion of organic material, indicating wet and acidic soil conditions. Microfossils are well preserved in period 3. Ericaceous heath and scrub vegetation reached a stable minimum. Wet forest taxa *Syzygium*, *Nuxia verticillata*, *Labourdonnaisia* type and Melastomataceae became more abundant. These taxa also occur as stunted vegetation on bare soils. A sharp increase of charcoal is recorded at 9 cm core depth. A large fire event could have supported the increase of wet forest species and grasses (Poaceae). Erica shrubs need a longer period to regenerate after fire in Mauritius (Vaughan and Wiehe, 1937; Baider and Florens, pers. comm.), allowing stunted wet forest vegetation and opportunistic grasses to take over areas of ericaceous vegetation. Compared to period 2, *Pandanus* screw pine and associated fern-rich marsh lost abundance, but waterlogged areas remained present in these exposed uplands. At present-day, 11 species of *Pandanus* can be found in Le Pétrin (Baider and Florens, pers. comm. 2012), making it a hotspot in the Mascarenes for *Pandanus* diversity. Cyperaceous vegetation may reflect marshy vegetation, and can also become more abundant after fire. *Stillingia* can be associated both with marshy conditions and stunted vegetation. The strong decrease of *Cyathea* tree ferns may reflect human disturbance; i.e. the effect of competitive invasive species, fire and selective logging (Vaughan and Wiehe, 1937).

The increase in charcoal and the stable presence of taxa reflecting anthropogenic disturbance suggests that the upper 12 cm of the core reflects the period of colonization. Currently, plantations of pine (*Pinus* spp.), tea (*Camellia sinensis*) and sugar cane (*Saccharum officinarum*) occur in the vicinity of Le Pétrin (Fig. 1); species that are also reflected in the pollen record (Fig. 4). The wind-pollinated she-oak, *Casuarina equisetifolia*, was usually planted along the coast (Rouillard and Guého, 1999). Guava (*Psidium cattleianum*) is considered an invasive plant in forests and in azonal upland vegetation where it forms extremely dense thickets (Vaughan and Wiehe, 1937). Queensland poplar, *Homalanthus*, is an ornamental plant introduced in the 20th century; it is a common weed in cultivated land, but it is also found in the last remnants of upland forest (Kueffer and Mauremootoo, 2004). Judging the time of appearance, we interpret Poaceae in our record as a signal of human disturbance. Some unknown pollen taxa are only present in this period, strongly suggesting that these taxa reflect exotic plants.

Fig. 6. Diatom percentage diagram of sediment core Le Pétrin (650 m elevation, Mauritius) showing downcore changes in representation of the most important diatoms. Diatom zones are based on CONISS cluster analysis.

Period 3 is characterized by burning (see charcoal record), the presence of disturbed vegetation (see records showing human influence), and a more open landscape which can partially explain the high pollen concentration of the sediments (Fig. 5). Diatoms were only recorded in this period (Fig. 6). The spectra between 11 and 4 cm were dominated by *Frustulia rhomboides*, *Anomoeoneis seriensis* and *Anomoeoneis seriensis* var. *brachysira*; taxa that prefer waters with low pH and low conductivity (Patrick and Reimer, 1966; Gaiser and Johansen, 2000). The slight increase around 7–8 cm in *Eunotia bilunaris* var. *mucophila* may point to lower water levels (Patrick and Reimer, 1966). The uppermost 3 cm of the core shows an increase of *Navicula* aff. *subtilissima*, *Cymbella naviculiformis* and *Cymbella* sp. These taxa prefer aerial environments and peat bogs (Gasse, 1986), suggesting that the bog around the coring site may have expanded. The onset of the diatom record indicates that a water body developed which supported the interpretation of other proxies that at least local environmental conditions, and possibly also regional climatic conditions, became moister.

6. Discussion

The transition from zone PET-2 to zone PET-3 at 12.5 cm core depth results from changes in the records of *Erica*, *Pandanus*, and *Securinega* type, as well as the appearance of indicators of human disturbance. However, visual inspection of the pollen record shows that introduced plants are first registered by their pollen at 15 cm core depth. The level of 15 cm core depth seems a more accurate moment of the start of human impact on the vegetation. Theoretically, we can compare known introduction dates (Kueffer and Mauremootoo, 2004) of selected plants with the ages of the start of their pollen records. However, the age at 15 cm depth, as calculated from linear accumulation rates between radiocarbon dates, predates the start of colonization (AD 1638). It shows that for such a comparison the required chronological control of the sediment record is not available.

The lower part of the core (115–30 cm) reflects a very slow sediment accumulation. These sediments of earlier Holocene age and of glacial age are barren of microfossils due to oxidation, and likely contain hiatuses. Moreover, sediment accumulation is expected to have been continuous only when marshy conditions prevailed. Drier conditions allow all sedimentary scenarios varying between slow accumulation, interrupted accumulation, and erosion.

In an earlier palynological investigation, Straka (2001) published on the vegetation history of the heathlands of Le Pétrin (Fig. 7). We were unable to identify the exact location of the coring site of Straka. The studied core was 190 cm deep and included an uncalibrated radiocarbon age at 170 cm depth (dated interval 160–180 cm core depth) of 22,700 ^{14}C yr BP. In contrast to our record, the sediments provided adequate pollen spectra over the full 190 cm length of the core. Pollen counts were calculated and graphed on the basis of a pollen sum of 200 grains and fern spores. This alternative design of the pollen sum means that both pollen records cannot be compared in detail. Both records surpass the Last Glacial Maximum. However, both pollen abundance levels as well as species composition differ between the pollen records. In contrast to our record, ericaceous vegetation is restricted to the upper half of the record in Straka's paper. In our record, the presence of Poaceae is related to the period of human intervention, but Straka's record also shows Poaceae during glacial times. Both scenarios are not mutually exclusive as the Poaceae family includes exotic as well as native taxa. According to our interpretation, the abundance of Poaceae might have increased after a local fire. In general, grasses are resistant to fire owing to the location of their meristem at close distance to the ground. Both records show the presence of forest taxa in low abundances. The records of Asteraceae, Lycopodiaceae, *Eugenia*, Euphorbiaceae, and Apiaceae are also comparable in both records. The presence of aquatic vegetation in Straka's record points to a coring site close to permanent stagnant water, or a location close to a branch of the local drainage system. More than half of the

Fig. 7. Pollen percentage diagram (digitized) of a sediment core collected in Le Pétrin heathland (Straka, 2001), showing from left to right: uncalibrated ^{14}C age, downcore changes of main ecological groups, records of individual taxa, pollen sum values, CONISS cluster dendrogram, and an environmental characterization.

identified arboreal species in Straka's record are not native (Bosser et al., 1976–onwards), although most taxa are native in Madagascar.

According to the chronicles (e.g. Moree, 1998; Grihault, 2005) the Dutch colonized the island in AD 1638, resulting in a rapid transformation of the landscape. Later, as colonizers changed, the impact became more profound and this seems to coincide with the 12.5 cm level in our record. During the first two centuries of colonization, the record shows a rapid deforestation and expansion of crop cultivations. Currently, less than 5% of original forest is left (Safford, 1997). Our new pollen record shows that ericaceous heath and *Pandanus* marsh were abundant during pre-colonial times in the exposed

uplands above 600 m elevation. A pollen record from Kanaka Crater, situated a few kilometers east of Le Pétrin, shows evidence that in the past the ericaceous heathland covered a more extensive area in the central uplands than currently (Van der Plas et al., 2012; De Boer et al., 2013). The common perception that the island was almost entirely forested before human colonization (Cheke, 1987) seems an oversimplification, perhaps fuelled by observations from the coast. Today, ericaceous heath occurs on bare lava slabs and immature and highly laterized soils (Vaughan and Wiehe, 1937). *Pandanus* marsh is found within just 200 m from the coring site on water-logged soils at one extreme; at the other extreme, dry ericaceous

Fig. 8. Schematic figure showing changing edaphic conditions in relation to vegetation change at Le Pétrin heathland. (a) Period of mainly glacial age corresponding with pollen zone PET-1: pollen is poorly to not preserved due to exposure and oxidation. The few well-preserved pollen grains are plausibly anachronistic. Sediments were formed as a result of weathering and the landscape may have been covered by exposed vegetation. (b) Period corresponding to pollen zone PET-2: drainage properties of the soil had changed allowing marshy conditions to develop in the depressions, while heath and later thicket vegetation prevailed in areas at 'higher' elevation. (c) Period corresponding to pollen zone PET-3: marshy conditions developed and the proportion of stagnant water increased, resulting in sediments rich in organic material. Heath and thicket vegetation remained present at 'higher' elevations.

heath is found on highly drained rocky soils (Fig. 2). *Sideroxylon* thicket reflects intermediate conditions. We argue that this might reflect the setting of our record (Fig. 8): ericaceous heath giving way to marshy conditions, species of wet forest that formed thickets, mixed up with scrub as stunted plants. Accumulation of sediments and plant derived organic elements, shown in our core (Fig. 8), must have gradually changed edaphic conditions, making the soil locally suitable for other types of vegetation. Natural or human-induced fires and invasion of exotic species might have more recently started to replace natural ericaceous vegetation with grassy vegetation.

7. Conclusions

The sediment record from a heathland area located at 650 m elevation in Mauritius shows upland vegetation that changed composition before and after human arrival. The sediments of last glacial age contain a poor pollen signal but it is evident that heathland occurred as a natural biome in these exposed uplands with poorly developed soils. The wet environmental conditions reflected by the pollen and diatom spectra suggest locally wet conditions during Holocene times. Marshy vegetation occurred in waterlogged depressions, ericaceous heathland grew on better drained soils, and wet forest was restricted as stunted vegetation in the heathlands and on the surrounding slopes. The colonization of Mauritius in AD 1638 is documented by a sudden appearance of exotic species, deforestation, fire, and increasing abundances of grasses reflecting degraded vegetation. We conclude that a gradual change in edaphic conditions reduced the extent of ericaceous vegetation in the central uplands before colonization.

Fossil pollen records in isolated islands are an adequate tool for baseline studies in which the native proportion of the present-day flora is assessed (van Leeuwen et al., 2008; Connor et al., 2012). The present pollen record identifies natural vegetation dynamics in the Mauritian uplands, shows evidence of landscape degradation reflecting the period of colonization, and provides indications on the native status of individual taxa.

Acknowledgments

Sediments were collected within the framework of an NWO funded research project (2300155042) to HH and EjdB. We thank the Mauritius Sugar Industry Research Institute for their logistic support and Roshan Beersingh for the assistance in the field. Annemarie Philip is thanked for preparing pollen and diatom samples. We thank Dr. Stephen Rucina for the support with pollen identification and we thank Bas van Geel for the documentation of non-pollen palynomorphs. We also thank Stefan Engels for his valuable comments on the manuscript. Finally, we thank the team members of the International Dodo Project for inspiration and support during field work.

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