

Full Length Research Paper

Determinants of vegetation composition and diversity of a moist forest-savanna boundary in south-eastern Zimbabwe

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Determinants of a forest-savanna boundary were investigated around Chirinda forest, south-eastern Zimbabwe. Vegetation data were collected in 60 plots along ten 200 m-transects demarcated across the forest boundary. Geology, soil properties, physiography and fire were recorded as explanatory variables. Species composition changed significantly across the boundary, with 100% species turnover between extreme ends of the distance gradient, indicating a strong environmental influence on the transition from forest to savanna. Species diversity ($F = 8.06$, $p < 0.01$) and species richness ($F = 16.73$, $p < 0.001$) were significantly lower inside the forest than outside. Measured explanatory variables significantly ($F = 8.4$, $p < 0.01$) accounted for 52% of the variation in species data. Soil moisture, soil depth, fire, geology and slope were significant boundary determinants. All forest plots were on dolerite but not all dolerite areas supported forest. This indicates the importance of geology in determining the position of the forest edge but it becomes less important in some areas where altitude, soil moisture, soil depth and fire are more important. Therefore, Chirinda forest is not a relic of what was once a larger forest neither is it a progenitor of a larger forest-to-be, but the position of its boundary is determined by a complex hierarchy of interacting determinants.

Key words: Chirinda, determinants, ecotone, forest boundary, moist forest, species diversity, Zimbabwe.

INTRODUCTION

In the southern African subcontinent, moist evergreen forests are found mainly on mountains and valleys in high rainfall areas. Just like in many parts of the world (Sollins, 1998; Hooper et al., 2004), their structure, composition and distribution are influenced by a variety of factors including climate, altitude, edaphic conditions and fire (Muller, 1991). Most of these forests exist in the form of isolated, species-diverse patches that are often embedded within mosaics of non-forest vegetation supporting lower species diversity. These forests have been subjected to varying degrees of disturbance by anthropogenic (e.g. encroachment by human settlements and fire) and natural factors (e.g. cyclones), hence some of them may be in a state of change. Agricultural and human settlement expansion have led to significant encroachment upon forests (Mitchard et al., 2011)

resulting in large-scale exploitation, severe deforestation and fragmentation. This has prompted concerns for the need to improve our understanding of local-scale dynamics of these forest patches in order to properly plan for their improved conservation and protection because of their inherently high biodiversity.

Even though the general ecology of moist forests is relatively understood (Corlett and Primack, 2011), knowledge gaps concerning patch dynamics caused by disturbances still exist, including whether such forest patches are progenitors of larger forests-to-be (Timberlake, 1992a, b) or whether they are relics of what were once larger forests which have now been reduced by the individual or interactive effects of climate change, fire, and other human activities (Mitchard et al., 2011; Favier et al., 2004). To gain more insights into these

issues, studies of forest boundaries are of paramount importance. In the past, much attention has been paid to vegetation dynamics in forest gaps in tropical moist forests (Shugart, 2002; Bugmann, 2001) but the dynamics of forest boundaries have received much less attention. The boundaries between forest and non-forest vegetation are often sharp, which raises the question of what factors determine the positions of such boundaries. Related questions concern the stability of the forest boundary over time and the nature of the differences in ecological processes on either side of the boundary.

Forests may end abruptly due to natural changes in environmental gradients or artificially, due to anthropogenic influences. Forest boundaries may be very dynamic, naturally stable or maintained in near-stable states by external factors such as fire and/or grazing. It is the complexity introduced by the various factors that has led to difficulties in understanding forest boundary dynamics. The forest boundary creates microclimatic gradients that result in differences in environments between the forest interior and the non-forest areas (Ranney et al., 1981; Hennenberg et al., 2008). Such conditions are likely to favour the establishment of certain species and not others. In this context, the influence of soil moisture and other edaphic changes at the forest-savanna boundary is particularly important (Furley, 1992; Hopkins, 1992). The ecotone between forest and non-forest areas often has high plant densities and diversity, and represents the juxtaposition of two contrasting habitats. Along the ecotone, there is generally a high incidence of wind and animal activity (Ranney et al., 1981), especially mammals and frugivorous birds which impact both negatively and positively on seed dispersal. Ecotones are reported to offer transitional habitats that appear to be areas of evolutionary dynamism (Smith et al., 2001). The extent of such areas in Africa is about 1.28 million km² (Mayaux et al., 2004), which is quite significant.

In southern Africa, forest patches with sharp, abrupt boundaries are common in Mozambique, Malawi, South Africa and along the eastern highlands of Zimbabwe, including Chirinda forest. There are suggestions that Chirinda forest is a small relic of what was once a much larger forested area which has now been reduced in the last few hundred years by gradual climatic changes (Goldsmith, 1976), while some maintain that the forest boundary is determined by the extent of dolerite soils (Muller, 1991). One widely discussed idea is the possibility of allowing the forest to expand by improving its protection from fire (Timberlake, 1991), since such anthropogenic disturbances such as fire and grazing are known to maintain forest boundaries (Bucini and Hanan, 2007). The main objective of this study was, therefore, to investigate the determinants of floristic composition and diversity of Chirinda forest boundary, and determine whether the distribution and composition of plant species across the boundary suggest expansion, contraction or stability of the forest boundary. This is important for forest

protection and conservation considerations.

MATERIALS AND METHODS

Study area

The study was carried out in Chirinda forest (32°42' E, 20°26' S), south-eastern Zimbabwe. The forest is about 30 km to the south east of Chipinge town (Figure 1). The forest is the south-easternmost extremity of moist forest distribution in Zimbabwe. It is a typical example of Muller's (2006) 'medium altitude' moist forest that is under proper conservation. According to Muller (2006), a 'medium altitude' rain forest (in southern African context) is a moist forest that occurs between 850 and 1350 m above sea level. Chirinda forest is surrounded by communal settlements, commercial timber plantations (of *Eucalyptus* and *Pinus* species) and small-scale commercial farming units.

It is a gazetted Forest Land managed by the Forestry Commission of Zimbabwe, and covers 947 ha, of which 606 ha is moist evergreen forest. The forest is dominated by *Chrysophyllum gorungosanum*, *Craibia brevicaudata*, *Khaya anthotheca* and *Trichilia dregeana* in upper canopy layer while *Tannodia swynnertonii*, *Strychnos meliodora* and *Drypetes gerrardii* are common in the sub-canopy (Muller, 2006). The forest lies on two broad highlands, rising from 1076 to 1250 m in altitude. These highlands essentially subdivide the forest into a southern half and a northern half, with a saddle in between. Three rivers (Zona, Chinyika and Musangazi) have their sources in the forest. The geology of the area comprises red and purple phyllitic mudstones interbedded with pale fine- to medium-grained feldspathic sandstones of the Upper Argillaceous series of the Pre-Cambrian Umkondo System (Watson, 1969). Fine-grained dolerite sills have intruded into these sandstones forming a cap over much of the higher ground. The area receives an average annual rainfall of 1466 mm (Timberlake, 1994a). Average winter and summer temperatures are 14 and 20°C, respectively.

Plot demarcation and vegetation assessments

The five vegetation types surrounding the forest identified by Mapaure (1997) were used as strata for the placement of transects. Ten belt transects (A to J), each measuring 200 m long and 20 m wide, were demarcated across the forest boundary, two in each vegetation type. Each transect was perpendicular to the forest boundary, with 100 m on either side of the forest boundary. Each belt transect was subdivided into ten 20 m × 20 m contiguous plots, 5 on either side of the boundary. Plot boundaries were marked by wooden pegs driven into the soil and marked with red reflective tape. From the forest boundary going to either side, the first, third and fifth plots (making a total of 60 plots) were sampled as described subsequently. Plots along each transect were assigned identification codes such that they were coded 1 or 2 if they were inside or outside the forest, respectively. Then they were numbered according to their positions relative to the forest boundary (1 = at forest boundary on either side, 3 = third plot from boundary on either, etc). Thus, the first plot outside the forest along transect A was A21 while the first plot inside the forest on the same transect was A11.

In each plot, all plant species were identified and assigned to height categories: < 0.5 m, 0.5 to 3 m, 3 to 6 m, and > 6 m. The height classes were arbitrarily chosen based largely on the nature of the vertical stratification of the vegetation. All the plants in height classes >3 m were assessed in the 20 × 20 m plots whilst those in height classes <3 m were assessed in a 5 m × 5 m subplot nested within the larger plot.

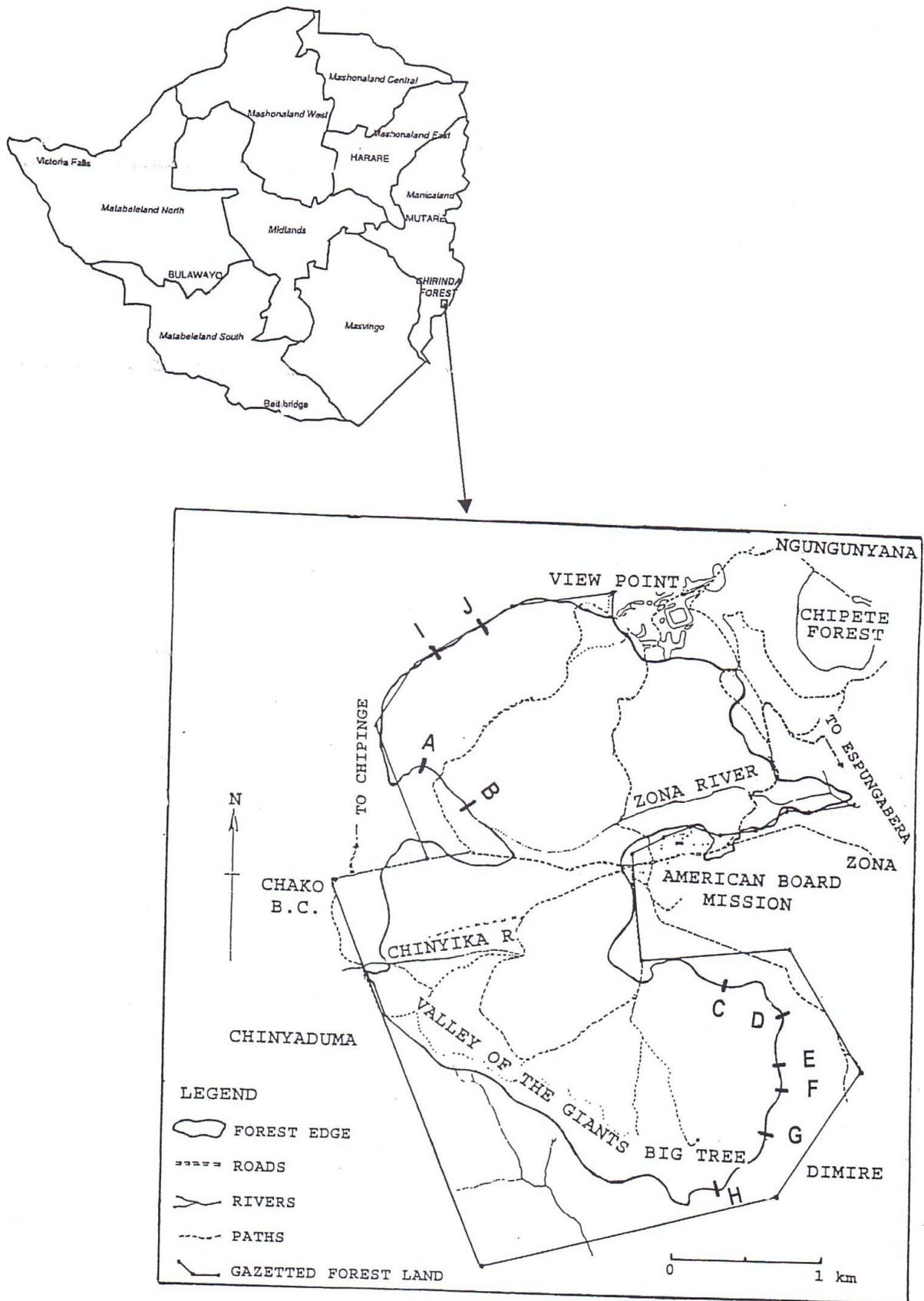


Figure 1. The location of Chirinda Forest in south-eastern Zimbabwe.

Measurement and assessment of explanatory variables

Soil samples were collected from depths of 0 to 20 cm while the soil depth was determined by continuing to auger to >60 cm or until bedrock was hit. Soils were collected from five positions (four corners and the centre), mixed and sub-samples taken for moisture determination and chemical analyses. Soil moisture was gravimetrically determined while chemical analyses for Cation Exchange Capacity (CEC), Total Exchangeable Bases (TEB) and free Iron were done following standard procedures (Anderson and Ingram, 1993). In each plot, the geology was determined from any exposed bedrock and soil type. The slope of each transect was determined by analysing a map of physical features of the area. Other factors recorded were presence of grazing, woodcutting and fire.

Data analyses

Detrended Correspondence Analysis (DCA) was applied on species presence/absence data to infer gradients in vegetation data. This was done using CANOCO for Windows Version 4.1 package (ter Braak and Šmilauer, 2002). Shannon diversity indices were calculated in CANOCO and a t-test was used to test for their differences between the forest and non-forest plots. Canonical Correspondence Analysis (CCA) (in CANOCO) was used to explore species-environment relationships using the same vegetation data matrix used for DCA and an explanatory data matrix with geology, soil moisture, distance from forest edge, slope, soil depth, TEB, CEC and free Fe as the test variables. The significance of the influence of explanatory variables on vegetation data was tested using Monte Carlo Permutation tests available in CANOCO. The importance of each variable in influencing vegetation data was tested using forward selection of variables. Differences in species richness and diversity among the forest, savanna and boundary were tested using Oneway ANOVA, with Tukey's test as the *post hoc* analysis.

RESULTS

Detrended Correspondence Analysis of the data resulted in a clear separation (along Axis 1) between forest and savanna plots with very little overlap between them (Figure 2). In general, plots close to the forest edge, from either side (e.g. marked A11 or A21), were closer to the centre of the spread while plots furthest away from the forest edge (e.g. marked A15 or A25) are positioned at the opposite extremes of the scatter along axis 1, mirroring the physical situation on the ground (Figure 3). DCA axes 1 and 2 accounted for 58 and 22% of the total variation, respectively. There are more than 4 DCA units between the two extreme ends of the scatter along the first axis, indicating a 100% species turnover along that distance gradient. There is no clear gradient associated with Axis 2. A total of 252 plant species were recorded in the study area. Species diversity was significantly lower in the forest than in the savanna and than in the forest boundary ($F = 8.06$, $df = 2$, $p < 0.01$) (Table 1, Figure 2). A similar pattern was evident for species richness ($F = 16.73$, $df = 2$, $p < 0.001$; Table 1). Some species occurred typically in the forest while others were only confined to the savanna vegetation. A suite of species

was also associated with the forest boundary but most of these are ubiquitous species that could be found in either of the other two habitats. Table 1 shows a list of selected common woody species which typified these three categories.

Canonical correspondence analysis (CCA) confirmed the grouping evident in DCA (Figure 4). CCA axes 1 and 2 accounted for 53 and 24% of the total variation, respectively. The overall influence of the measured explanatory variables on species data was significant ($F = 8.4$, $p < 0.01$). Forward selection of variables indicated that there was a significant change in vegetation data along the distance gradient ($F = 6.11$, $p < 0.001$). The tested variables explained 52% of the observed variation in species data. Soil moisture (19%; $F = 2.33$, $p < 0.001$), soil depth (15%; $F = 1.76$, $p < 0.001$), fire (13%; $F = 1.64$, $p < 0.01$), and slope (12%; $F = 1.52$, $p < 0.001$) all significantly influenced the vegetation. Geology, TEB, free Iron and CEC were not significant. CCA separated the two geological formations (sandstone and dolerite) along both the first and second axes such that all forest plots fell on doleritic but not all areas underlain by dolerite supported the *C. gorungosanum*-dominated moist forest. The influence of fire and soil moisture was important in some areas, especially the south-eastern section (transects E, F, G), which coincided with the windward side of the highland. The north-western part (transects I, J) and the middle saddle (transects A, B) were mainly associated with steeper slopes and drier soils, and thus supported savanna comprising woodland and bushland with *Bridelia micrantha* and *Psidium guajava* as the most commonly occurring species, respectively.

DISCUSSION

Moist forests generally occur in wetter environments and savannas in drier ones. The amount of precipitation received from rainfall in the study area is lower than the normal requirement for typical moist forest development. Muller (2006) states that for moist forest development to occur in eastern Zimbabwe, rainfall should be at least 1200 mm per annum. The extra moisture in the study area that supports forest development comes in the form of orographic drizzle, made possible by a number of factors: the high ground, a south-easterly aspect, and the tall trees facilitate the release of this extra moisture from the low clouds. The forest may have originated from the combined effects of geology, rainfall and topography.

The sudden change in species composition across the forest boundary evident in the DCA ordination gives an indication of how slow (and how difficult) the change from one vegetation type to another is, if it is taking place at all. This suggests a strong environmental barrier against a change from one type to another. Adejuwon and Adesina (1992) noted that a plant community will extend its range of distribution in all directions until some

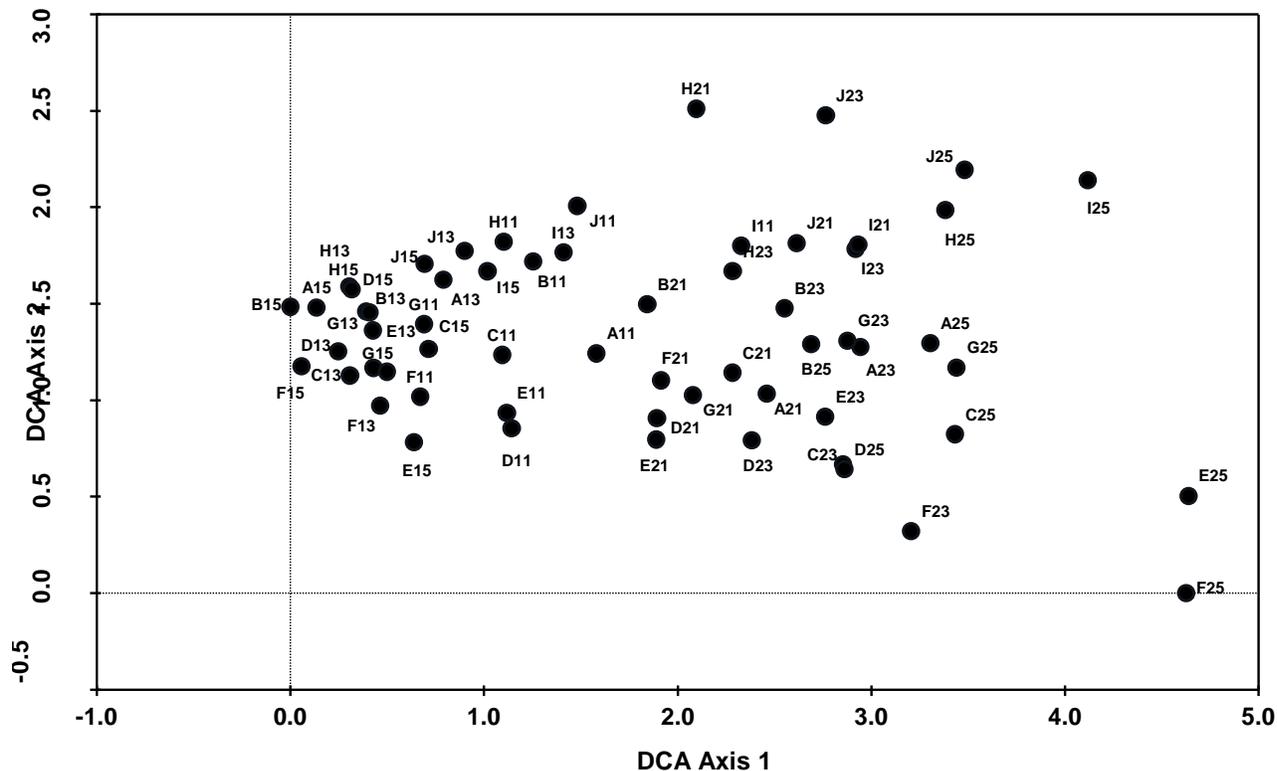


Figure 2. Detrended Correspondence Analysis (DCA) ordination diagram showing the grouping of plots from transects (A to J) across the forest boundary.

detrimental environmental factor prevents normal existence. There is up to a 50% change in species composition between contiguous quadrats just across the forest edge and a 100% species turn-over at the extreme ends of the gradient (Figure 3). The sudden change in species composition and vegetation physiognomy (from forest to savanna) is brought about by an abrupt change in pedological conditions.

Canonical correspondence analysis (CCA) separated sandstone from dolerite areas, indicating the importance of geology in determining the position of the forest edge. However, geology becomes less important in some parts of the forest boundary, especially the south-eastern boundary where altitude and soil depth are more important. These observations suggest that the soils derived from geology have to be of a certain minimum depth in order to support forest trees. Given this influence of geology on the extent of the forest at present, the suggestion that Chirinda forest may be a relic of what was once a larger forest seems unlikely. Therefore, the position of the forest is determined by a hierarchy of interacting factors in different places. As pointed earlier, geology is a very important determinant of the position and extent of the forest boundary, the forest occurring on richer dolerite soils and the savanna woodland vegetation mostly on poorer soils derived from sandstone, but not all soils derived from dolerite support forest. Some areas

under dolerite soils supported grassland. This masked the importance of geology in the analysis by forward selection of variables resulting in it becoming less significant than other factors. Ellery et al. (1992) developed a decision tree model indicating grasslands to occur under conditions of shallow soils resulting from several causes including an indurated B-horizon or existence of an impervious rock. Hence, shallow dolerite soils could not support forest but grassland.

It may also be hypothesized that the grassland area occurring on dolerite may have been originally forest which was cleared and is now being maintained by fire, provided that the minimum soil depth for forest development was available. This assertion is supported by CCA where fire was a significant factor in those parts of the forest boundary. Fire has an effect of promoting savanna and suppressing forest (Cochrane and Laurance, 2002). Even though fire may negate the establishment of seedlings of forest tree species in otherwise suitable localities in the adjacent savanna vegetation (such as the south-western boundary where the forest seems to have the potential to expand), its effect on the forest in general is minimal. The current situation indicates that the forest has not contracted despite these threats. This is due to a number of reasons: first, the forest is sufficiently protected by the authorities to keep such threats to a minimum; second, the evergreen forest

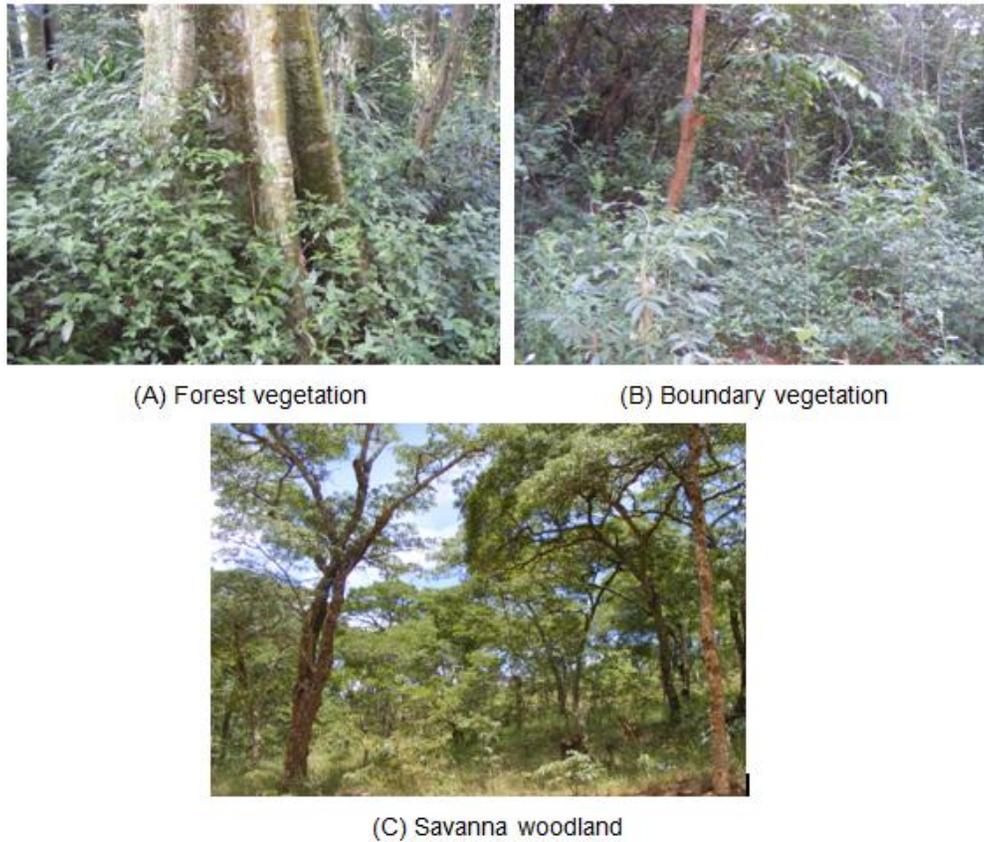


Figure 3. Close-up photos showing structural differences between the forest with buttressed *Chrysophyllum gorungosanum* tree (A), the boundary vegetation close to a road (B) and savanna woodland dominated by *Brachystegia spiciformis* (C).

Table 1. Differences in Shannon diversity indices and species richness among forest, savanna and boundary habitats (similar superscripts for each attribute indicate no significant differences). Ten most common woody plant species found in each habitat are also shown (numbers in parentheses indicate the frequency of occurrence).

| Attribute | Forest | Savanna | Boundary |
|---|--|---|------------------------------------|
| Shannon diversity | 3.39 (± 0.06) ^a | 3.74 (± 0.06) ^b | 3.58 (± 0.07) ^b |
| Species richness | 28.0 (± 1.13) ^a | 42.2 (± 2.8) ^b | 41.2 (± 1.8) ^b |
| Most common woody species (10 selected) | <i>Acacia pentagona</i> (100%) | <i>Bridelia micrantha</i> (83%) | <i>Albizia gummifera</i> (80%) |
| | <i>Chrysophyllum gorungosanum</i> (100%) | <i>Diospyros lycioides</i> (63%) | <i>Carissa bispinosa</i> (60%) |
| | <i>Craibia brevicaudata</i> (60%) | <i>Euclea divinorum</i> (80%) | <i>Casearia battiscombei</i> (65%) |
| | <i>Diospyros abyssinica</i> (90%) | <i>Harungana madagascariensis</i> (53%) | <i>Clausena anisata</i> (65%) |
| | <i>Landolphia buchananii</i> (77%) | <i>Heteropyxis dehniae</i> (50%) | <i>Croton sylvaticus</i> (90%) |
| | <i>Rawsonia lucida</i> (83%) | <i>Lantana camara</i> (77%) | <i>Keetia gueinzii</i> (45%) |
| | <i>Rothmannia urcelliformis</i> (87%) | <i>Parinari curatellifolia</i> (50%) | <i>Pavetta comostyla</i> (45%) |
| | <i>Strombosia scheffleri</i> (63%) | <i>Psidium guajava</i> (87%) | <i>Peddiea africana</i> (85%) |
| | <i>Tabernaemontana ventricosa</i> (100%) | <i>Rhus transvaalensis</i> (67%) | <i>Teclea nobilis</i> (75%) |
| | <i>Tannodia swynnertonii</i> (80%) | <i>Toddallia asiatica</i> (70%) | <i>Tiliacora funifera</i> (50%) |

does not readily burn because it is sufficiently moist to keep out fires; third, apart from the presence of *Lantana camara* and a few lianes in some places, the forest edge

does not present much fuel for fire to burn into the forest. Whilst there is an environmental limit to the forest in terms of expansion afore-noted, the forest could contract

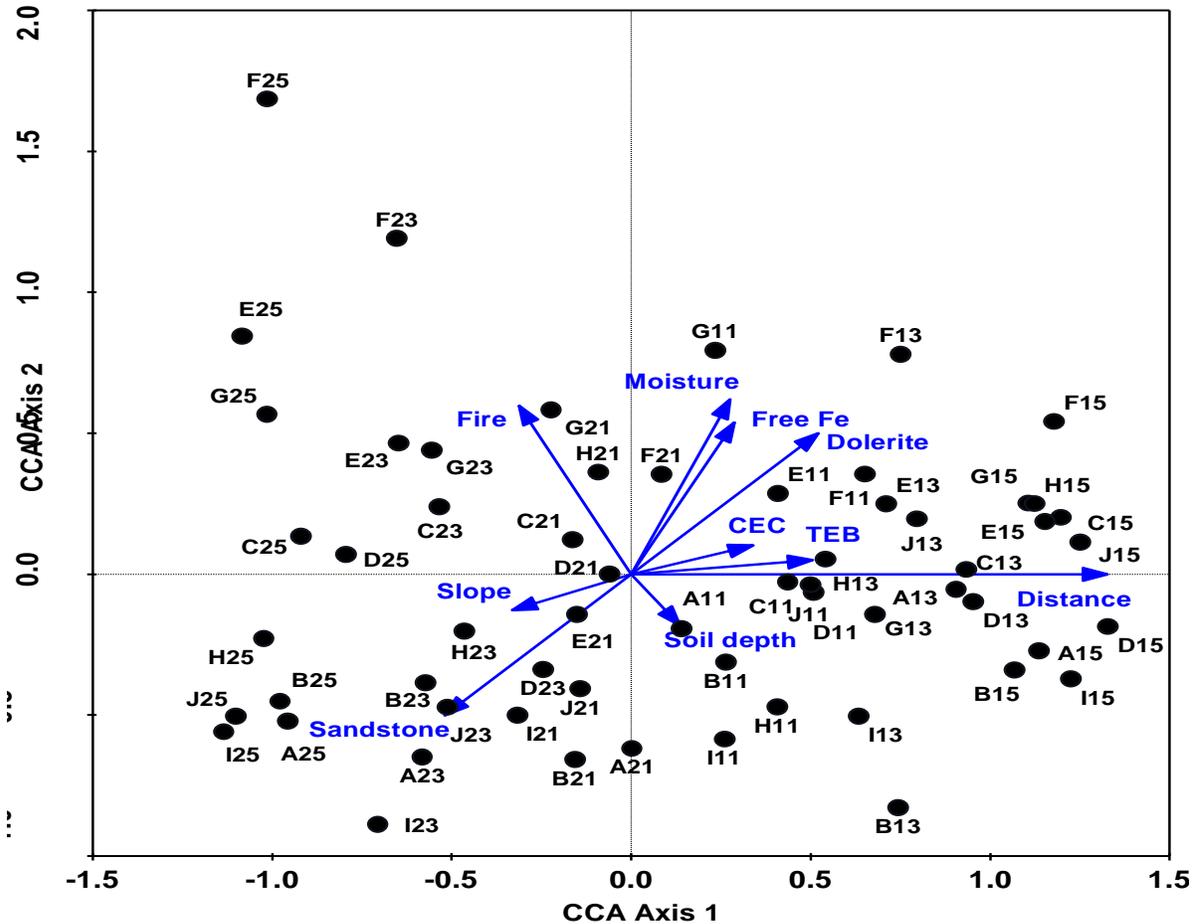


Figure 4. Canonical correspondence analysis (CCA) ordination diagram showing the grouping of plots from transects (A to J) across the forest boundary in relation to the measured explanatory variable indicated by arrows. The relative size of each arrow indicates the importance of that variable along the direction it is pointing.

through various reasons, especially fire and logging activities at the forest boundary. These human-induced disturbances are becoming of increasing concern around the forest. Fire seems to be one of the major anthropogenic factors on the increase in the area, especially in recent years where encroachment on the forest has increased. This has been exacerbated by the economic hardships and could have a profound effect on the vegetation of the buffer zone, especially in areas adjacent to the Dimire settlements in the south-eastern and southern parts. Traditional human activities such as the use of fire have been reported to strongly influence vegetation succession at the forest-savanna boundaries (Favier et al., 2004). Mujuru and Kundhlande (2007) noted that the northern section of the forest was logged in the past but the forest has recovered and there is no difference in species diversity between the two sections. The effect of fire on the dynamics of the vegetation within the gazetted area has sparked some debate even from several decades ago (Armitage, 1965), especially with reference to the possibility and desirability of extending the forest. The current study suggests that the overall

increase in bush cover observed on the aerial photographs by Timberlake (1992a; 1994b) was a result of a combination of re-growth after abandonment of cultivation followed by fire protection, but not forest expansion. Some authors (e.g. Favier et al., 2004) reported forest expansion over savanna after control of fires, which differs from the current situation in Chirinda.

Grazing by livestock next to the forest does not really present a big problem. The affected area is quite small and grazing has positive effect of reducing the herbaceous layer thereby reducing the fuel for fire (Davies et al., 2010). However, the observed significant settlement encroachment against the forest boundary in the south-eastern side is a cause for concern. This dynamic is a real threat to forest conservation since wood-cutting activities are on the increase. Woodcutting may undermine forest integrity by altering microclimatic conditions in the affected areas and, in the long-term, change the structure and species composition (Hall et al., 2003). If uncontrolled, this may lead to genetic erosion through loss of unique species and habitats. A combination of wood cutting and fire along the forest edge

could eventually force the forest to recede. From the preceding account, it is therefore concluded that Chirinda forest is not a relic of what was once a larger forest as hypothesized by some authors. Neither is it a progenitor of a larger forest-to-be, but the position of its boundary is determined by a complex hierarchy of interacting factors in the different places around the forest.

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