

Article

# Berenty Reserve—A Gallery Forest in Decline in Dry Southern Madagascar—Towards Forest Restoration

Vanessa Winchester <sup>1,\*</sup>, Kate Hardwick <sup>2</sup>, Hantaranina Rasamimanana <sup>3</sup>, Sahoby M. Raharison <sup>4</sup>, Anne Mertl-Millhollen <sup>5</sup> , Holger Gärtner <sup>6</sup>  and Janet McCrae <sup>7</sup>

<sup>1</sup> School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, UK

<sup>2</sup> Royal Botanic Gardens, Kew, Wellcome Trust Millennium Building, Wakehurst, Ardingly, West Sussex RH17 6TN, UK; k.hardwick@kew.org

<sup>3</sup> Ecole Normale Supérieure, University of Antananarivo, Antananarivo 101, Madagascar; hantani1@yahoo.fr

<sup>4</sup> Lycée Ambohimilaza Miray, Cisco Antananarivo, Avaradrano, Antananarivo 101, Madagascar; raioby@gmail.com

<sup>5</sup> Department of Anthropology, 128 University of Oregon, Eugene, OR 97403-1218, USA; hplam\_1998@yahoo.com

<sup>6</sup> Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland; holger.gaertner@wsl.ch

<sup>7</sup> 20 Aston Street, Oxford, OX4 1EP, UK; jemccrae12@btinternet.com

\* Correspondence: vanessa.winchester@geog.ox.ac.uk; Tel.: +44-(0)-186-555-7600

Received: 22 October 2017; Accepted: 8 January 2018; Published: 15 January 2018

**Abstract:** Berenty Reserve, a fully protected gallery forest beside the Mandrare River is renowned for its lemurs, but the continuous canopy of the main forest is shrinking, fragmenting and degrading. The aim of this study, before any restoration can be considered, is to investigate why canopy-cover is declining and define the forest's vegetation status and composition. Our study includes analysis of tamarind age (the dominant species) and regeneration, forest extent, climate and soil. Measurement of trunk circumference and annual rings indicated a median age of 190 years, near the accepted maximum for tamarinds. There is no regeneration of tamarind seedlings under the canopy and an invasive vine, *Cissus quadrangularis* suffocates any regeneration on the forest margins. A vegetation survey, based on fifteen transects, broadly characterized three forest areas: continuous canopy near the river, transitional canopy with fewer tall trees, and degraded dryland; the survey also provided a list of the 18 most common tree species. Ring counts of flood-damaged roots combined with measurement to the riverbank show that erosion rates, up to 19.5 cm/year, are not an immediate threat to forest extent. The highly variable climate shows no trend and analysis of forest soil indicates compatibility with plant growth.

**Keywords:** degrading; tamarind age; regeneration; invasive vine; vegetation survey; erosion

## 1. Introduction

Madagascar is one of the richest countries on Earth in terms of biodiversity, endemism and range of habitats, but the combination of a rapidly growing human population coupled with extreme poverty constitutes a serious threat to its uniquely diverse flora and fauna. In the dry south, with the highest percentage of endemic plants on the island, forests are burnt for charcoal production, planted with maize or sisal or degraded by cattle pasturing [1]. Much has been written about the need for conservation [2–4], but there have been few surveys of the dryland vegetation [5] and little is known concerning the growth requirements of the local species. There is no information on successional patterns [6] or which species could be termed pioneer or climax and, excluding one reforestation project on the southwestern side of Madagascar focused on planting eucalyptus and tamarind trees for

local use [7], regeneration of a gallery forest aiming at re-establishing its structure, productivity and species diversity has, to the authors' knowledge, never been attempted.

Gallery forests form as corridors along rivers or wetlands running through arid or semi-arid landscapes. The riparian zone offers fertile alluvial soil, a more reliable water supply at depth and better drainage than is available to the vegetation beyond the immediate river valley. As a result, the boundary between the gallery forest and the surrounding woodland or grassland is usually abrupt, with an ecotone only a few metres wide, as is the case at Berenty Private Reserve.

The reserve, embracing patches of forest on the banks of the Mandrare River and famous for its lemurs, is among the very few remaining securely protected gallery forests in southern Madagascar. However, since the 1980s researchers have noticed that the canopy of the dominant species, *Tamarindus indica* (tamarind), has been fragmenting and shrinking [8]: this is of particular concern since tamarinds are a keystone resource for lemurs. That the forest exists at all and has not been lost, as have most other gallery forests in Madagascar, is due to the foresight of the de Heaulme family, who set the forest aside as a conservation area 80 years ago and have protected it ever since. Although only 330 ha in area, the reserve has an importance far beyond its size: studies of its six species of lemur have been ongoing for the last 50 years and as a centre for eco-tourism and student education it has a preminent position in spreading knowledge of this fragile, unique and potentially vanishing ecosystem [9].

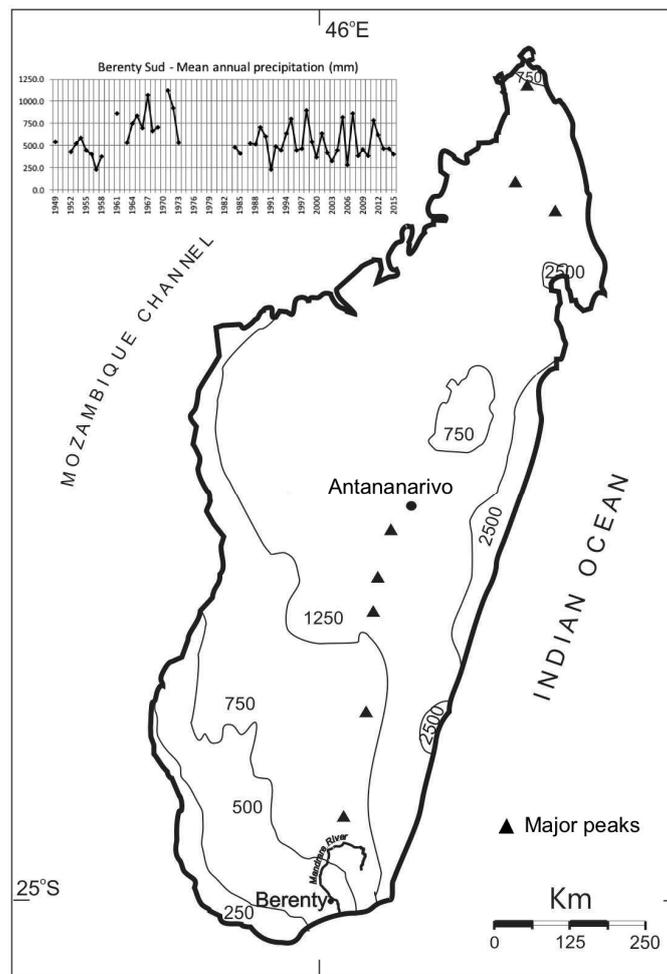
Previous studies have shown that the main forest area, Malaza, includes at least three different vegetation zones [10], which can be further subdivided into six vegetation types [8]. Maps of the zones produced in 1973 and 1995 show that in 1973 the continuous canopy gallery forest formed a belt about 250 m at its deepest mainly along the western section of the Malaza riverbank, with patchy cover along the bank to the east. The south-east side is more open with occasional large trees surrounded by grass, scrub and thorny thickets. By 1995, the dense tamarinds near the river showed a 25% decrease in canopy cover, with the more open areas expanding. Fire is a minor problem; three small patches were set alight in Malaza, one east of the central north-south trail in 1998 and the other two on the western edge of the same trail in 2006, all were quickly extinguished by watchful guardians and reserve staff.

This present study sets out to provide a background for forest restoration. Several restoration methods have been developed and most approaches involve planting tree seedlings, but many tree planting projects fail, due to the planting of inappropriate species, inadequate planting techniques and post-planting maintenance regimes, particularly when using native tree species about which little is known. Although most of these applications have been in humid tropical zones, some of the lessons learned can be carried over to dryland reforestation: principally, investigation of the reasons for forest degradation, the importance of a preliminary survey of the target forest and the advisability of an initial planting program to trial different cultivation practices [11]. The first two of these reasons are the main objects of this study: an investigation of the reasons for forest decline and a vegetation survey to assess the existing balance of species in the gallery forest and identify what intervention may be needed to support or accelerate regeneration. The long-term aim is to arrest the decline of the continuous canopy forest and restore biodiversity levels to those typical of the remaining forest fragments, thus conserving key resources for the lemurs and other endangered fauna.

## 2. Methods and Materials

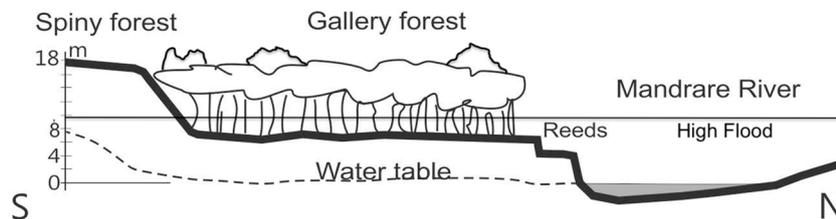
### 2.1. Study Area

Berenty lies 25 km from the southern coast ( $25^{\circ}00' 35.50'' 18' 28.50''$  E) and west of the coastal range in a relative rain shadow with average annual precipitation of 500 mm (Figure 1). Cyclones affecting southern Madagascar occur intermittently [12], but the forest structure, with an approximately uniform canopy height and the deep taproots of the tamarinds, is well adapted to resist cyclone events.



**Figure 1.** Precipitation map with isohyets (mm), with inset of Berenty precipitation data: note the exceptional flood in 1971. Data courtesy of Mr Rakotomalala, Berenty.

There are three main forest areas in the reserve, Malaza, Ankoba and Bealoka, and each have different management histories [13]: Malaza, covering approximately 100 ha is located on the floodplain on an outside bend of the Mandrare River where grazing has been excluded since 1936. A 10 m high ancient river terrace backed by spiny forest defines part of its southern boundary (Figure 2).



**Figure 2.** Generalised north-south cross section of Malaza forest showing the river at average annual low-flow, bank-side growth of reeds (*Phragmites mauritianus*) on a lower terrace frequently eroded by floods, height of intermittent high floods (in 1971 up to 1.5 m above forest floor) and an upper, ancient terrace rising up to 10 m above the gallery forest floodplain.

Tourist amenities and fields encompass the remaining perimeter. Dry ancient river channels and sandbars dissect the forest floor. Tree cover within the forest varies from dense tamarind forest, at its

densest along the riverbank, to open scrub and grassland interspersed with impenetrable thickets of thorny scrub, with *Capparis sepiaria* and *Azima tetracantha* among the most common. Plant species beginning to invade the open areas include *Agave sisalana* and *Opuntia monacantha* [14], used as a defence to keep cattle out of the reserve, but the most prolific invasive species is the succulent African vine, *Cissus quadrangularis*, growing wherever there is sunlight, climbing in great suffocating waves to the tops of isolated trees.

Ankoba, joined by a forest corridor to Malaza, is a 15 ha patch of mature secondary-growth forest. It was originally farmed by the locals and then used as a sisal nursery. In the 1950s it was allowed to revert to forest, with the addition of exotic *Pithecellobium dulce* [15] (p. 34). Bealoka, where grazing has been excluded since 1985, lies 4.5 km to the northwest and covers around 110 hectares. It is separated from Ankoba by Berenty village and sisal fields. Not included in this study are Rapily/Analalava, a 60 ha disjointed strip of spiny forest south of Malaza and Anaramalangy, a 45 ha patch east of Malaza once abandoned to *Cissus*, but now being cleared.

## 2.2. Objectives

The field work has three main objectives: the first is to establish why the forest is shrinking; the second is to carry out a vegetation survey, including names of the most common trees for eventual restoration, and the third is to investigate riverbank erosion rates to determine if the forest riverside margin is threatened. A further objective is an analysis of the soil composition across the Malaza floodplain, since for any eventual forest restoration an understanding of the organic, mineralogical, pH and moisture content of the soils is essential.

## 2.3. Tree Age

A random sample of 48 trunk circumferences was measured in Malaza and Ankoba at 95 cm height; eleven stem cores were taken, at the same height, with a 10 mm increment-boring tool. Only three of the cores reached the central pith due to exceptional wood hardness (we broke two boring tools). The cores were dried, mounted and fine-polished until the annual ring widths were clearly visible. Ring widths were measured using the LINTAB system and TSAP-Win software [16,17]. To find tree age in the reserve, tamarind circumference measurements were converted to radii and each radius divided by the average ring-width value. This provides tree age above the coring position; to find true age, years of growth below the core must be added to the ring count: a mean growth rate was derived from nine seedlings and saplings from 3 to 337 cm tall, aged one to 18 years, taken from a range of environments across the reserve.

## 2.4. Vegetation Survey

The main vegetation areas were surveyed using the rapid site assessment approach for data collection recommended by Elliott et al. [18] (pp. 72–77; 124). The procedure, defining five stages outlining the health of a forest, is designed as a broad-brush approach for assessing levels of forest degradation to aid the determination of the most suitable restoration strategy. However, the five stages are designed for the analysis of forests that have suffered most from human intervention. At Berenty, Malaza the main forest, has been protected from outside disturbance since the 1930s and thus the decline in forest cover here may mainly be due to natural causes and only the first three of Elliott's stages were considered relevant. Saplings and small trees, under 30 cm girth but over 50 cm tall, are termed 'regenerants' by Elliott et al. [18] (p. 72):

- Stage 1: at least 25 regenerants per circle, few shrubs and grasses and a high number of tree seedlings.
- Stage 2: at least 25 regenerants per circle, a moderate to low cover of shrubs and tree cover that is frequently insufficient to shade out the grasses. Large-tree numbers are declining as are seedling numbers.

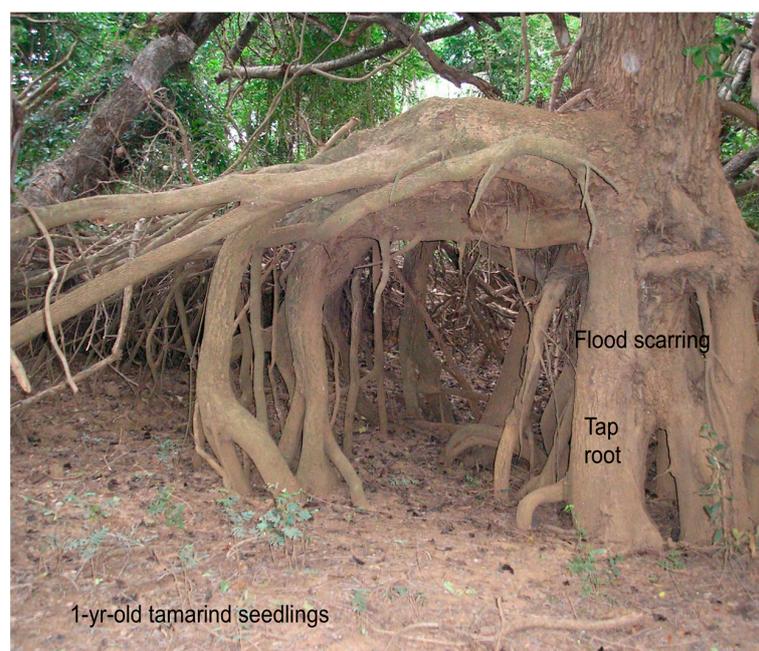
- Stage 3: fewer than 25 regenerants per circle, shrubs and grasses dominate, large trees are rare and seedling numbers are greatly reduced.

The vegetation survey was based on transects laid out on set compass bearings, with 10 m diameter circles established every 25 m. To avoid edge effects [19], wherever possible circles were initiated 20 m from any trail or path. The circles were defined using 5 m lengths of cord attached to a central pole. We aimed to include 10 circles per transect (i.e., 250 m), but a number of transects were shorter due to the thorny impenetrability of the undergrowth.

Within each circle, as well as regenerants, we recorded the number of trees with stems over 30 cm girth at breast height (large trees) and numbers of seedlings under 30 cm tall. Tamarind seedlings were counted separately as these have been of particular interest in previous studies [9,20]. Lianas and vines were classified as few, moderate or many (0–4; 5–9; 10<). The percent cover of shrubs and grasses was estimated as low, moderate or high, with their measured height range, and the percent cover of bare soil and numbers of dead trees. The short transect, T2, following a line of dead trees was included to see if this made a difference as regards forest growth.

### 2.5. Riverbank Erosion and Roots

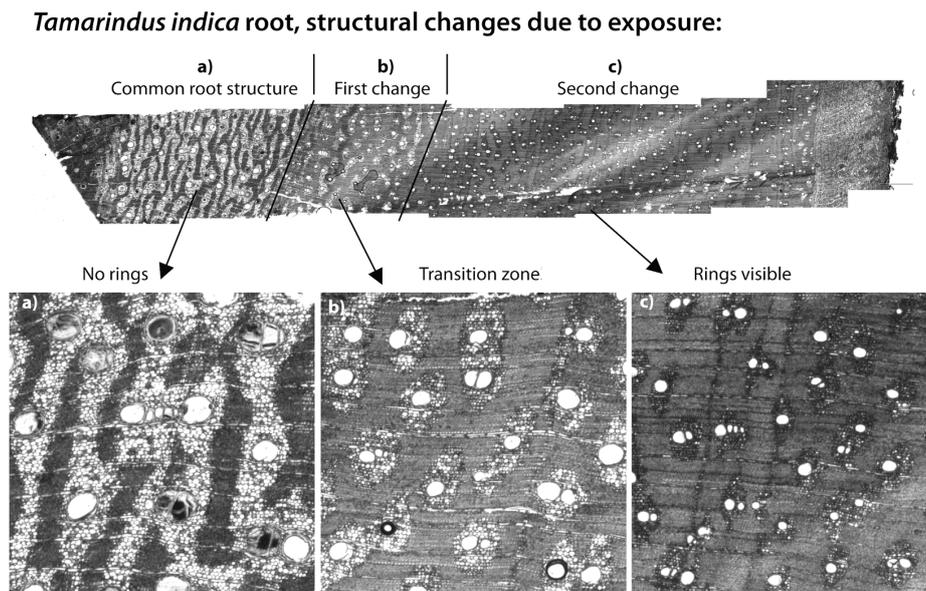
The extent of canopy cover could also be threatened by riverbank erosion (Figure 3).



**Figure 3.** Bank-side tamarind roots exposed by floods at Ankoba. Flood dates and rates of erosion can be estimated from anatomical changes in roots damaged by catastrophic flooding.

Incipient bank erosion can be dated from the year root cells become more stem-like with smaller and more densely packed thicker cell walls, providing more rigid support (Figure 4) [21]. Sections cut from damaged roots similarly provide a date for exposure, with this defined by the ring dating the year of damage [22]. Average annual erosion rates were calculated by dividing the distance from the damaged root to the eroded bank by the number of years since damage occurred.

Fifteen damaged roots were sectioned and dried in the sun, fine-polished in the laboratory and examined under a microscope, with a camera attachment for details and a high-resolution scanner used to view whole sections. This is an important necessity since annual rings may only be seen in part of a section due to trauma or wound callusing and may be eccentric in relation to root centres. Micro-sections were cut from some of the roots using a GSL1 microtome [23].



**Figure 4.** Root micro-section tamarind root sample from the eastern end of the Malaza riverbank. Structural changes due to gradual exposure: (a) Common root structure; (b) First structural change: root potentially close to the surface but not exposed; (c) Second structural change, root fully exposed.

## 2.6. Soil Analysis and Leaf Identification

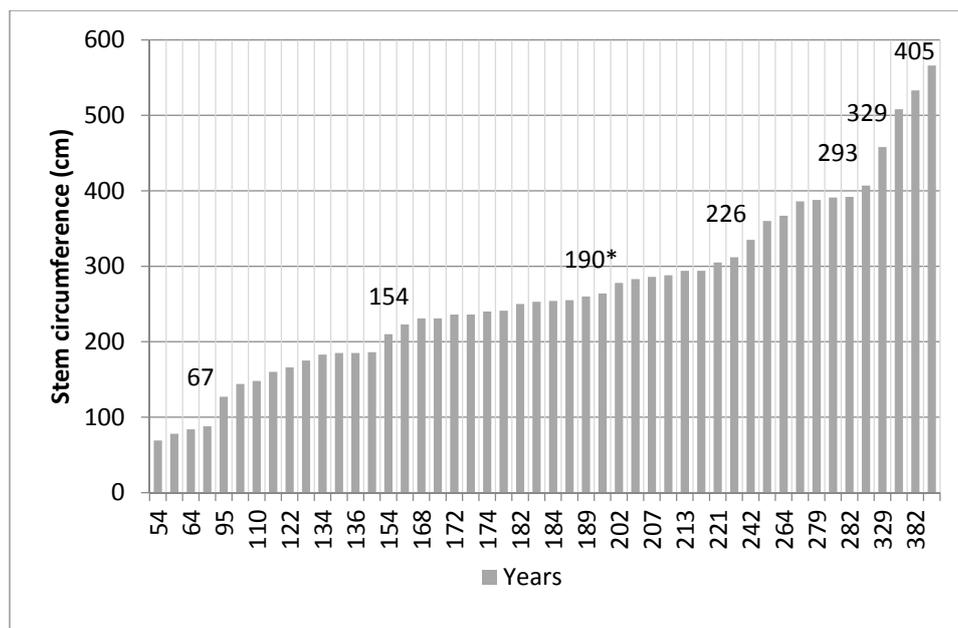
A total of twenty-four soil samples were taken, at 25 cm below leaf litter, from the transects and also from the river bank, mid-forest and in the degraded area. These were analyzed in Oxford to provide information on the suitability of the forest soil for seedling transplantation. For chemical analysis, a Dionex IC DX500 Chromatograph was used for determination of organic and inorganic ions using 1 g soil in 100 mL water. Iron was analysed using atomic spectroscopy, with 2 g in 10 mL EDTA 0.05 M. The organic content was calculated using the loss on ignition (LOI) method, with a sample size of 2 g dry weight and exposure time of 5 h at 550 °C [24]. A Malvern Master-sizer 2000, with the programme Gradistat, was used for soil particle size analysis [25]. Three soil samples were taken, also at 25 cm depth, to provide moisture measurements.

Identification of tree species was a priority. Specimens of each species were collected and dried and given their local names on site by the chief forest guardian Mr Remanonja, while Latin names were provided by Professor Rasamimanana. The specimens were then compared with a photographic collection left by a previous researcher. Specimens were mounted in a book and given to botanists at the Kew Madagascar Conservation Centre in Antananarivo for future reference and a photographic record was sent to botanists at the Muséum National d’Histoire Naturelle (MNHN) in Paris.

## 3. Results

### 3.1. Tree Age and Regeneration

Tree ages were derived from a combination of two values: an average core ring-width measurement of 0.225 cm, with this value agreeing with that obtained from a nine-year direct growth study [26], and an average value of five years extrapolated from a mean growth rate of 18.7 cm/year, below coring height. A histogram of the age structure of the tamarinds shows that two of the trees from Ankoba, at the lowest end of the distribution, are 54 and 67 years old, while the central cohort sampled in Malaza is aged between 154 and 226 years, with a median age of 190 years (Figure 5); the four trees in the upper range are aged from 323–405 years. On the forest floor, there are large numbers of one-year-old tamarind seedlings, but no young saplings: this does not, however, extend to lower canopy species, which regenerate plentifully under tamarinds.



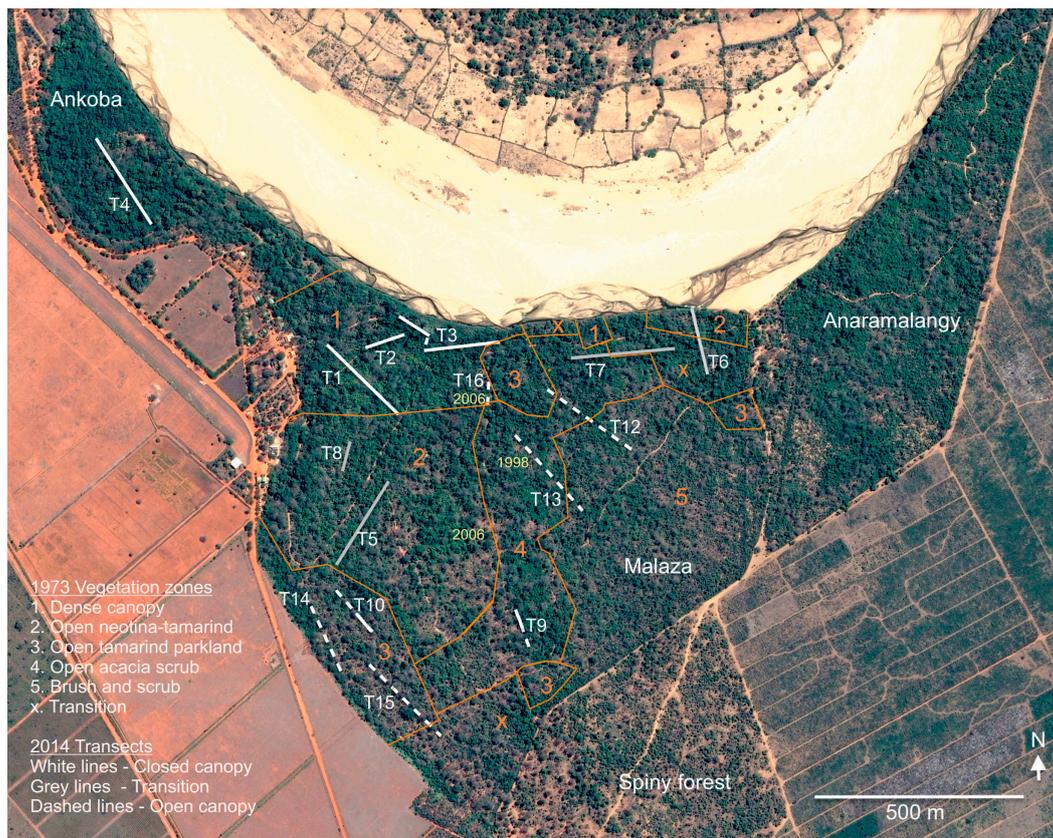
**Figure 5.** Tamarind tree age in Ankoba and Malaza. Note that exceptionally advantaged trees can attain ages between 300–400 years; whereas the usually accepted age is 200 years. 190\* is the median age in Malaza of the central cohort (154–226 years).

### 3.2. Vegetation Survey

Figure 6 shows the positions of the transects carried out in 2014, together with the outlines of the 1973 vegetation zones, as drawn by Blumenfeld-Jones [8] (p. 73), superimposed over a Google Earth June 2013 view of the forest. Comparison of the 1973 zones with the 2013 vegetation suggests that, at the scale of the 2013 satellite view, zone 1 appears relatively unchanged, despite the 25% decrease in canopy cover described by Blumenfeld-Jones [8] (p. 81); by 2013 half of zone 2, and large areas of 3 and X have fragmented together with the southern end of zone 4. Zone 5 has expanded north into zone 4 and into the smaller zone 3 areas, with almost no big trees and an extensive cover of shrubs, vines and grasses.

The positions of the three areas burnt in 1998 and 2006 show that the vegetation has to some extent regenerated over the interval, with the scar left by the 1998 fire reduced in size (it formerly covered almost a hectare), the small 2006 fire nearest the river is recovering and only the 2006 fire in the centre of the forest is still open.

In Table 1, the transects, listed in descending order of the average number of large plus small (regenerant) trees, illustrate the three stages defining the health of the forest [18]. Regeneration is at its highest under the continuous canopy of stage 1, apart from an extraordinary number of small trees in T9, an old riverbed. Average small tree numbers are reduced under the stage 2 canopy, but the ratio of small to large trees is at its highest, with this signaling the transitional character of the vegetation, while shrub and grass cover is mostly in the low to moderate range. In stage 3 transects, the low ratio between small and large trees and their overall low numbers highlights the degraded character of the area, with shrub and grass cover moderate to high.



**Figure 6.** View of Ankoba and Malaza with the river at low water. The red lines show the positions of the vegetation zones as defined in 1973. The 2014 transects are numbered and dates mark the locations of the 1998 and 2006 burns. The ‘dogleg’ transect, T3, crosses the riverside trail where it touches the riverbank.

**Table 1.** Rapid site assessment data for transects, divided into 3 stages. The transects are arranged in descending order of average large plus small trees, defined as ‘regenerants’ by Elliott et al. [18]. Regenerants are saplings and small trees <30 cm girth. Short transect lengths are italicized and highlighted. Averages are based on counts per circle in each transect. Standard deviations (SD) indicate considerable variability between circles.

| Malaza<br>1936                          | Ankoba<br>1950            |                |                |                | River<br>bed                |                     |                   |                | Bealoka<br>1985      | Burnt<br>1998       |                |                 | River<br>Bed   | Burnt<br>2006       |                    |                    |
|---|---------------------------|----------------|----------------|----------------|-----------------------------|---------------------|-------------------|----------------|----------------------|---------------------|----------------|-----------------|----------------|---------------------|--------------------|--------------------|
| <i>Transect</i>                         | 1                         | 3              | 3              | 4              | 5                           | 6                   | 7                 | 8              | 9                    | 10                  | 11             | 12              | 13             | 14                  | 15                 | 16                 |
| Length (m)                              | 250                       | 250            | 250            | 250            | 250                         | <b>150</b>          | 250               | 75             | <b>100</b>           | 125                 | 250            | 250             | 250            | 225                 | 250                | <b>50</b>          |
|   | STAGE 1—continuous canopy |                |                |                | STAGE 2—transitional canopy |                     |                   |                | STAGE 3—open dryland |                     |                |                 |                |                     |                    |                    |
| <b>Average large + regenerants – SD</b> | 80<br>21.0                | 61.7<br>12.8   | 58.9<br>20.6   | 55.7<br>11.5   | 46.8<br>21.9                | 46<br>12.2          | 40.9<br>12.6      | 37.6<br>1.9    | 37.2<br>27.1         | 35.2<br>14.9        | 33.0<br>13.9   | 13.1<br>9.3     | 14.7<br>12.4   | 14<br>9.3           | 13.8<br>9.2        | 9.5<br>3.5         |
| Average large trees (>30 cm girth) – SD | 7<br>5.4                  | 9.7<br>4.0     | 7.3<br>2.9     | 6.9<br>3.0     | 4.0<br>2.4                  | 4.5<br>1.6          | 3.1<br>2.0        | 2.6<br>0.9     | 1.5<br>0.5           | 3<br>2.6            | 4.4<br>2.0     | 2.9<br>5.4      | 1.8<br>2.7     | 1.9<br>1.8          | 2<br>1.7           | 2<br>2.0           |
| Average regenerants (<30 cm girth) – SD | 73.1<br>20.1              | 52<br>13.9     | 51.6<br>20.3   | 48.9<br>1.9    | 42.8<br>22.7                | 41.5<br>11.7        | 37.8<br>12.2      | 35<br>1.6      | 35.7<br>27.0         | 32.2<br>12.5        | 28.6<br>12.4   | 10.2<br>8.4     | 12.9<br>10.8   | 12.1<br>8.4         | 11.9<br>8.0        | 7.5<br>1.5         |
| Average all seedlings (<50 cm ht)       | 22.9                      | 35.0           | 34.5           | 40             | 17.3                        | 32.8                | 32                | 19.6           | 54.3                 | 17.2                | 27.2           | 3.7             | 2.4            | 13                  | 8.2                | 2.5                |
| Average tamarind seedlings              | Not counted               | 8.5            | 11.7           | 8.4            | 0.2                         | 2.5                 | 0.9               | 0.6            | 27                   | 0.6                 | 9.5            | 0.2             | 0.1            | 3.9                 | 0.3                | 0                  |
| Shrub cover ht range (cm)               | low<br>10–200             | low<br>100–150 | low<br>7–150   | low<br>10–200  | low/mod<br>15–200           | low/high<br>130–800 | low/mod<br>30–200 | low/mod<br>200 | low/mod<br>50–150    | mod/high<br>200–250 | low<br>20–200  | mod<br>25–200   | mod<br>30–200  | mod/high<br>100–300 | mod<br>100–200     | low/high<br>70–150 |
| Lianas/vines nos of circles.            | Few<br>1<br>3             | mod<br>3       | many<br>7<br>1 | many<br>7<br>2 | many<br>3<br>6              | many<br>1<br>4      | many<br>1<br>6    | many<br>1<br>3 | many<br>3<br>6       | many<br>1<br>4      | many<br>2<br>6 | many<br>6<br>4  | many<br>4<br>5 | many<br>2<br>6      | many<br>7<br>1     | many<br>1<br>1     |
| Grass cover % ht-range (cm)             | low<br>5–10               | low<br>0–10    | low<br>5–10    | low<br>5–20    | low/mod<br>10–50            | low/high<br>0–10    | low/high<br>5–150 | high<br>10     | low/high<br>15–75    | mod<br>15–100       | low5<br>–15    | high<br>100–150 | high<br>5–500  | low/mod<br>5–100    | mod/high<br>20–280 | high<br>30–40      |
| Bare soil % cover                       | 3.2                       | 0              | 1              | 0              | 0.5                         | 4                   | 0                 | 0.2            | 0.1                  | 0.1                 | 0.9            | 4.7             | 2              | 0.1                 | 2.5                | 1                  |
| Dead trees                              | 11                        | 6              | 1              | 12             | 8                           | 4                   | 7                 | 2              | 4                    | 8                   | 5              | 9               | 10             | 0                   | 3                  | 0                  |

(i) On each transect, circles of 10 m diameter are spaced 25 m apart; (ii) Shrub and Grass cover %: low = 0–33%; moderate = 34–66%; high = 67–100%; (iii) Lianas and vines (principally *Combretaceae* and *Cissus*) in circles: few = 0–4; moderate = 5–9; many = 10+.

Comparison of the average number of seedlings in each of the three stages is also indicative of stage: highest in stage 1 areas, including T2, where a line of acacia trees was blown down in a wind storm in 1999 [27] and lowest in the degraded open dryland. In stage 2, the T9 riverbed is again an exception with an extraordinary number of seedlings of all species, but otherwise seedling numbers are variable. The average tamarind seedling numbers are generally moderate to low in the other stages. Of note is that despite the eight years difference between the two burns, covered by transects T13 and T16, they contain closely similar seedling counts, with only one tamarind seedling in T13 and none in T16. Grass and shrub cover is least in stage 1 but variable elsewhere, while percentages of bare soil follow no pattern.

Figure 7 presents the data as a graph showing averages of both small and large trees declining across the stages, as expected given the sampling criteria. Shrub and grass cover under the dense canopy of stage 1 is low as is shrub cover for half of the transitional stage 2, although the presence of grass here is highly variable. In stage 3, shrubs and grasses (mainly *Panicum maximum*) dominate. The incidence of dead trees, peaking in T2 and T10, is also highly variable showing no pattern. Vines and lianas could not be quantified due to sampling difficulties.

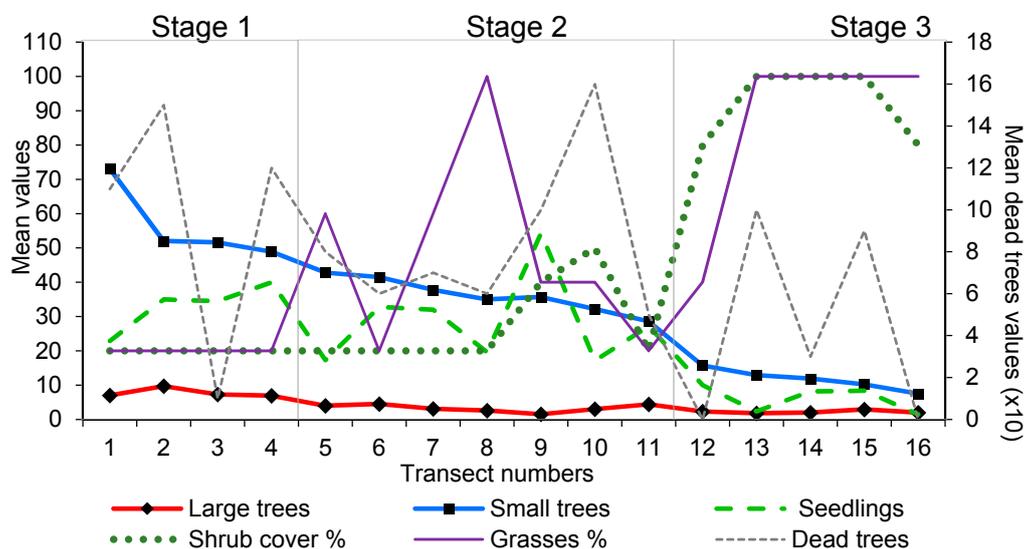


Figure 7. Graph of the data from Table 1 showing the inter-relationship of the six main factors across the three stages.

In Table 2, species are listed in descending order of percent occurrence in all transects in each vegetation type: continuous canopy, transitional and dryland. Other species are doubtless present, but are insufficiently common to occur in any of the transects (for example, there are a number of *Ficus* spp. found elsewhere in Malaza). The single record of *Cordia caffra* (a native from mainland Africa) suggests that the species is not yet a threat to the mainly endemic tree population in the forest and probably never will be since the presence of large specimens in the tourist precinct imply that the species has been in the area for some time. Table 2 also shows that *Euphorbia* does not grow under the continuous canopy and that *Salvadora angustifolia* is the only one of the listed species to grow solely in the dryland area. Not shown in the table, but also growing in the dryland, are several species from the spiny forest including sisal (*Agave sisalana*) from the nearby fields and a thick growth of tall grasses, thriving even beside the narrower trails wherever there are openings letting in light.

**Table 2.** Transect tree species classified according to habit and habitat. Short transects are highlighted.

| Transect (T)                      | 1              | 2   | 3   | 4   | 5              | 6   | 7   | 8   | 9   | 10  | 11  | 12             | 13  | 14  | 15  | 16  | %        |
|-----------------------------------|----------------|-----|-----|-----|----------------|-----|-----|-----|-----|-----|-----|----------------|-----|-----|-----|-----|----------|
| <b>DRYLAND</b>                    | <b>STAGE 1</b> |     |     |     | <b>STAGE 2</b> |     |     |     |     |     |     | <b>STAGE 3</b> |     |     |     |     |          |
| <i>Enterospermum*</i>             | x              | x   |     | x   | x              | x   | x   | x   | x   | x   |     | x              | x   | x   | x   | x   | <b>7</b> |
| <i>Strychnos madagascariensis</i> | x              | x   | x   | x   |                | x   | x   | x   | x   | x   | x   | x              | x   | x   |     |     | <b>7</b> |
| <i>Euphorbia*</i>                 |                |     |     |     | x              | x   |     | x   | x   | x   | x   | x              |     | x   | x   |     | <b>5</b> |
| <i>Hazunta modesta</i>            | x              | x   |     | x   | x              |     | x   | x   |     |     | x   | x              |     |     | x   |     | <b>5</b> |
| <i>Grewia*</i>                    |                |     |     | x   | x              |     | x   |     |     | x   |     | x              | x   |     | x   |     | <b>4</b> |
| <i>Salvadora angustifolia</i>     |                |     |     |     |                |     |     |     |     |     |     | x              | x   | x   | x   |     | <b>2</b> |
| <b>LOWER CANOPY</b>               |                |     |     |     |                |     |     |     |     |     |     |                |     |     |     |     |          |
| <i>Celtis philippensis</i>        | x              | x   | x   | x   | x              | x   | x   | x   | x   | x   | x   | x              | x   | x   | x   | x   | <b>8</b> |
| <i>Rinorea greveana</i>           | x              | x   | x   | x   | x              | x   | x   | x   | x   | x   | x   | x              | x   | x   | x   | x   | <b>8</b> |
| <i>Crataeva excelsa</i>           | x              | x   | x   | x   | x              | x   | x   | x   | x   | x   | x   | x              | x   | x   | x   | x   | <b>8</b> |
| <i>Quisioianthe papinae</i>       | x              | x   | x   | x   | x              | x   | x   | x   | x   |     | x   | x              |     | x   | x   | x   | <b>7</b> |
| <i>Celtis bifida</i>              | x              | x   | x   | x   |                |     | x   |     |     |     | x   | x              | x   | x   | x   |     | <b>6</b> |
| <i>Rubiaceae sp. **</i>           | x              | x   | x   | x   | x              | x   | x   | x   |     |     |     | x              |     |     | x   | x   | <b>6</b> |
| <i>Tricalysia sp. **</i>          | x              | x   | x   | x   |                |     |     |     |     |     |     | x              |     | x   |     | x   | <b>4</b> |
| <i>Celtis gomphophylla</i>        |                |     |     | x   |                |     |     |     |     |     | x   |                |     |     |     |     | <b>1</b> |
| <i>Cordia caffra</i>              |                |     |     |     |                |     | x   |     |     |     |     |                |     |     |     |     | <b>-</b> |
| <b>UPPER CANOPY</b>               |                |     |     |     |                |     |     |     |     |     |     |                |     |     |     |     |          |
| <i>Tamarindus indica **</i>       | x              | x   | x   | x   | x              | x   |     |     | x   | x   | x   | x              | x   | x   | x   |     | <b>7</b> |
| <i>Albizia polyphilla</i>         | x              | x   | x   | x   | x              | x   | x   |     |     |     | x   | x              |     | x   |     |     | <b>6</b> |
| <i>Neotina isoneura</i>           | x              | x   | x   | x   | x              |     |     | x   |     |     | x   |                |     | x   | x   | x   | <b>5</b> |
| <i>Acacia roovumae</i>            | x              |     | x   | x   |                |     | x   |     |     | x   | x   |                |     | x   | x   | x   | <b>5</b> |
| <b>TOTAL SPECIES</b>              |                |     |     |     |                |     |     |     |     |     |     |                |     |     |     |     |          |
| Dryland species                   | 3              | 3   | 1   | 4   | 4              | 3   | 4   | 4   | 3   | 4   | 3   | 6              | 4   | 4   | 5   | 1   |          |
| Lower canopy                      | 7              | 7   | 8   | 7   | 5              | 5   | 6   | 5   | 4   | 4   | 6   | 7              | 4   | 6   | 5   | 7   |          |
| Upper canopy                      | 4              | 3   | 4   | 4   | 3              | 2   | 4   | 1   | 1   | 4   | 3   | 2              | 2   | 4   | 3   | 1   |          |
| <b>AVERAGE spp./circle</b>        | 1.4            | 3.2 | 1.3 | 1.5 | 1.2            | 1.6 | 1.4 | 3.3 | 2.0 | 2.4 | 1.2 | 1.5            | 1.1 | 1.4 | 1.3 | 4.5 |          |

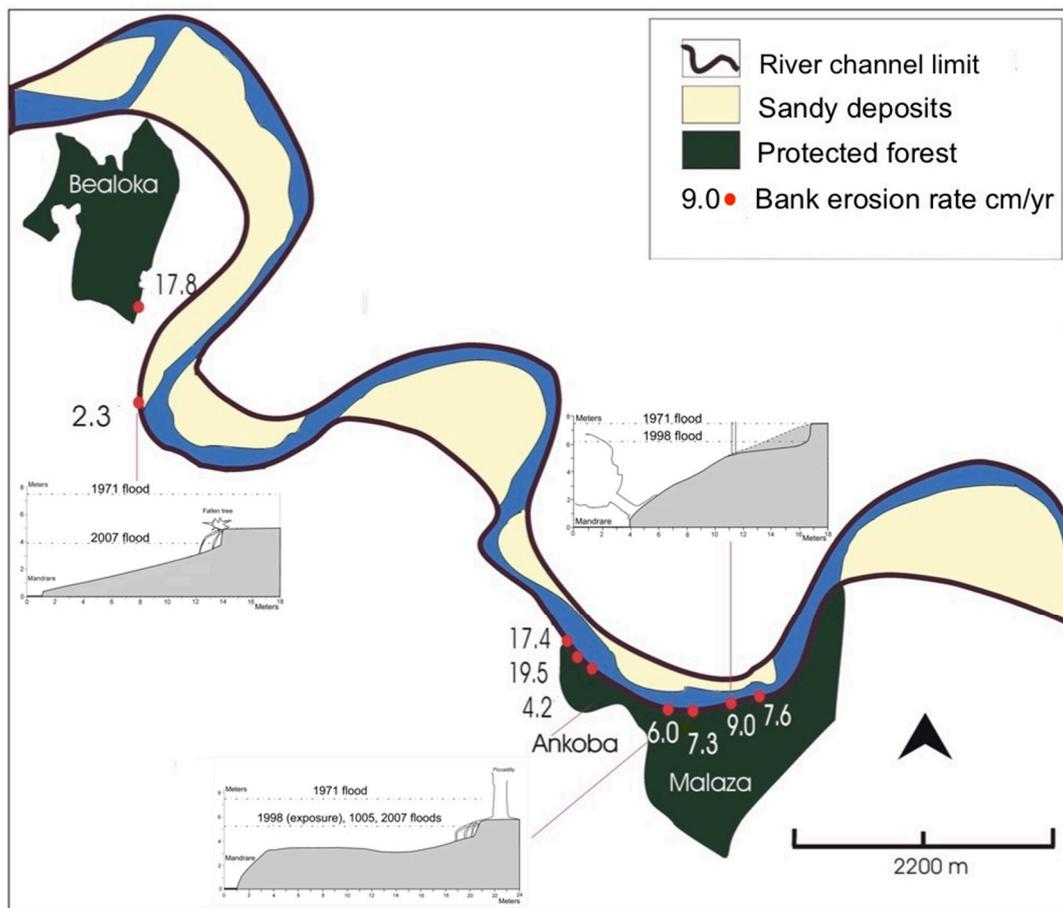
Average canopy height: dryland—10 m; lower canopy—12 m; upper canopy—20 m. \* At least two species; \*\* Species that are native but probably not endemic; -*Cordia caffra* is non-native and should not be planted in forest; %Guide as to the relative percentage of species to plant to approximate the distribution of species in the natural; ecosystem

### 3.3. Riverbank Erosion

Root section ring counts show damage in three main flood years since 1998 (Figure 8). According to root damage, the bank towards the northern end of Ankoba is the most threatened, with maximum projected erosion of 19.5 cm/year, while on the Malaza bank erosion averages between 6 and 9 cm/year (Figure 9)



**Figure 8.** Tamarind root section from the Ankoba riverbank. The section shows changes in structure from root to stem-type cells after the damage that occurred in the 1998 flood (Figure 9) when the root was first exposed to the air and subsequently during the floods of 2005 and 2007.



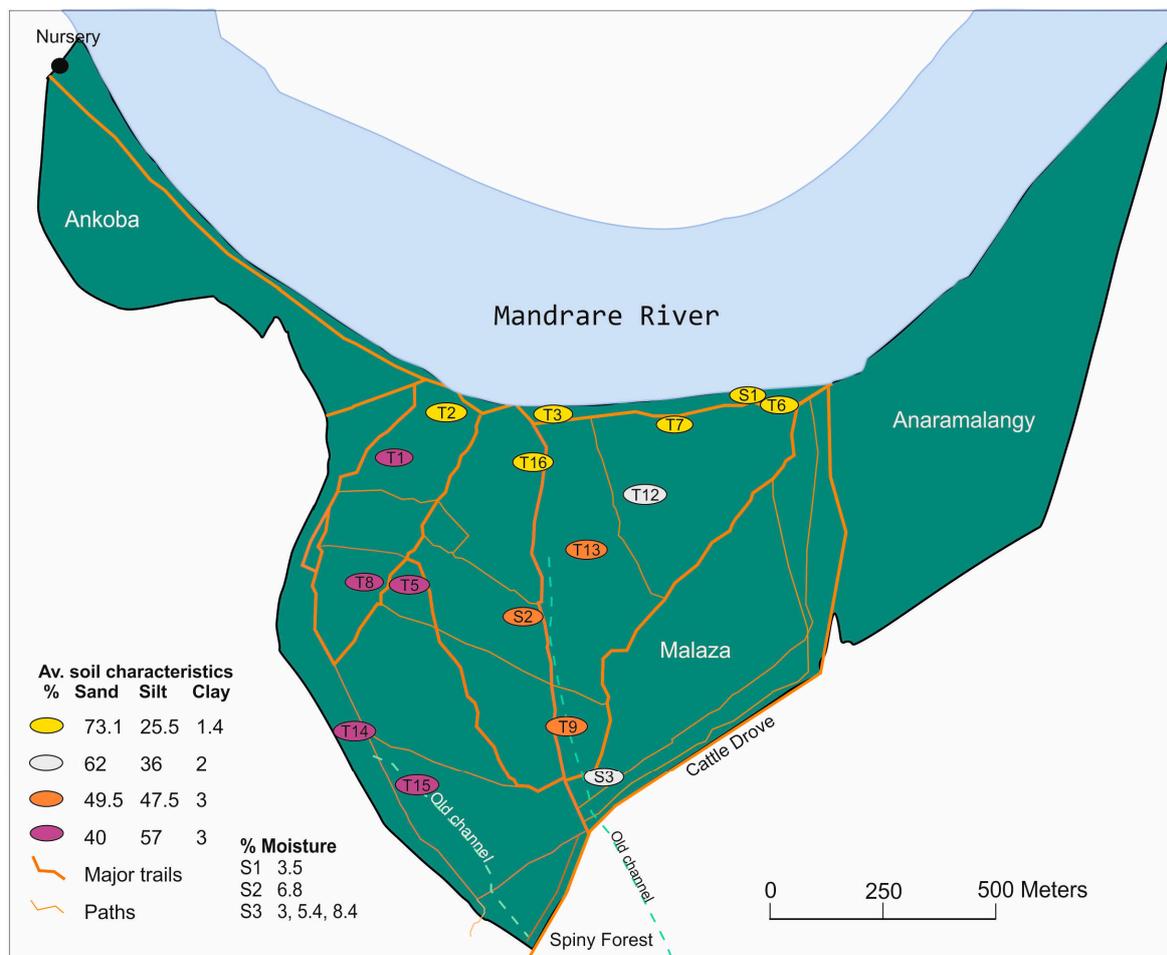
**Figure 9.** Berenty Reserve with the Mandrare river at low water and the range of different bank profiles with dated flood heights: 1971 was the highest flood on record. The local people practice transient cultivation on inside channels and bends.

### 3.4. Soil Analysis

The soils in Malaza can be divided into four domains (Figure 10): riverbank, south, centre-east and west. Near the river, the average sand percentage compared with silt is high and clay is low (73.1%, 25.5%, 1.4%). In two widely separated sites, one within 250 m of the river (T12) and the other near the southern margin in the open area east of the central trail (S3), the sand content is almost twice that of silt, and clay is moderately increased compared with the riverbank (62%, 36%, 2%). In the centre of Malaza, the sand to silt ratio is nearly even and the clay percentage is raised (49.5%, 47.5%, 3%), while on the west side of the forest the percentage of sand is reduced and silt predominates, with clay remaining the same as in the centre (40%, 57%, 3%).

The organic content of the soil averages 12%, with the notable exception of 38% at T9 in the old river channel running beside the central trail where leaf litter is particularly deep; here, as a consequence of the high organic content, cation values are high compared with the other transects influencing the soil's ability to hold onto essential nutrients [28]. Elsewhere anion values are variable from a low of 62 ppm in T11, a dry channel in Bealoka, to 1110 ppm at the start of T3 in Malaza. Other raised values are found in transects T5 and T16.

Levels of salinity are well below concentrations that could reduce growth. They are highest on the riverbank, T3, at 53.3 ppm and T7, at 45.4 ppm. Elsewhere they are within the range 23–43 ppm. Phosphorous at T16 is high (336 ppm compared with an average elsewhere of 55 ppm), with an anomalous pH of 4.4. At all other transects pH values are approximately neutral ranging from 6.5 to 7.6, with most nutrients optimally available and a range highly compatible with plant growth.



**Figure 10.** Soil sampling sites: The T samples are from the 2014 transects and the S1–S3 sites included soil moisture measurements.

Soil readings from T16, the small burnt patch, show an exceptionally low pH and a high phosphate and iron content, with this suggesting that the sample could contain urine; nevertheless, the high average number of tree species on the site, with as yet no upper canopy species, imply that this area is as suitable for seedlings as elsewhere.

Soil moisture measurements show that the driest site is near the river under the continuous canopy at S1, with high sand content. At S2, mid-forest where there was more silt than sand, moisture was over twice that of S1, while S3 showed highly variable results.

#### 4. Discussion

##### 4.1. Tamarind Age and Regeneration

The young ages of 54 and 67 years of the two trees from Ankoba are consistent with the known age of this secondary forest. However, the four trees between 329 and 405 years old (Figure 5) are a surprise, since the generally accepted age for tamarinds is 200 years. Evidently, these trees are growing in exceptionally advantageous locations. The oldest, growing on the edge of a large clearing in Ankoba, which measured 28 m tall, died in 2010 (Alison Jolly personal communication).

Blumenfeld-Jones [8], who detailed canopy changes over a 22-year period (1973–1995), suggests that the whole forest may be in transition to a dryer forest type, with the pattern of change in vegetation boundaries along the eastern section of the riverbank reflecting the overall drying of the forest due to changing dynamics of the river. However, our study of riverbank erosion rates reveals that there have

been only small changes over the period, hence changes in river dynamics are unlikely to have affected the forest. Climate change might be implicated, but the precipitation data (Figure 1) show no trend, with droughts or floods occurring every few years, although warming temperatures may have contributed to drying.

Blumenfeld-Jones also carried out an extensive study of tamarind regeneration [8] (pp. 69–85), she found almost no tamarind seedlings (between 1–2 m tall) growing less than 15 m from large tamarinds and none in canopy gaps around dead tamarinds. She also found that tamarind abundance was uncorrelated with canopy cover or soil type and that young trees tended to grow in clusters in all forest types especially along the sides of the wider trails. Overall, she concludes that young tamarinds mostly survive in scattered patches not already overhung by mature tamarinds: this confirms our findings. The lack of tamarind saplings under mature trees suggests either a toxic effect [29–31] or some other negative plant–soil feedback [32].

Measurement of tamarind annual ring widths revealed widely differing patterns making comparison impossible; hence, neither age decline in ring-width nor climate-related trends could be determined due to ring eccentricity, a common growth feature of older tamarinds.

#### 4.2. *Cissus Quadrangularis*, Pests and Pathogens

*Cissus* is a major problem in the reserve, stifling regeneration especially on the margins of the dense canopy [33,34]. There is no record of when *Cissus* originally arrived in Berenty; evidently it was well established by 1983 when a program of vine clearance was initiated, following which tree growth was found to improve [35]. Nevertheless by 2007, *Cissus* was widespread covering between 50% to 60% of Malaza [15], with this being particularly a problem for regeneration around dense canopy margins and wherever trees are dead or dying and there is full sunlight.

Pests and pathogens, particularly insects and fungi, form a vital part of the ecosystem in any forest [36], but at Berenty there are no obvious signs that they are causing forest decline; although the leaves of individual trees are frequently mined by insects, termites favour the smooth bark of *Neotina* and dying tamarinds are often associated with *Phellinus adamantinus*. This last is a species of wood-rot fungus identified for us by Leif Ryvarden (Botanical Institute University of Oslo) who affirmed that it is not usually pathogenic on living trees.

#### 4.3. Climate

There are no local records of historical temperatures, but meteorological data from Taolagnaro (Fort Dauphin) indicate that since the 1950s annual temperatures have increased by 0.2 °C [37]. This small increase, together with highly variable local rainfall since the 1980s (Figure 1), suggests that if changes in forest cover are climate-related they are more likely linked to vegetation distribution and microclimatic variations than to any changes in regional climate.

River and water table levels vary seasonally and floods are likely to be important in the life cycle of the trees [38]. One of the growth variables for a riverine climate is distance from the river, with riverside vegetation providing shade, evapotranspiration and humid air that, cooling the microclimate, contrasts with the hot dry air over the open areas, the fields and the spiny forest fragments on Malaza's southern and eastern margins. In flood years the river can top its banks and flow over a meter deep across the forest floor (Figures 2 and 9) and although recurrent droughts can be disastrous for lemurs [13], droughts in terms of gallery forest survival are normal. In order to survive, many of the tree species have deep taproots, so that even when the river dries completely their roots can reach the saturated zone below the water table [39].

#### 4.4. Growth Variables

Gallery forests survive as spatial and temporal mosaics at different successional stages, with complex inter-related patterns of cause and effect closely related to micro-environmental variations. The short transect of T2 was included to see if a line of dead trees made a difference

to regeneration, but although *Capparis sepiaria* grows around the dead trunks, growth elsewhere is similar to that in the other stage 1 transects. Otherwise, growth variations are likely to be linked to minor topographic features, for although the forest floor is generally characterised as flat (Figure 2), former river-channels and sandbars have left numerous dips and gentle rises in the floodplain. These channels, containing more leaf-litter than elsewhere will, during high floods, retain moisture for longer than the flatter surroundings providing favourable seedbeds for species regeneration. This is illustrated by the high numbers of seedlings and saplings and few large trees in the T9 channel bed, with this strongly suggesting more frequent floods over recent decades than formerly (Figure 1). Growth in transect T15 along the other old channel further from the river does not appear to have been similarly advantaged.

An additional variable is provided on the western forest boundary by the planting of exotic species to provide cooling shade around the tourist facilities. The presence of this shelterbelt may be one reason why the neighbouring forest can be placed in stage 2 and has not declined to stage 3.

The 3–4 m wide forest trails may also be affecting the microclimate: Rambeloarivony and Jolly [13] remark that temperatures are noticeably higher by the wider trails than in the surrounding forest. In general, wherever the continuous canopy remains intact and 1 m wide trails through the forest are narrow and shaded, the penetration of hot air and light is reduced and vines, shrubs and grasses are largely excluded, but wide trails by providing channels for hot air may hasten forest fragmentation [40].

The generally high species presence in each transect, especially lower canopy species (Table 2), suggests that Malaza, left to regenerate on its own with the only intervention being *Cissus* removal, might eventually recover, but with a warming climate and under the pressure of drying as ageing trees die this could be a race against time.

#### 4.5. Limitations

The choice of where to place transect lines and their lengths was partly controlled by the nature of the undergrowth; wide-scale clearance of prickly shrubs and strangling vines was impractical and thus the representation of the forest as a total ecosystem is incomplete.

Counts of the numbers of young trees in sampling circles were complicated by the growth of multiple stems in ‘clumps’ so that it was unclear if the stems were individual trees or shoots from a single initial stem. We counted all stems, but this could be a mistake since lemurs also eat seedling leaves possibly stimulating new shoots from the root-collar, with this subsequently buried by leaf litter and hidden by the expansion of the root system. The raised count of small trees in T1 may be due to this effect, but the similarities with the assessment data in the other stage 1 transects indicate that the findings are otherwise reasonably representative.

In Table 1, the addition of standard deviations shows the high degree of variability within transects. There was also high variability between circles in shrub and grass cover, but no standard deviations are given because it was impossible to provide realistic percentages due to patchy grass cover and the aerial cover of vines and lianas being often much greater than their ground cover.

A simple count of tamarind seedlings (Table 1) does not include seedling age; the limited size of seedlings suggests that they seldom thrive beyond a year (Figure 3), with this due to an unidentified negative effect. Whatever the cause, the death of tamarind seedlings under the dense canopy has implications for succession.

*Cissus* distribution is under-represented in the data. Although it was recorded wherever it occurred in the transects, we were unable to penetrate the heavily invaded areas and thus the data presented in Table 1, especially in stage 3 areas, do not give a true picture of its prevalence and for that reason *Cissus* is not included in Figure 7. Bare soil was also excluded as a factor of minor importance in Malaza.

Table 2 only shows the presence or absence of species, not their frequencies in each transect. Hence, to some extent this masks differences in forest character. For example, in Bealoka species diversity is similar to that in Malaza at T1 (excluding *Neotina* and *Celtis bifida*), but possibly due to grazing

history, trees are more widely spaced resulting in this transect being placed at the lower limit of stage 2 (Table 1). The main difference is that in the Malaza bank-side forest mature tamarinds predominate compared with T4 in Ankoba and T11 in Bealoka where canopies are more open. However, the high number of tamarind seedlings in Bealoka suggests that, if this forest remains protected and is kept clear of *Cissus*, a continuous tamarind canopy might develop in time, with this signaled by the growth of tamarind saplings.

We classified tree growth in Table 2 as dryland, lower and upper canopy rather than “pioneer” and “climax” as recommended by Elliott et al. [18] (p. 46) since there is no information on the growth characteristics of the endemic species of the region. Hence, our definitions apply to habit and habitat rather than species position in succession.

#### 4.6. Future Intervention and Work

In Malaza and Bealoka, the de Heulme family have already established a programme of systematic clearance of *Cissus quadrangularis*, with work starting from *Cissus*-free areas and working towards the more infested areas. *Cissus* requires light and does not grow under a dense canopy. However, even in the ‘clean’ areas, these forests will need to be regularly searched to remove any new invasions since *Cissus* can re-sprout from the smallest fragments. In the long term, the battle can only be won by persistent clearance and the planting of trees to out-shade the vine.

Minimum intervention termed “accelerated natural regeneration” by Elliott et al. [18] (pp. 118–123) in stage 2 areas, could include weeding of grasses and clearance of competing shrubs. The list in Table 2 suggests areas where species are missing that could benefit from addition of seedlings. For example, tamarind (in T8), *Neotina* (T6, T7, T9, T10) and *Acacia* (T5, T6, T8, T9, T10). A further intervention that could moderate hot air invasion in Malaza could be to plant upper canopy species where these are lacking to shade the wider trails.

Other topics for future work could include a comparison of temperature differences beside wide and narrow trails in relation to vegetation and a controlled nursery study of the reasons for tamarind seedling inhibition under the tamarind canopy; measurement of seedling growth in the nurseries; and, if feasible, regular measurement of water table levels in the nursery water well for comparison with the precipitation data gathered at Berenty; and finally a more extensive survey of the forest’s tree species and continuation of the specimen collection for future reference.

Large-scale reforestation in the degraded areas should be preceded by an experimental planting trial lasting at least three years to investigate optimum planting distances and growing conditions, species inter-relationships and soil conditions for the native trees [18]. For the planting trial and eventual reforestation, two tree nurseries have been established with enough space to propagate tree seedlings: Table 2 provides guidelines as to the approximate percentages of seedlings to plant for reforestation.

### 5. Summarizing Remarks

Our 2014 survey enabled us to divide the forest into three vegetative stages: continuous canopy, transitional canopy and open dryland. The decline in forest canopy cover in Malaza, although largely protected from human interference, results from a combination of three major factors: senescence of tamarind, the dominant tree species; a lack of its regeneration under the canopy; and the invasion in open spaces of the exotic vine, *Cissus quadrangularis*.

- Firstly, almost 50% of the tamarinds in Malaza are nearing the accepted 200-year life span of the species, although this study finds that exceptionally advantaged specimens can live twice as long (Figure 5).
- Secondly, the loss of ageing tamarinds and lack of tamarind regeneration under the continuous canopy will lead to changes in vegetation character. Either lower-canopy species will predominate, with *Neotina*, *Acacia*, *Albizia* and the occasional surviving tamarind providing a thin upper canopy (as in our Stage 2 zone); or

- thirdly, wherever there are large sunlit gaps *Cissus* will invade and overwhelm all seedlings and young trees, as is currently occurring in stage 3 areas and increasingly in stage 2 (Figure 6).

Table 1 illustrates the decline in canopy cover (average large plus small trees) across the three stages, with seedling survival particularly challenged in stage 3 areas. The high variability both within and between transects is likely related to microhabitat variations especially as regards dead tree locations, trails or former river channels, with T9 a particular example of an old channel with deep leaf litter that has recently become highly favourable for plant growth as witnessed by the exceptional number of saplings and seedlings, but few mature trees.

Table 2 supplies a list of the most common tree species for planting in a recommended three-year experimental planting trial. Such a trial is mandatory to avoid costly and time-consuming mistakes and to ensure that the integrity of the forest remains uncompromised before attempting any larger-scale reforestation. It is intended that the selection of common native trees will, in time, form a nucleus for the repopulation of the forest with ecological processes and functions matching those of the existing continuous canopy areas [18] (pp. 124–125).

Although riverbank erosion rates between 2.3 and 19.5 cm/year indicate that the forest is not immediately at risk from erosion, tamarind regeneration along the riverbank [41] provides a slim margin for re-growth at best, with seedlings and young trees caught between damaging flood events, embracing reeds and the negative effect of overhanging mature tamarinds (Figure 3). The problem is that the gallery forest at Berenty is limited to the existing area since riparian sites outside the reserve are used by the local people for transient cultivation and thus the forest cannot evolve along the riverbank over time. Hence, the urgent need for planting trials to provide a basis for forest restoration.

Soil characteristics, although variable, are supportive of plant growth. Sand predominates near the riverbank, where coarse particles are the first to be deposited by fast-flowing floodwaters, while the fine particles of silt and clay are held in suspension and deposited where flooding has lost its impetus over the western and southwestern reaches of Malaza. The open dryland areas to the east and around the central trail hold an intermediate soil position suggesting an intermediate position as regards flood deposition, with soil moisture levels reflecting soil composition rather than canopy cover.

According to Tadross et al. [37], climate warming in southern Madagascar is likely to increase, but modelling of temperature and precipitation trends is ill-constrained, being confounded by high inter-annual variability. It is foreseen that Indian Ocean warming is likely to result in fewer but more intense cyclones.

The data gathered in this study are intended to assist development of a restoration strategy in an ecoregion where there is very little information on species growth habits or requirements. If the dense canopy continues to shrink at the rate indicated by Blumenfeld-Jones et al. [8], in twenty years there may be very little forest left for the lemurs; ecotourism will collapse and the de Heaulme family, the local people and the wider world will lose a unique ecosystem.

**Acknowledgments:** Funding for Vanessa Winchester was provided by the Percy Sladen Memorial Fund and the Appleyard fund administered by the Linnean Society of London. The late Alison Jolly contributed to the expenses of Anne Mertl-Millhollen, Hantanarina Rasamimanana, Vanessa Winchester and the students Tolotra Randrianirina and Mirana Ratovolol from the École Normale Supérieure, Madagascar. James Tysell (USA), the students Camille Kaynor and Cassondra Gavazza (University of Oregon) and Dee Wallace (Portland State University), are all warmly thanked for their valiant help in the field as is Mona Edwards of the School of Geography and the Environment, Oxford, (UK) who carried out the soil analysis. Lastly, we thank the de Heaulme family for their support and encouragement during our work at Berenty. Two anonymous referees are thanked for their helpful comments.

**Author Contributions:** Vanessa Winchester conceived, researched and wrote the paper; Holger Gärtner sectioned and photographed the root samples, described the cell structures and assisted at the referee stage. Kate Hardwick and Anne Mertl-Millhollen, contributed ideas, context and wordsmithing. Hanta Rasamimanana, Sahoby Raharison and Janet McCrae all helped in the field work.

**Conflicts of Interest:** The authors declare no conflict of interest.

## References

1. Waeber, P.O.; Wilmé, L.; Ramamonjisoa, B.; Garcia, C.; Rakotomalala, D.; Rabemananjara, Z.H.; Kull, C.A.; Ganzhorn, J.U.; Sorg, J.-P. Dry forests in Madagascar: Neglected and under pressure. *Int. For. Rev.* **2015**, *17*, 127–148. [[CrossRef](#)]
2. Vieira, D.L.M.; Scanot, A. Principles of natural regeneration of dry tropical forests for regeneration. *Restor. Ecol.* **2006**, *4*, 11–20. [[CrossRef](#)]
3. Aronson, J.; Vallauri, D.; Jaffré, T.; Lowry, I.I. PP 2005: Restoring dry tropical forests. In *Forest Restoration in Landscapes: Beyond Planting Trees*; Mansourian, S., Vallauri, D., Eds.; Springer Science + Business Media, Inc.: New York, NY, USA, 2005; pp. 285–290. [[CrossRef](#)]
4. Scales, I.R. The future of conservation and development in Madagascar: Time for a new paradigm? *Madag. Conserv. Dev.* **2014**, *9*, 5–12. [[CrossRef](#)]
5. Seddon, N.; Butchart, S.; Tobias, J.; Yount, J.W.; Rémi Ramanampamonjy, J.; Randrianizahana, H. Conservation issues and priorities in the Mikea Forest of south-west Madagascar. *Oryx* **2000**, *34*, 287–304. [[CrossRef](#)]
6. Sussman, R.W.; Rakotozafy, A. Plant Diversity and Structural Analysis of a Tropical Dry Forest in Southwestern Madagascar. *Biotropica* **1994**, *26*, 241–254. [[CrossRef](#)]
7. Kassi N'Dja, J.K.; Decocq, G. Successional patterns of plant species and community diversity in a semi-deciduous tropical forest under shifting cultivation. *J. Veg. Sci.* **2008**, *19*, 809–820. [[CrossRef](#)]
8. Blumenfeld-Jones, K.; Randriamboavonjy, T.M.; Williams, G.; Mertl-Millhollen, A.S.; Pinkus, A.; Rasamimanana, H. Tamarind recruitment and long-term stability in the gallery forest at Berenty, Madagascar. In *Ringtailed Lemur Biology*; Jolly, A., Sussman, R.W., Koyama, N., Rasamimanana, H., Eds.; Springer Science + Business Media, LLC: New York, NY, USA, 2006; pp. 69–85. ISBN 978-0-387-34126-2.
9. Jolly, A. Berenty Reserve, Madagascar: A long time in a small space. In *Long-Term Field Studies of Primates*; Kappeler, P.M., Watts, D.P., Eds.; Springer-Verlag: Berlin/Heidelberg, Germany, 2012; pp. 1–464. ISBN 978-3-642-22513-0.
10. Budnitz, N.; Dainis, K. Lemur catta: Ecology and Behaviour. In *Lemur Biology*; Tattersall, I., Sussman, R.W., Eds.; Plenum: New York, NY, USA, 1975; pp. 219–236.
11. Kuaraksa, C.; Elliott, S. The use of Asian *Ficus* species for restoring tropical forests ecosystems. *Restor. Ecol.* **2012**, *21*, 86–95. [[CrossRef](#)]
12. Fitchett, J.M.; Grab, S.W. A 66-year tropical cyclone record for south-east Africa: Temporal trends in a global context. *Int. J. Climatol.* **2014**, *34*, 3604–3615. [[CrossRef](#)]
13. Jolly, A.; Koyama, N.; Rasamimanana, H.; Crowley, H.; Williams, G. Berenty Reserve: A research site in southern Madagascar. In *Ringtailed Lemur Biology*; Jolly, A., Sussman, R.W., Koyama, N., Rasamimanana, H., Eds.; Springer Science + Business Media, LLC: New York, NY, USA, 2006; pp. 32–42. ISBN 978-0-387-34126-2.
14. Binggeli, P. Cactaceae, *Opuntia* spp., Prickly Pear. In *The Natural History of Madagascar*; Goodman, S.M., Benstead, J.P., Eds.; University of Chicago Press: Chicago, IL, USA, 2003; pp. 257–268.
15. Rambeloarivony, H.; Jolly, A. Berenty Reserve: Past, Present and Future. In *Leaping Ahead. Developments in Primatology: Progress and Prospects*; Masters, J., Gamba, M., Génin, F., Eds.; Springer Science + Business Media: New York, NY, USA, 2013; Volume 153, pp. 353–359.
16. Rinn, F. Eine neue Method zur Berechnung von Jahrringparametern. Auszug aus der Diplomarbeit. Ph.D. Thesis, Universität Heidelberg, Heidelberg, Germany, 1988; pp. 1–86.
17. Rinn, F. *TSAP-Win Time Series Analysis and Presentation for Dendrochronology and Related Applications*; Version 0.53 for Microsoft Windows; Rinn Tech.: Hedelberg, Germany, 2003; pp. 1–88.
18. Elliott, S.; Blakesley, D.; Hardwick, K. *Restoring Tropical Forests: A Practical Guide*; Kew Publishing: Royal Botanic Gardens, Kew, UK, 2013; pp. 72, 118–125. ISBN 978-1-84246-442-7. Available online: <http://www.forru.org/en/content.php?mid=78> (accessed on 14 November 2017).
19. Harris, L.D. Edge effects and conservation of biotic diversity. *Conserv. Biol.* **1988**, *2*, 330–332. [[CrossRef](#)]
20. Mertl-Millhollen, A.S.; Rambeloarivony, H.; Miles, W.; Kaiser, V.A.; Gray, L.; Dorn, L.T.; Williams, G.; Rasamimanana, H. The influence of tamarind tree quality and quantity on *Lemur catta* behavior. In *Ringtailed Lemur Biology*; Jolly, A., Sussman, R.W., Koyama, N., Rasamimanana, H., Eds.; Springer Science + Business Media, LLC: New York, NY, USA, 2006; pp. 102–118. ISBN 978-0-387-34126-2.

21. Gärtner, H.; Schweingrube, F.H.; Dikau, R. Determination of erosion rates by analyzing structural changes in the growth pattern of exposed roots. *Dendrochronologia* **2001**, *19*, 81–91.
22. Gärtner, H. Tree roots. Methodological review and new development in dating and quantifying erosive processes. *Geomorphology* **2007**, *86*, 243–251. [[CrossRef](#)]
23. Gärtner, H.; Lucchinetti, S.; Schweingruber, F.H. New perspectives for wood anatomical analysis in Dendrosciences: The GSL1-microtome. *Dendrochronologia* **2014**, *32*, 47–51. [[CrossRef](#)]
24. Heiri, O.; Lotter, A.F.; Lemcke, G. Loss on ignition as a method for estimating organic and carbonate content in sediments: Reproducibility and comparability of results. *J. Paleolimnol.* **2001**, *25*, 101–110. [[CrossRef](#)]
25. Ryzak, M.; Bieganski, A. Methodological aspects of determining soil particle-size distribution using the laser diffraction method. *J. Plant Nutr. Soil Sci.* **2011**, *174*, 624–633. [[CrossRef](#)]
26. Koyama, N.; Soma, T.; Ichino, S.; Takahata, Y. Home range of ringtail lemur troops. In *Ringtailed Lemur Biology*; Jolly, A., Sussman, R.W., Koyama, N., Rasamimanana, H., Eds.; Springer Science + Business Media, LLC: New York, NY, USA, 2006; pp. 86–101.
27. Rasamimanana, H.; Ratovonirina, J.A.; Jolly, A.; Pride, E. Storm Damage at Berenty Reserve. *Lemur News* **2000**, *5*, 7–8.
28. Hazelton, P.; Murphy, B. Interpreting soil test results: What do all the numbers mean? *Eur. J. Soil Sci.* **2007**, *58*, 1219–1220.
29. Parvez, S.S.; Parvez, M.M.; Fujii, Y.; Gemma, H. Allelopathic competence of *Tamarindus indica* L. root involved in plant growth regulation. *Plant Growth Regul.* **2003**, *41*, 139–148. [[CrossRef](#)]
30. Parvez, S.S.; Parvez, M.M.; Nishihara, E.; Gemma, H.; Fujii, Y. *Tamarindus indica* L. leaf is a source of allelopathic substance. *Plant Growth Regul.* **2003**, *40*, 107–115. [[CrossRef](#)]
31. Parvez, S.S.; Parvez, M.M.; Fujii, Y.; Gemma, H. Differential allelopathic expression of bark and seed of *Tamarindus indica* L. *Plant Growth Regul.* **2004**, *42*, 245–252. [[CrossRef](#)]
32. Mangan, S.A.; Schnitzer, S.A.; Herre, E.A.; Mack, K.M.; Valencia, M.C.; Sanchez, E.I.; Bever, J.D. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* **2010**, *446*, 752–755. [[CrossRef](#)] [[PubMed](#)]
33. Martínez-Izquierdo, L.; García, M.M.; Powers, J.S.; Schnitzer, S.A. Lianas suppress seedling growth and survival of 14 tree species in a Panamanian tropical forest. *Ecology* **2016**, *97*, 215–224. [[CrossRef](#)] [[PubMed](#)]
34. Addo-Fordjour, P.; Rahmad, Z.B.; Shahrul, A.M.S. Effects of human disturbance on liana community diversity and structure in a tropical rainforest, Malaysia: Implication for conservation. *J. Plant Ecol.* **2012**, *5*, 391–399. [[CrossRef](#)]
35. Crowley, H.M. *Berenty Reserve Management Plan*; Wildlife Preservation Trust International: Philadelphia, PA, USA, 1995.
36. Dietze, M.; Matthes, J.H. A general ecophysiological framework for modelling the impacts of pests and pathogens on forest ecosystems. *Ecol. Lett.* **2014**, *17*, 1418–1426. [[CrossRef](#)] [[PubMed](#)]
37. Tadross, M.; Randriamarolaza, L.; Rabefitia, Z.; Zheng, K.Y. *Climate Change in Madagascar; Recent Past and Future*; Climate Systems Analysis Group, University of Cape Town: South Africa; World Bank: Washington, DC, USA, 2008; pp. 1–17. Available online: <http://www.csag.uct.ac.za/%7Eemtadross/Madagascar%20Climate%20Report.pdf> (accessed on 1 October 17).
38. Rasamimanana, N.; Ratsirarson, J.; Richard, A.F. Influence de la variabilité climatique sur la phénologie de la forêt de la Réserve Speciale de Beza Mahafaly. *Malagasy Nat.* **2012**, *6*, 67–82.
39. Duan, L.; Liu, T.; Wang, X.; Luo, Y.; Wang, W.; Liu, X. Water table fluctuation and its effects on vegetation in a semi-arid environment. *Hydrol. Earth Syst. Sci. Discuss.* **2011**, *8*, 3271–3304. [[CrossRef](#)]
40. Costello, J.F.; Leeder, J.; Strang, M. Drivers of the distribution of a dominant riparian tree species (*Eucalyptus coolabah*) on a dryland river system, Diamantina River, Lake Aire Basin. Paper 2667, Hydrology-ecology interactions, G9. In Proceedings of the 11th International Symposium on Ecohydraulics, Melbourne, Australia, 7–12 February 2016; The University of Melbourne: Melbourne, Australia, 2016.
41. Ranaivoson, T.; Brinkmann, K.; Rakouth, B.; Buerkert, A. Distribution, biomass and local importance of tamarind trees in south-western Madagascar. *Glob. Ecol. Conserv.* **2015**, *4*, 14–25. [[CrossRef](#)]

