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Rapid succession of plant associations on the small ocean island of Mauritius at the onset of the Holocene

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ABSTRACT

The island of Mauritius offers the opportunity to study the poorly understood vegetation response to climate change on a small tropical oceanic island. A high-resolution pollen record from a 10 m long peat core from Kanaka Crater (560 m elevation, Mauritius, Indian Ocean) shows that vegetation shifted from a stable open wet forest Last Glacial state to a stable closed-stratified-tall-forest Holocene state. An ecological threshold was crossed at ~11.5 cal ka BP, propelling the forest ecosystem into an unstable period lasting ~4000 years. The shift between the two steady states involves a cascade of four abrupt (<150 years) forest transitions in which different tree species dominated the vegetation for a quasi-stable period of respectively ~1900, ~1100 and ~900 years. We interpret the first forest transition as climate-driven, reflecting the response of a small low topography oceanic island where significant spatial biome migration is impossible. The three subsequent forest transitions are not evidently linked to climate events, and are suggested to be driven by internal forest dynamics. The cascade of four consecutive events of species turnover occurred at a remarkably fast rate compared to changes during the preceding and following periods, and might therefore be considered as a composite tipping point in the ecosystem. We hypothesize that wet gallery forest, spatially and temporally stabilized by the drainage system, served as a long lasting reservoir of biodiversity and facilitated a rapid exchange of species with the montane forests to allow for a rapid cascade of plant associations.

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1. Introduction

Small and remote oceanic islands provide natural laboratories to study evolutionary processes and dynamic histories of their biomes in relation to climate change (Whittaker and Fernández-Palacios, 2007). The island of Mauritius, located about 900 km east of Madagascar in the Indian Ocean (Fig. 1) with a surface area of 1865 km², offers such an opportunity. This island is of volcanic origin and was formed 8–10 million years ago (Montaggioni and Nativel, 1988). Phytogeographical analysis shows that the Mauritian flora was stocked with plants mainly originating from East Africa and Madagascar (Whittaker and Fernández-Palacios, 2007;

Warren et al., 2010). There are no long-term records showing how biodiversity developed; present-day levels of diversity are high for an oceanic island setting (Groombridge, 1992; Myers et al., 2000; Kreft et al., 2008; Florens et al., 2012). These high levels of diversity plausibly developed through rafting and zoochory, followed by local speciation and relatively low rates of extinction. Island speciation explains the high proportion of endemics in Mauritius (Baider et al., 2010).

Pleistocene ice ages had a significant impact on the altitudinal distribution of the main plant associations in the East African mountains (e.g. Hedberg, 1951, 1964; Coetzee, 1967; Van Zinderen Bakker and Coetz, 1988; Hemp, 2005, 2006; Kiage and Liu, 2006; Street-Perrot et al., 2007; Schüller et al., 2012), here considered equivalent to biomes or ecosystems (Dickinson and Murphy, 1998). In East African savannas and lowland forests, changes in climatic humidity caused significant spatial changes in plant distributions during Pleistocene and Holocene times (Vincens et al., 2005, 2007;

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Fig. 1. Elevation map of Mauritius showing the sites Kanaka Crater (current study; Van der Plas et al., 2012) and Le Pétrin (De Boer et al., submitted for publication). The inset shows the location of Mauritius in the Indian Ocean compared to Africa and the latitudinal position of the ITCZ in December. The westbound South Equatorial Current flows along Mauritius all year round.

Gasse et al., 2008; Kröpelin et al., 2008; Rucina et al., 2009). Considering the insular setting and the geographical location of Mauritius at $\sim 20^\circ\text{S}$, several mechanisms may have contributed to past environmental change, such as astronomical forcing (Partridge, 1997; Gasse, 2000; deMenocal et al., 2000; Schefuss et al., 2005; Tierney et al., 2008; Verschuren, 2009), changing Indian Ocean sea surface temperatures (SSTs) (Prell et al., 1980), changes in the monsoon system and annual distribution of precipitation (Fleitmann et al., 2007; Vincens et al., 2007; Thomas et al., 2009; Tierney et al., 2011), and the Indian Ocean Dipole (IOD) (Saji et al., 1999; Marchant et al., 2006). Low sea level stands during the Last Glacial Maximum (LGM) let the surface of Mauritius increase by $\sim 30\%$ (Camoïn et al., 2004; Warren et al., 2010). Today, 70% of Mauritius' surface is below 300 m above sea level (asl) and only 8% of its surface reaches above 500 m asl. This specific island topography hardly allows individual plant species or plant associations to migrate altitudinally or latitudinally, a setting much in contrast to that of the mountains of Madagascar and East Africa.

Pollen records represent an important source of information as to how long-term ecological change affected the abundance of individual plant taxa as well as the overall vegetation. Dry palm-rich woodland and ebony (*Diospyros*) forest in Mauritius were most conspicuous at low elevations. Lower montane forest, moist forest and wet montane forest grew on slopes. In the flat uplands around 500 m elevation ericaceous heath, *Pandanus*-dominated marsh, and scrublands are common. Van der Plas et al. (2012) provided a first document of the dynamic history of montane forest. De Boer et al. (submitted for publication) showed the long-term ecological history of ericaceous scrubland. The pollen records of De Boer et al.

(submitted for publication) and Van der Plas et al. (2012) suggest that changes in climatic humidity were the most important drivers of past environmental change. There was no support for impact of the latitudinal migrations of the Intertropical Convergence Zone (ITCZ) on the vegetation driven by the 21 kyr precession cycle of the Earth's orbit (Kutzbach, 1981; Berger and Loutre, 1991). Instead, an important dampening effect of the IOD on long-term climate change was suggested. Stable temperatures across the LGM, and during the Last Glacial to Holocene transition, are known from the Tanzanian Eastern Arc Mountains (Mumbi et al., 2008; Finch et al., 2009). These studies suggested that moist Indian Ocean air masses caused long-term ecosystem stability.

Van der Plas et al. (2012) used a relative low-resolution pollen record from Kanaka Crater and showed that Last Glacial and Holocene forest compositions were stable, reflecting 'steady states'. In this study we use a sub-centennial sampling resolution of up to 20 years in order to analyze forest dynamics meticulously. We document for the first time a cascade of four abrupt forest transitions at the onset of the Holocene, reflecting a montane forest response to climate change alternative to migration. We hypothesize on the possibility that this suite of rapid ecological transitions is the result of montane forest crossing a tipping point (Scheffer and Carpenter, 2003; Lenton et al., 2008; Scheffer et al., 2009; Lenton, 2011). We discuss the role of biodiverse gallery forest to facilitate a rapid exchange of species with montane forest and allowing for a rapid succession of plant associations. Finally, we evaluate from a paleo-ecological perspective the native or introduced status of plant taxa.

2. Study area

2.1. Geology, geography and climate

Mauritius, Réunion and Rodrigues together form the archipelago of the Mascarene Islands (Fig. 1). Mauritius is located between $19^\circ 50'$ and $20^\circ 51'$ S latitude, and $57^\circ 18'$ and $57^\circ 48'$ E longitude. Upland areas above 500 m asl cover only 8% of the island and volcanic peaks ($<2\%$ surface) reach up to 828 m asl. Kanaka Crater ($20^\circ 24'$ S; $57^\circ 31'$ E) lies at 560 m asl in the southern mountains. It has a regularly formed cone-shape with a diameter at the top of ~ 300 m. Volcanic activity lasted until ~ 25 thousand years ago in the northeast part of the island (Montaggioni and Nativel, 1988). The age of Kanaka Crater and its period of volcanic activity are unknown. The center of the crater preserves 19.8 m of soft sediments (Van der Plas et al., 2012) and the surface consists of a mire without open water.

The winds over the Indian Ocean change significantly with the seasons and are driven by the latitudinal displacement of the ITCZ. In the Northern Hemisphere winter, the air over southern Asia is cooler and denser than the air over the ocean. The resulting pressure gradient leads to a low-level northerly or north-easterly airflow from the Asian landmass to south of the equator, forming the northeast monsoon (Colling, 2002). After crossing the equator, the airflow is turned west by the Coriolis force and converges with southeast trades at latitudes of 10° – 20°S . This is the rain season in Mauritius during which tropical cyclones and depressions may affect the island (Senapathi et al., 2010). As the year progresses, the Asian landmass heats up and the high pressure over Asia weakens. By May/June, a low pressure area has developed in Asia, causing a sudden change in wind direction to a southerly/south-westerly wind, blowing across the region until October. This is the southwest monsoon, the stronger component of the Indian Ocean monsoon.

On astronomical time-scales, the ITCZ is driven by the Earth's precessional cycle (Kutzbach, 1981; Pokras and Mix, 1987; Berger and Loutre, 1991; Cruz et al., 2005), resulting in a latitudinal

migration of the ITCZ at a frequency of 19–23 kyr. As a consequence, Mauritius may experience maximum and minimum precipitation events about every ~ 10 kyr. However, tropical oceanic islands might be buffered during dry phases by elevated topography-driven orographic rains and the direct influence of relatively high SST (Cronk, 1997; Trend-Staid and Prell, 2002; Rosell-Melé et al., 2004). Anomalously high SST and associated rainfall can be propagated by the IOD. The IOD is a coupled ocean–atmosphere system that occurs inter-annually in the tropical parts of the Indian Ocean (Saji et al., 1999; Marchant et al., 2006) and is characterized by changes in SST between the western and eastern parts of the Indian Ocean, independent from the general Indian Ocean circulation (Saji et al., 1999).

The mean annual temperature (MAT) is 22 °C near Mauritius at sea level and the mean annual precipitation (MAP) is 2100 mm. Depending on relief and orientation of the slopes, MAP varies from 800 mm in the western coastal lowlands to 1400 mm in the eastern coastal lowlands, and over 4000 mm in the uplands. Only 74 mm of mean precipitation is registered during the driest month (October) (Padya, 1989). MAP exceeds evapotranspiration in the central uplands (Padya, 1989).

2.2. Vegetation and human occupation

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 (Vaughan and Wiehe, 1937; Cheke and Hume, 2008). Wet forest grew on slopes and higher and wetter grounds and covered about 50% of the island. Azonal plant communities included heath formations or stunted thickets on shallow rocky soils, and in the wet areas on poorly drained soils marshes with screw pine (*Pandanus*) occurred (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 (Fig. 2), resulting in a more mosaic-pattern vegetation cover rather than a zonal pattern.

Human colonization started in AD 1638 after which the island became rapidly deforested (Vaughan and Wiehe, 1937). By 1872 the palm-rich woodland biome was virtually lost (Safford, 1997; Cheke and Hume, 2008). Despite the small size of the island (c. 40×60 km) and the long history of botanical inventories, native 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). According to the 2010 inventory, the angiosperm flora includes 691 species, 39.5% of which are considered as endemic (Baider et al., 2010). Today, native vegetation suffers from many introduced invasive alien plants (Lorence and Sussman, 1986; Safford, 1997; Florens, 2008; Caujapé-Castells et al., 2010). The number of introduced plants far outnumber the number of native species (Bossier et al., 1976-onwards). An estimated number of 1675 species have been introduced (Kueffer and Mauremootoo, 2004), although there is some doubt as to which part of the present flora can be considered as native.

Presently, Kanaka Crater is mainly surrounded by plantations of pine, sugar cane and tea. The crater walls were strongly deforested between 1975 and 1989. Remnants of degraded natural forest closest to Kanaka Crater occur as gallery forest along the drainage

system (Safford, 1997). The area around Kanaka Crater receives ~ 3600 mm MAP, making it potentially suitable for moist to wet forest (Fig. 2).

3. Materials and methods

The 10 m long sediment core Kanaka-1 was collected with a Russian Corer in 50 cm increments. There is a small gap from 418 to 428 cm core depth. The sediment matrix consists of homogeneous ‘root-peat’ without other recognizable plant macrofossils. A chronological framework of the sediment column is based on 11 accelerator mass spectroscopy radiocarbon ages. The age–depth model of the sediment core was produced using Bayesian modeling routine Bacon (Blaauw and Christen, 2011). The core was divided into 51 10-cm long vertical sections, and accumulation rates were modeled for each section through combining the dates with prior information. The surface was assumed to be of recent age (AD 2010 ± 5). Since Kanaka Crater lies within the southern hemisphere, the radiocarbon dates should ideally be calibrated using the southern hemisphere calibration curve SHCal04 (McCormac et al., 2004). However, since this curve only extends to 11 cal ka BP (thousands of years before AD 1950), we used the northern hemisphere curve IntCal09 (Reimer et al., 2009), applying a southern hemisphere offset of 40 ± 20 ^{14}C yr (Hogg et al., 2009). Dates were assumed to have a student-*t* distribution on the ^{14}C scale, instead of the default Gaussian distribution (Christen and Perez, 2009). The prior information applied (see Blaauw and Christen, 2011) was a gamma distribution for sedimentation time (shape 1.5, mean 50 yr/cm), and a beta distribution for the accumulation variability between neighboring depths (strength 4, mean 0.7).

Details on sample preparation are described in Van der Plas et al. (2012). For pollen analysis, minimal 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). We also used the African Pollen Database (<http://medias3.mediasfrance.org/apd/accueil.htm>) for identifications and have asked several African pollen experts for help with determination. All pollen taxa, except undeterminable pollen grains, were included in the pollen sum; fern spores, fungal spores, and non-pollen palynomorphs were excluded. Pollen and spore taxa were categorized into the following ecological groups: (1) heath and scrub, (2) marsh, (3) montane forest, (4) taxa currently not accepted as native (Bossier et al., 1976-onwards), (5) (higher ranked) taxa with diffuse or unspecified ecological requirements, (6) unidentified pollen grains, and (7) fern spores. Pollen diagrams were plotted with TILIA 1.5.12 (Grimm, 1993, 2004) software. Zonation was based on CONISS analysis, included in the TILIA program.

Modern vegetation associations (Fig. 2) are recognized in the pollen spectra. However, several characteristic trees such as *Calophyllum*, *Cassine*, *Harungana madagascariensis* and *Diospyros* are not reflected in this pollen record although their pollen grains are identifiable. This led us decide to group all arboreal taxa in the category ‘montane forest’. *Erica* heath and *Sideroxylon* thickets have many species in common and both vegetation associations could not be distinguished in the pollen spectra (De Boer et al., submitted for publication). *Pandanus*, *Pilea* and *Dracaena* are, at least partly, wind pollinated and may therefore be overrepresented in the pollen record. In continental records pollen from *Pilea* (Urticaceae) and *Ficus* (Moraceae) are distinguishable (Straka et al., 1964-onwards, listed in Hooghiemstra and Van Geel, 1998). As both genera contain respectively twelve and five native species (Bossier

Fig. 2. Altitudinal ranges of the most important native taxa making up the main biomes in Mauritius above 150 m elevation. The right hand columns show the indicator value of taxa with respect to succession stage (column d) and their pollination syndrome (column e). Column c shows a characterization of mean annual rainfall for the main biomes. Taxa indicated in red have been identified in the Kanaka pollen record; blue taxa have been identified in other sites in Mauritius (De Boer et al., submitted for publication). Abbreviations: Cli = climax, Pio = pioneer, MSu = mid succession, Ane = anemochory (wind), Zoo = zoochory (animals), Ent = entomochory (insects), Orn = ornithochory (birds), Chi = chiropterochory (bats). The question marks in column e indicate an uncertainty in pollination syndrome. High-ranked taxa may comprise multiple species and are not specific for a particular forest type. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

et al., 1976-onwards) and the pollen morphological variability is unknown, we decided not to try differentiate between *Pilea* and *Ficus*. Although *Pilea* is a ground herb and *Ficus* a canopy tree, both genera grow predominantly in wet montane forests.

We performed a principal component analysis (PCA) to summarize the pollen data and explore temporal trends in the pollen data. PCA is an indirect linear ordination method and provides a means to identify the main gradients in the species assemblage data (Legendre and Birks, 2012). We used square-root transformed percent abundances of the pollen taxa that are included in the pollen sum, and we did not use downweighting of rare taxa. The PCA was performed using CANOCO v 4.5 (Ter Braak and Šmilauer, 2002).

The main temporal trends in taxon diversity were explored by calculating species turnover between the pollen spectra (MacDonald et al., 2008). The species turnover between two adjacent pollen samples is obtained by calculating a dissimilarity coefficient (DC) and dividing it by the time interval between the two samples. A DC between two spectra is the distance between two points in an n -dimensional space, where n is the number of pollen types (Bennett and Humphry, 1995). Pollen data were interpolated to produce intervals between samples equidistant in time. Two curves of species turnover were calculated due to the differences in sedimentation rate. The first curve interpolates samples at 80-yr resolution and covers the Holocene period. The second curve

interpolates samples at 1000-yr resolution and covers the entire record. All taxa included in the pollen sum with values >5% were included in the analysis. To balance the effect of dominant taxa and to downweight the number of rare pollen types, a signal-noise DC was used (Prentice, 1980). Noise is determined by calculating a ratio of small-scale variation of a sub-interval to the overall variation of the complete interval (Bennett and Humphry, 1995). Noise may be more important at intervals with finer resolution, resulting in artificially higher rates of change. To guard against this, two different interpolation intervals were applied.

4. Results

The age-modeling routine Bacon automatically excluded the date at the bottom of the core (Fig. 3). This date at 9.96 m depth is much younger than all samples below 6 m depth, pointing to contamination of the sample. The age of the sediment sequence ranges from ~35.6 ka BP at 1000 cm to 0.125 ka BP at 1 cm core depth. The upper 10 cm of the sediment core corresponds to the period of human presence in Mauritius. The age-depth model basically shows a slow sedimentation rate during the Last Glacial and a faster sedimentation rate during the Holocene. Confidence intervals (95%) for the age-depth model ranged from 315 yr at 46 cm core depth, to several millennia at the slowly accumulating and lower-resolution dated lower part of the core (550–1000 cm depth) (Fig. 3).

Fig. 3. Age model of Kanaka-1 sediment core. Upper panels indicate stability Markov chain Monte Carlo run, accumulation rate (green prior distribution, grey posterior), and memory (green prior distribution, grey posterior). Grey scales in lower panel indicate chronological uncertainty; darker grey indicates more likely ages. Red line shows 'best' age-depth model based on weighted mean from age distributions. Dark blue shapes are the calibrated ^{14}C dates, blue shape indicates the calendar date of the surface. Vertical bars indicate the position of the pollen samples against calibrated age. This improved age model differs from the one presented in Van der Plas et al. (2012). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

We recognized 124 different pollen types in the 208 analyzed pollen samples; 50% of the pollen types could be identified to family level at least. Of the counted pollen grains 99% were identified, as many of the 62 unidentified pollen types are rare. Fifteen unknown pollen types in the pollen record of Van der Plas et al. (2012) have been identified in this paper. The records of all paly-nomorphs (Supplementary information Fig. S1) are shown as ecological groups, reflecting temporal changes in the proportions of the main plant associations (Fig. 4). Sample scores of the first two PCA axes, explaining 41% (axis 1) and 10% (axis 2) of the variance, and the species turnover calculations of pollen taxa involved are shown on a linear time scale (Fig. 5). Compared to the record of Van der Plas et al. (2012), the additional 108 pollen spectra caused the zone boundary at 825 cm to shift to 498 cm in the present record and caused zone KAN1-5 to be divided into four subzones (Table 1). The additional 108 pollen spectra were taken between 550 cm and 1 cm core depth, strongly increasing the sample resolution of this interval between minimally ~20 to maximally ~200 yr (Fig. 3 and Table 1). Compared to Van der Plas et al. (2012) we now identified rapid ecological events and strengthened long-term trends, making calculations of species turnover meaningful.

Period 1 (pollen zone KAN 1-1) – Heath and scrub vegetation was continuously present during the Last Glacial. The proportion of montane forest increased mainly due to increasing proportions of *Syzygium*, *Nuxia*, *Weinmannia* and *Pilea/Ficus* type. The dominant taxa *Nuxia*, *Weinmannia* and *Tambourissa purpurea* type indicate moist to wet open canopy forest (Fig. 2). The abundant presence of tree fern *Cyathea* also points to moist to wet forest. Mascarene *Weinmannia* and to a lesser extent *Nuxia* typically germinate on stem bases of *Cyathea* (Derroire et al., 2007; Rivière et al., 2008). *Artemisia afra* type indicates the presence of open woodland and forest margins. Species turnover is low, pointing to ecological stability (Fig. 5). *A. afra* type, Cycadaceae, *Hydrocotyle* type, *Alchornea* type and *Laurembergia tetrandra* are currently listed as exotic to the Mauritian flora (Bossier et al., 1976–onwards). Potentially, pollen can be transported over large distances (Van der Knaap et al., 2012) depending on pollen production, pollen morphology and atmospheric conditions. However, the dominant southeast tradewinds blowing over Mauritius persist throughout the year (Schott and McCreary, 2001; Barrows and Juggins, 2005) making a steady supply of pollen grains from Africa unlikely. The prolonged presence of pollen from *A. afra* type, Cycadaceae, *Hydrocotyle* type, *Alchornea* type and *Laurembergia tetrandra* taxa during this period indicates that these taxa have grown on the island and should be considered as native. The erratic occurrence of aerodynamic *Podocarpus* pollen grains in the record is interpreted as reflecting occasional long-distance transport from the nearest locations in Madagascar.

Period 2 (pollen zone KAN 1-2) – The pollen record showed small changes at 24.6 cal ka BP. The abundance of montane forest decreased while *Pandanus* marsh and heath and scrub became more abundant. This change is also indicated by higher values of species turnover (Fig. 5), and coincides with the onset of the LGM episode. *Cyathea* was less abundant from the LGM to the Lateglacial, suggesting this period was drier than period 1, but presence of wet forest continued in the area. Species turnover during the Lateglacial is low showing ecological stability continued after the LGM.

Period 3 (pollen zone KAN 1-3) – At the transition from the Lateglacial to the Holocene a sequential change in the species composition is registered (Fig. 5 and Fig. S1) and species turnover is high. Heath and scrub became rare and *A. afra* type disappeared from the pollen record, suggesting that exposed areas such as the rim of the crater became forested. *Syzygium*, *Psiloxylon mauritianum* and Cycadaceae became important forest elements, pointing to open and wet forest. *Psiloxylon mauritianum* germinates in particular on either bare sloppy ground or on rotting fallen logs where

abundant light is available. The presence of *Cyathea* tree ferns and *T. purpurea* type, *Allophylus* and *Olea* growing there as trees of intermediate height also support the indication that open and wet forest prevailed.

Period 4 (pollen zone KAN 1-4) – At the transition to period 4, Cycadaceae and *Syzygium* became rare. Their dominant position was taken over by *Eugenia*, *Dracaena* type and *Securinega* type. As *Eugenia* is more resistant to dry conditions than *Syzygium* we infer decreasing climatic moisture. This shift is the most dramatic transition of the record, as scores on the first PCA axis change to negative values and species turnover is highest (Fig. 5). Higher abundance of Cyperaceae, *Pandanus* T.mau-131, and *Lycopodium* may reflect the development of the local vegetation in the crater. In general, *Pandanus* marsh decreased in abundance indicating decreasing climatic moisture in general and/or an improved drainage of the crater. *Dracaena*, *Psiloxylon mauritianum*, *Nuxia* and *Weinmannia* were important trees and point to open moist to wet forest. Other trees of intermediate height are *Aphloia theiformis*, *T. purpurea* type, *Allophylus*, *Molinaea* and Sapindaceae. Around 9.1 cal ka BP *Eugenia* disappeared abruptly for ~100 yr, returning for a short interval only around 9.0 cal ka BP. Simultaneously, the other myrtaceous taxa *Psiloxylon mauritianum* and *Syzygium* decreased in abundance, while proportions of other taxa were relatively stable. The suddenness and brevity of change in all three myrtaceous records is remarkable. In the 19th century, outbreaks of wood borer attacks had a short but significant impact in Mauritian forests (Cheke & Hume). We speculate that a pest or disease outbreak could have rapidly knocked down the dominant myrtaceous trees during this interval.

Period 5 (pollen zone KAN 1-5a) – Montane forest taxa *Nuxia*, *Eugenia*, *Psiloxylon mauritianum*, *Syzygium*, *Allophylus* and *Weinmannia* all decreased in abundance and *Pandanus* screw pine expanded, indicating that marsh and wet soils became more abundant. Species turnover is low. At the end of this period proportions of sapotaceous trees increased in the montane forest.

Period 6 (pollen zone KAN 1-5b) – *Pandanus* decreased in abundance and sapotaceous trees started to dominate the forest, coinciding with high species turnover. Representatives of the Sapotaceae family typically form tall shady forest. Also, higher values of *Pilea/Ficus* type is indicative of closed mature canopy forest. *Allophylus*, *Securinega* type and several euphorbiaceous species typically occur as high understorey trees in this tall forest. Currently, Sapotaceae-dominated forests occur in drier environments than forests dominated by *Eugenia*-, *Syzygium*-, and *Nuxia*-*Weinmannia*.

Period 7 (pollen zone KAN 1-5c) – Sapotaceae decreased in abundance and *Pandanus* increased. *Olea* type and *Molinaea* were present as understorey trees in the tall sapotaceous forest. Between 4.9 and 4.3 cal ka BP *Nuxia* suddenly increased in abundance. A substantial mortality among Sapotaceae trees at 4.9 cal ka BP may have been the cause that *Nuxia* and *Weinmannia* trees became temporarily more abundant; these species germinate well on dead logs and stumps where abundant moisture and light is available (Derroire et al., 2007; Rivière et al., 2008). Within a period of ~80 years *Nuxia* occupied an important role in the open forest.

Period 8 (pollen zone KAN 1-5d) – After *Nuxia* forest had been abundant during some 500 years, forest composition returned to the assemblage characteristic of period 7. Toward the end of this period, the proportion of *Dracaena* decreased and *Eugenia* became more abundant.

Period 9 (pollen zone KAN 1-6) – Presence of *Nuxia*, *Weinmannia*, *Syzygium*, *Eugenia* and *Acalypha* indicates open wet forest. In open patches *Acalypha* typically forms 2–3 m high dense thickets reflecting an early secondary succession. Historical records show that *Aphloia theiformis* was abundantly present near Kanaka Crater. In the upper 10 cm of the record, representing the last ~400

Fig. 4. Pollen percentage diagram of core Kanaka-1 (Mauritius, 560 m elevation) analyzed at 10-cm increments from 1000 to 550 cm core depth, and 3.3-cm increments from 550 to 1 cm core depth. Data are plotted on a linear depth-scale. From left to right are shown: radiocarbon ages, depth, lithology, pollen concentration (pollen cm^{-3} of sediment), main diagrams of biome categories with a pollen sum including (left) and excluding (right) *Pandanus* marsh taxa, ecological categories of pollen and spores, charcoal presence, pollen sum values, pollen zones, and the CONISS cluster dendrogram.

Fig. 5. Pollen percentage diagram of core Kanaka-1, showing selected records involved in species turnover events. Data are plotted on a linear time-scale. Taxa are arranged from highest abundance during the Last Glacial (left) to taxa with highest abundance during the Holocene (right). Also shown: depth, recognized periods, PCA sample scores and calculated species turnover between sample intervals. The first PCA axis separates period 1–3 from period 4–9. The second PCA axis clusters periods 1–2, 3–4, 5–8 and period 9 (see also Fig. S2).

Table 1
Period specific information of pollen record Kanaka-1.

Period	Age interval (cal ka)	Pollen zone	Depth interval (cm core depth)	# of samples	Average resolution (yr)
1	35.6–24.6	KAN1-1	1000–745	26	~450
2	24.6–11.5	KAN1-2	745–495	36	~1100 (lower part) ~80 (upper part)
3	11.5–9.6	KAN1-3	495–449	14	~140
4	9.6–8.5	KAN1-4	449–368	21	~50
5	8.5–7.6	KAN1-5a	368–315	16	~60
6	7.6–6.8	KAN1-5b	315–268	14	~50
7	6.8–4.3	KAN1-5c	268–138	39	~60
8	4.3–2.3	KAN1-5d	138–55	25	~80
9	2.3–recent	KAN1-6	55–1	17	~130

years, a suite of rare pollen taxa is registered for the first time, such as *Psidium cattleianum* (Myrtaceae, strawberry guava), *Clidemia hirta* and *Osbeckia octandra* (Melastomataceae), *Nymphoides indica* (Menyanthaceae), sugar cane (Poaceae), and *Camellia* (tea).

5. Discussion

5.1. Steady states

Long-term rainfall patterns in northern and southern Africa are linked to changes in the different monsoons, which on their turn are linked to precession-driven variations in the latitudinal range of the ITCZ (Gasse, 2000; deMenocal et al., 2000; Schefuss et al., 2005; Fleitmann et al., 2007; Tierney et al., 2008). Based on organic biomarkers from Lake Challa in southern Kenya, Verschuren (2009) demonstrated that equatorial Africa experienced high rainfall when the insolation gradient between the hemispheres was large, and either the southwest or northeast monsoon was intensified. Wet periods in Lake Challa were inferred around ~22.5, 11.5 and 1.5 cal ka BP. In Mauritian uplands, continuous presence of montane forest suggests that no significant changes in climatic moisture have occurred during the last ~35,600 years (Fig. 4). Nonetheless, maximum representation of wet forest during the periods of ~28–24.8, 9.6–8.5 and 2.3–0 cal ka BP, suggest that Mauritius might have been affected by the precession-driven migration of the ITCZ at half-precessional time-scales. Independent climate proxies are needed to clarify the effects of changing monsoon activity in Mauritius.

Stable climate conditions in Mauritius are reflected by low species turnover in montane forest between ~35.6 and ~11.5 cal ka BP and from ~7.6 to 2.3 cal ka BP, reflecting steady states. These stable hydrological conditions are supported by long-term effects of orographic rains and warm water masses in the Indian Ocean. Both characteristics are little responsive to Pleistocene climate change (Prell et al., 1980; Cronk, 1997; Trend-Staid and Prell, 2002; Rosell-Melé et al., 2004; Marchant et al., 2006; Whittaker and Fernández-Palacios, 2007). Based on planktonic foraminifera assemblages Barrows and Juggins (2005) estimated that during the LGM the subtropical waters around Mauritius were less than 1 °C colder than at present. A potential explanation for this small temperature change is that tropical waters from the Indian Ocean were not exported by the Agulhas Current into the Atlantic Ocean. Instead, the subtropical Indian Ocean gyre continuously supplied warm waters to Mauritius. Small changes in SST overwrite any potential impact of orbitally-forced long-term rainfall patterns (Verschuren, 2009).

5.2. Regime shift

From ~11.5 to 7.6 cal ka BP, species associations changed dramatically in four steps in between the ecological stable periods. At

~11.5 cal ka BP the forest changed from a not-stratified *Nuxia-Weinmannia*-dominated open wet forest into a *Syzygium*-dominated open wet forest (period 3) that lasted ~1900 years. At ~9.6 cal ka BP *Syzygium* lost dominance and was replaced by *Eugenia*-dominated moist forest that lasted for ~1100 years (period 4). This forest showed little resemblance to the glacial signature forest, clearly reflected in the PCA diagram (Fig. 5; Fig. S2) where the pollen assemblages have shifted to the negative side of the first PCA axis. Simultaneously, species turnover shows maximum values of the record (Fig. 5). A third step occurred at c. 8.5 cal ka BP when *Eugenia*, and other forest elements such as *Nuxia*, *Weinmannia*, *Syzygium* and *Psiloxylon mauritianum* declined in abundance. Sapotaceous trees slowly increased during a period of 900 years and reached dominance around ~7.6 cal ka BP (period 5). During the following ~4300 years forest showed a stable composition and occurred as tall, stratified, late successional moist forest dominated by sapotaceous trees.

The initial change occurred at the Lateglacial to Holocene transition at 11.5 cal ka BP. The shift to Holocene global climatic conditions, such as high atmospheric levels of greenhouse gasses and the onset of the meridional overturning circulation possibly pushed the Mauritian montane forest biome into instability. Mayle and Bush (2007) showed that in the tropics the combination of lower temperature, precipitation, and atmospheric $p\text{CO}_2$ concentrations resulted in forest structurally and floristically different from today. The first event of species turnover was followed by short-lived discrete forest associations and a new equilibrium was reached after 4000 years. These subsequent events of species turnover do not coincide with climate events of a global or African significance. Therefore, we hypothesize that intrinsic drivers caused the forest succession (Williams et al., 2011). The impact of intrinsic drivers on tropical forests was discussed by Chambers and Silver (2007), Körner (2007), Lewis et al. (2007), Meir and Grace (2007), Pearman et al. (2008) and Osborne (2012). These insular reorganizations of montane forest composition contrast with spatial migration in continental settings and exemplify an alternative mechanism for montane forest response to climate change.

Scheffer and Carpenter (2003), Lenton et al. (2008), Scheffer et al. (2009) and Lenton (2011) defined a tipping point as an abrupt change when an ecosystem is forced to cross some threshold, triggering a transition to a new steady state at a rate determined by the ecosystem itself and faster than the cause. The four consecutive events between ~11.5 and ~7.6 cal ka BP occurred within three successive pollen samples each, which is equivalent to a period of up to 150 years. Assuming that the life time of one generation of a canopy tree can reach up to three centuries we infer that forest transitions occurred in less than two generations, and possibly within one. Based on growth rates and stem widths, the age of canopy trees such as Sapotaceae, *Eugenia* and *Cassine* are estimated to exceed 1000 years (Baider and Florens, 2006; Florens, 2008). The initial change at ~11.5 cal ka BP, globally coinciding with the start of the Holocene, is relatively small compared to the next three steps of forest change. This is supported by the PCA analysis showing that period 3 (~11.5–9.6 cal ka BP) is more similar to the glacial pollen spectra than to the Holocene spectra (Fig. 5; Fig. S2). The transition from period 3 to 4 might be considered as the moment that the biome crossed a critical threshold, propelling the forest ecosystem into an unstable period for the next ~4000 years. There is a change from 'open not-stratified' forest to 'closed, well-stratified late-successional' forest. The critical threshold can be considered as a bifurcation point separating one state (viz. open forest) from another (viz. closed-stratified forest). Theoretically, when reaching a critical threshold a system becomes slower in responding to perturbations from outside the system ('slowing down') (Dakos et al., 2008; Scheffer

et al., 2009) reflected by an increased autocorrelation, i.e. the change from one given time interval to another (Dakos et al., 2008). We explored the presence of increased autocorrelation (results not shown) but clear trends were not found. This may be explained by the low sediment accumulation during the Lateglacial resulting in a low ~550-yr resolution in the record (Fig. 3). Potentially, detection of increased autocorrelation in pollen records is a powerful tool, as it might provide an early warning signal of an ecosystem approaching its tipping point.

5.3. Long-term ecology and implications for conservation

Where had species that arrived as 'new' in the Holocene record taken their residence during glacial times? And where do species of the glacial forest reside during the Holocene? Rijdsdijk et al. (2009) unraveled the persistence of a thriving community of wet forest tree species in a small edaphically wet area set within a climatically dry zone in Mauritius during the mid-Holocene. We hypothesize that gallery forests bordering the drainage system offered a similar refugium for diversity. These azonal forests form long corridors potentially facilitating migration, and allow in insular settings to receive and supply diversity to zonal forests elsewhere (Vaughan and Wiehe, 1937; Mayle et al., 2007; Moat and Smith, 2007). In addition, the rapid species turnover observed at Kanaka may have been aided, at least for the many zoochoric species, by a rich fauna of seed disseminators (Cheke and Hume, 2008; Rijdsdijk et al., 2009). In Madagascar, rivers with headwaters at high elevations served as refugia, maintaining riparian forest where species retreated during the driest periods (Hannah et al., 2008). When conditions became wetter, riparian habitats extended into tributaries with lower headwaters, opening migration corridors for plants to (re-)establish in previously unsuitable areas (Hannah et al., 2008; De Boer et al., submitted for publication). However, dryness adapted taxa, such as *Erica*, *Trochetia* and *Artemisia* may benefit less from these landscape corridors. Currently, *Erica* heath is restricted to a small upland, but heathland covered larger areas during the Last Glacial (De Boer et al., submitted for publication).

Our pollen record suggests that amongst others Cycadaceae, *Artemisia*, *Hydrocotyle*, *Alchornea* and several palm species disappeared during Holocene times, long before human colonization started. One may wonder why these taxa became (locally?) extinct during the Holocene interglacial after the long sequence of Pleistocene changes. We find it most plausible that these taxa were extirpated from the island after human arrival and before biological inventories could register their native status. This argument appears particularly valid in view of the many new species which are still being discovered more than 350 years after humans colonized the island and despite only 5% of native habitat is left (Florens and Baider, 2006; Le Péchon et al., 2011; Baider et al., 2012). These observations illustrate that in insular settings knowledge of long-term ecological change has a high potential to improve conservation practice and policy (Burney and Pigott-Burney, 2007; Willis et al., 2007; Van Leeuwen et al., 2008; De Nascimento et al., 2009; Virah-Sawmy et al., 2009; Rull et al., 2010; Connor et al., 2012).

6. Conclusions

The present study gives an unprecedented view on the forest dynamics of the small oceanic island of Mauritius. Two periods with a low-level of species turnover, considered as steady states, are separated by a transitional period including a cascade of abrupt changes in forest composition at ~11.5, ~9.6, ~8.5 and ~7.6 cal ka BP. These transitions occurred within 150 years, i.e. two arboreal generations at the most. Steps of the cascade lasted ~1900, ~1100 and ~900 years, respectively. We hypothesize that this salient example of ecological

change is a functional answer to climate change when biota cannot migrate. Montane forest changed from an open wet forest dominated by *Nuxia*, *Weinmannia* and *Tambourissa*, to a *Syzygium-Psiloxylon-Eugenia* myrtaceous forest, and finally to drier high canopy forest dominated by Sapotaceae in the canopy and *Dracaena* in the understorey. Gallery forest with relatively stable moisture availability during all climatic episodes is assumed to constitute the reservoir of plant diversity from where species are recruited to form more extensive montane forests under favorable conditions.

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Appendix A. Supplementary material

Supplementary material related to this article can be found at <http://dx.doi.org/10.1016/j.quascirev.2013.02.005>.

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