The spatial distribution of elephants (*loxodonta Africana*) in relation to the spatial heterogeneity of vegetation cover in a Southern African agricultural landscape

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Abstract

We tested whether and how the probability of African elephant (*Loxodonta Africana*) presence was related to spatial heterogeneity of vegetation cover and in the agricultural landscape of the Sebungwe region in northwestern Zimbabwe in the early 1980s and early 1990s. We also tested to whether and how spatial changes in probability of elephant presence were related to changes in spatial heterogeneity the Sebungwe region between the abovementioned dates. A novel perspective was used to characterise spatial heterogeneity based on intensity (i.e. maximum variance in vegetation cover) and dominant scale (i.e. patch size at which intensity is manifested) while vegetation cover was estimated from a remotely sensed normalised difference vegetation index (NDVI) based on Landsat TM satellite imagery. The results indicated that the probability of elephant presence could be predicted reliably using intensity and dominant scale of spatial heterogeneity. Both the intensity and dominant scale of spatial heterogeneity explained 80 % and 93 % of the variance of the probability of elephant presence in the early 1980s and early 1990s respectively. The changes in the intensity and dominant scale of spatial heterogeneity predicted 89 % of the variance of the change in elephant presence between the 1980s and 1990s. The results of this study imply that if elephants are to be conserved in agricultural landscapes, it is important that wildlife management strategies aimed at sustaining wildlife species in agricultural landscapes take into account the spatial heterogeneity of vegetation cover, with particular attention to the dominant scale and intensity of spatial heterogeneity. In addition, the results imply the dominant scale and intensity perspective to the characterisation of spatial heterogeneity may improve the prediction of ecological patterns in the landscape such as determining the spatial distribution of wildlife species.

Key words: Dominant scale; Intensity; NDVI; Spatial heterogeneity; Wavelets; Zimbabwe

1. Introduction

Community based wildlife management programmes in the agricultural landscapes of Southern Africa such as the Communal Areas Management Programme For Indigenous Resources (CAMPFIRE) in Zimbabwe (Hoare and Du Toit 1999, Hulme and Murphree

2001, Logan and Moseley 2002) owe their existence to the sustained presence or persistence of wildlife species throughout these landscapes. However, wildlife species persistence in agricultural landscapes of Southern Africa, particularly in Zimbabwe, is increasingly being threatened by agricultural field expansion into the natural habitats (Cumming 1982, Cumming 1997a, Hoare 1999, Hoare and Du Toit 1999). The critical question for wildlife managers and ecologists is: how can sustained presence of wildlife in agricultural landscapes be ensured in the face of expanding agriculture? In other words, in what kind of agricultural landscape can wildlife species thrive? The answer may lie in understanding the kind of habitat conditions that can make elephants thrive within the unique context of agricultural landscapes in which fields divide natural habitats into discontinuous patches of different spatial arrangements. In such a landscape, it is not only the amount of natural habitat that is important for wildlife species persistence, but also the spatial arrangement (patch size and inter-patch distance) of habitat patches becomes particularly critical. Thus, to ensure wildlife species persistence in agricultural landscapes it is critical to understand how they respond to spatial heterogeneity (i.e. the patterning or patchiness in vital landscape properties such as vegetation cover (Legendre and Fortin 1989, Pickett and Rogers 1997, Gustafson 1998) that is introduced by the imposition of agricultural fields onto the natural habitat. Consequently, the need for ecological research to characterise wildlife species response to spatial heterogeneity in agricultural landscapes is critical.

Although empirical and theoretical literature suggests the importance of spatial heterogeneity to wildlife distribution (Turner 1989, Johnson*, et al.* 1992, Kareiva and Wennergren 1995, Turner*, et al.* 1997, Lynam and Billick 1999, Adler*, et al.* 2001), an understanding of the levels of spatial heterogeneity at which specific wildlife species can persist in agricultural landscapes is still rudimentary. This may stem from the lack of clarity in the characterisation of spatial heterogeneity (Sparrow 1999), suggesting that spatial heterogeneity needs to be properly characterised even before the wildlife response to spatial heterogeneity can be understood.

The quantification of spatial heterogeneity is an empirical approach based on observed data, thus it is a forerunner of the specific testable hypotheses about ecological patterns (Perry*, et al.* 2002). Traditionally, spatial heterogeneity has been quantified from remote sensing images by using two basic approaches: (a) the direct image approach, where straight reflectance or reflectance indices of remote sensing images are used to quantify spatial heterogeneity, using the original pixel size of the image (Goodchild and Quattrochi 1997); and (b) the cartographic or patch mosaic approach, where the image is subdivided into homogeneous mapping units through classification (Gustafson 1998). The first approach assumes that spatial heterogeneity is at the pixel size of the image and, in this case, it is only the reflectance values that change in space. The argument against this approach is that its choice of scale (i.e. window size) is arbitrary, thus it is subjective. Alternatively, using the patch mosaic approach to quantify spatial heterogeneity assumes a collection of discrete patches. Based on this approach, characterisation of spatial heterogeneity is highly dependent on the initial definition of mapping units by the researcher (Turner 1989). The argument against this approach is that patches have abrupt boundaries and the variation within the patches is assumed to be irrelevant (McGrigal and Cushman 2002). The patch mosaic model is parsimonious and has therefore become the operating paradigm. It is particularly valid where landscape patches have crisp boundaries, as with the regular landscapes of Europe (Pearson 2002). However, the model poorly represents spatial heterogeneity in landscapes that are characterised by gradients rather than discrete patches, for instance in savanna landscapes (Pearson 2002), and this leads to both loss of information and the introduction of subjectivity. Alternative approaches for characterising spatial heterogeneity remain underdeveloped.

In this study, a new approach to characterising spatial heterogeneity of continuously varying landscape properties such as percent vegetation cover is presented, based on intensity as well as the dominant scale. Intensity is defined as the maximum variance exhibited when a spatially distributed landscape property is measured with a successively increasing window size or scale. For example, measuring the variance in percent canopy cover along a 100 m long transect in a tree plantation with 10 m wide tree stands (with uniformly high canopy cover) that evenly interchange with 10 m wide bare ground (with nil canopy cover) at a successively increasing window size, starting from 1 m up to 100 m, would yield the maximum variance at a window size of 10 m. This maximum variance is the intensity of spatial heterogeneity. It is the scale or window size where the maximum variance in the landscape property is measured that is defined as the dominant scale of spatial heterogeneity. In other words, intensity and dominant scale of spatial heterogeneity are properties of a landscape that are inseparable. Note that our definition of scale follows that of (Levin 1992, Rietkerk *et al.* 2002) who define scale as the window or dimension (e.g. m, km, m^2, km^2) through which the landscape may be observed either in remote sensing images or by direct measurement. We therefore propose that spatial heterogeneity be defined and quantified using both intensity and the dominant scale at which the intensity is observed. Of course, grain (i.e. the initial observation scale or window size at which the data is collected) and extent (overall size of the study area) limits the range of the dominant scale that can be detected (Wiens 1989).

To properly elucidate the centrality of the intensity and the dominant scale in the characterisation of spatial heterogeneity, we present a simulation of tree canopy cover along three artificial transects (fig. 1). The tree canopy cover represented in the three artificial transects that stretch over 1000 m is sampled at an interval of 1 m. Thus, the interval of 1 m defines the grain (observation scale) while 1000 m defines the extent (overall length encompassed by the transect). The transects 1 and 2 have a dominant scale of spatial heterogeneity of 100 m, i.e. maximum variance is recorded at the window size of 100 m whereas transect 3 has a dominant scale of 200 m. The dominant scale of spatial heterogeneity in transects 1 and 2 is equal but the intensity of spatial heterogeneity is different. Next, a look at transects 1 and 3 shows that they have equal intensity of spatial heterogeneity but different dominant scales of spatial heterogeneity. Therefore, characterizing spatial heterogeneity in this example is incomplete if only either intensity or dominant scale of spatial heterogeneity is considered. Thus, we propose that both the intensity and dominant scale at which the intensity is observed describe spatial heterogeneity of a landscape. This method of characterising spatial heterogeneity in the landscape was developed and tested in (Murwira and Skidmore. 2003)

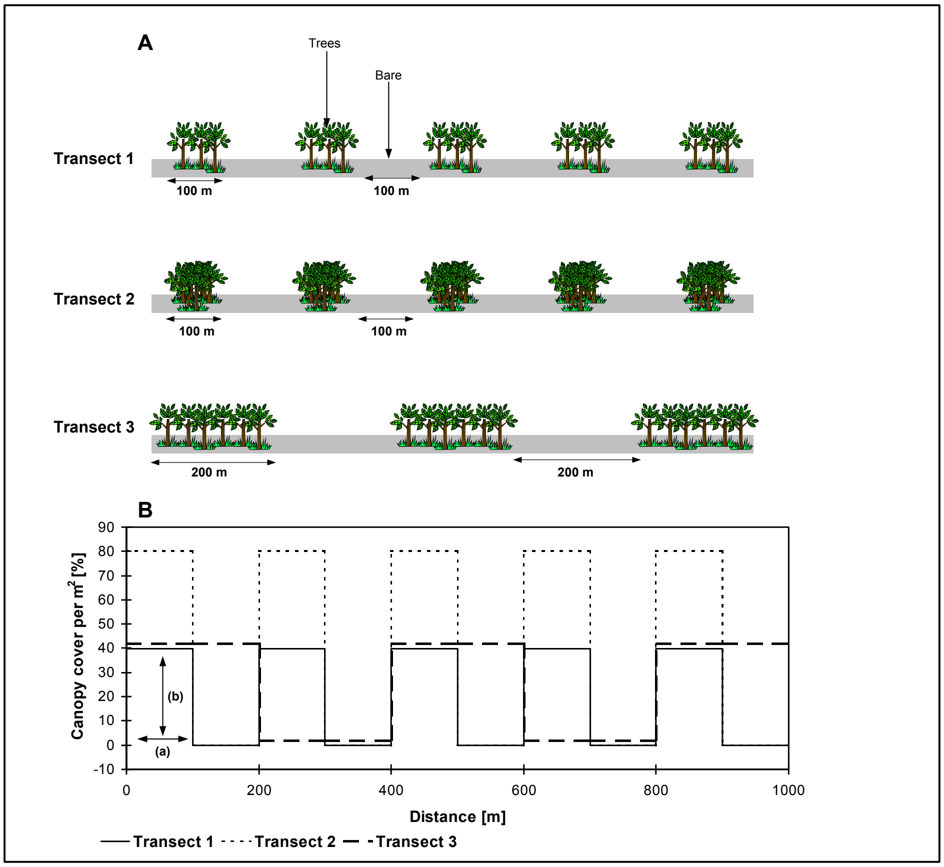


Fig. 1 Part (A) is three transects with alternating spaces of trees and bare ground. Part (B) shows the simulated tree canopy cover along each transect assuming that the cover measurements are made after every 1 m (i.e. grain = 1 m) and an extent of 1000 m. In this example, the dominant scale for transect 1 is represented by the horizontal dimension (a) whereas the intensity is represented by the vertical dimension (b).

The aim of this study was to test whether spatial heterogeneity in vegetation cover (estimated from the remotely sensed normalised difference vegetation index (NDVI)) was related to wildlife species distribution, particularly that of the African elephant (*Loxodonta Africana*) in the Sebungwe communal lands in Zimbabwe between the early 1980s and early 1990s. The specific objectives of this study were: (1) to test whether the distribution of the African elephant was significantly related the dominant scale and intensity of spatial heterogeneity and, (2) to test whether changes elephant presence between the early 1980s and early 1990s were related to changes in the dominant scale and intensity of spatial heterogeneity. But, firstly spatial heterogeneity was analysed as a preamble to fulfilling the above objective. For this, a wavelet transform was used to quantify spatial heterogeneity from an intensity and dominant scale perspective. Murwira and Skidmore (2003) demonstrated the utility of wavelets in characterising spatial heterogeneity from a dominant scale and intensity perspective.

The African elephant was selected for several reasons. Firstly, the Africa elephant is a keystone species of the African savanna (Hoare and Du Toit 1999) that need to be conserved. Secondly, the African elephant is on the list of the world's threatened species (Burton 1999) and is considered a conservation priority. Thirdly, the study area has been the only agricultural landscape in Zimbabwe outside the protected wildlife reserves with a healthy expanding elephant population (Cumming 1981). Nevertheless, this situation is increasingly being threatened by agricultural field expansion following the continual eradication of tsetse (*Glossina* sp.) since the 1960s. Thus, there is need of interventionist strategies to conserve the elephant. Fourthly, there water is not a limiting factor in the study area (Cumming 1981), and since the African elephant is a habitat generalist (Kingdon 2001) it has a potential of being anywhere in the study area and it is reasonable to hypothesise that the level of spatial heterogeneity may affect its distribution. Also, good survey data exists on the spatial distribution of the African elephant in the study area.

2. Materials and Methods

2.1. Materials

2.1.1 Study area

The study was based on the Sebungwe region in northwestern Zimbabwe (fig. 2). The Sebungwe region is composed of undulating topography with the average elevation of between 700 – 800 m above sea level. The region is characterised by a single wet season (November to March) with a mean annual rainfall of 680 – 700 mm, as well as a long dry season (April to October). Savanna woodlands and grasslands characterise the main natural land cover, i.e. Miombo woodland dominated by *Brachystegia spp.* and *Julbernardia globiflora spp,* Mopane dominated by *Colophospermum mopane spp,* Faidherbia woodland dominated by *Faidherbia albida spp,* Miombo-Mopane with co-dominance of *Brachystegia spp* and *Julbernardia globiflora spp* and *Colophospermum mopane spp* as well as Setaria dominated by *Setaria incrassata spp, Ischaemum afrum spp* and *Dicathium papillosum spp* (Timberlake*, et al.* 1993).

The Sebungwe contains of five wildlife reserves, interspersed with communal lands (fig. 2) that have varying degrees of agriculture and varying degrees of wildlife presence. Communal lands are a land category that are characterised by collective or community land ownership and they are subdivided into administrative or management units called wards (fig. 2). In the communal lands wildlife presence is affected by the ecological conditions such as the availability of vegetation cover rather than by conservation measures or laws like in the wildlife reserves, i.e. wildlife species are present provided there are necessities such as enough cover and water. Wildlife has to cross the communal lands when moving between the wildlife reserves. Thus, the communal lands also provide wildlife corridors that link the wildlife reserves.

The Sebungwe landscape evolved from a complex of different historical forces linked to the eradication of tsetse fly (*Glossina* sp.) and the related land use (fig.2). Historically, the Sebungwe region was home to both tsetse fly and a wide range of wildlife species until the 1960s when the tsetse belt began to continually dwindle as a consequence of the tsetse eradication programme that was meant to enable livestock ranging and arable agriculture, thereby relieving population pressure from elsewhere in the country (fig. 2). As tsetse fly was progressively destroyed since the 1960s, the valley began to be increasingly occupied by farmers (Cumming and Lynam 1997). By the mid-1980s immigration had accelerated and the threat of arable agriculture on the persistence of wildlife began to increase in parts of the Sebungwe (Cumming and Lynam 1997). The results were the varying degrees wildlife presence as a function of varying levels of arable agriculture (Hoare and Du Toit 1999).

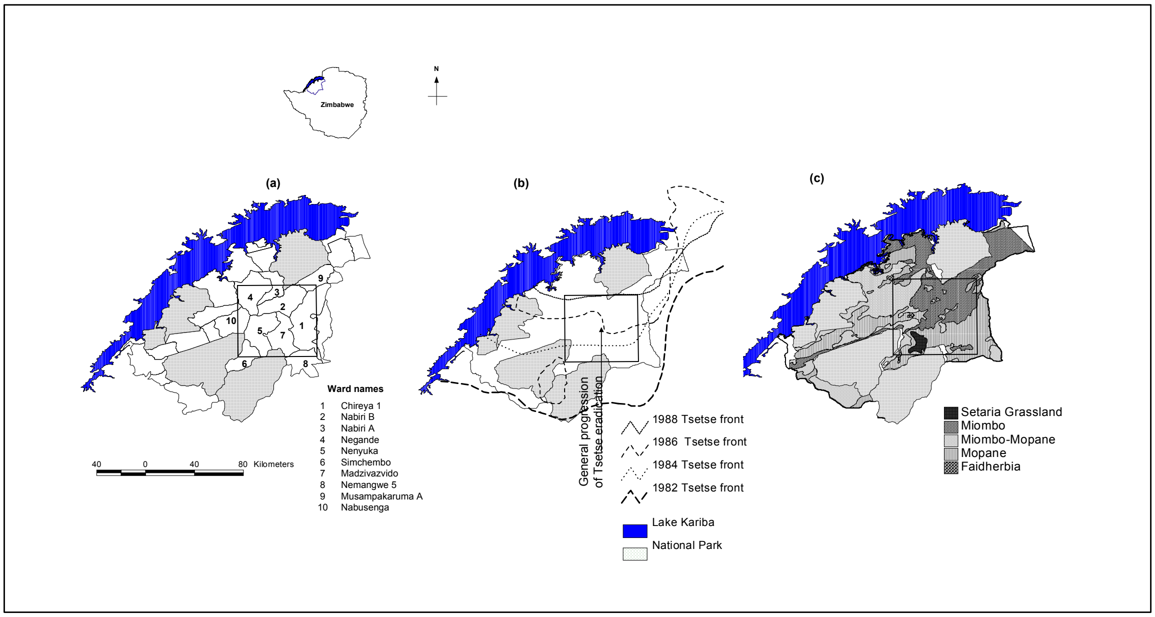


Fig. 2 The map of Zimbabwe showing the location of the Sebungwe region and (a) the wards and national parks (b) the history of the progression of tsetse eradication and (c) the main physiognomic-floristic vegetation classes in the communal lands based on (Timberlake, et al. 1993). The square box is a 61 km x 61 km area selected for this study.

This study is based on a 61 km x 61 km area (square box in fig. 2), mainly covering the communal lands. This study area was considered large enough for studying elephant distribution in the Sebungwe. Specifically, elephants in the Sebungwe region have an estimated range of between 83 km^2 to 263 km^2, approximating a horizontal length scale (horizontal dimension) of 9.1 km and 16.2 km, respectively (Guy 1976a, Dunham 1986). This makes the extent of the study area, i.e. 3721 km^2, which is at least 14 times the estimated range of the elephant in the Sebungwe large enough to study elephant distribution.

2.1.2 Elephant data

The data on the spatial distribution of elephants in the 1980s and 1990s were determined using respectively a combined 1981-1983 data set, and 1993-1995 data set. These data were obtained by the Department of National Parks and Wildlife Management of Zimbabwe's aerial surveys. The aerial surveys were carried out in the dry season, i.e. between August and October of the relevant years. This was considered an appropriate period for studying the effect of spatial heterogeneity on elephant distribution because the crop fields are fallow during this time. Crop fields tend to attract the elephants outside their normal natural range, thus making wet season (October to March) data less reliable for assessing the effect of spatial heterogeneity. In other words, an area that can be suitable for the elephant in the dry season can safely be assumed to be suitable in the wet season.

The data were in digital point map format. We considered the elephant distribution map of our study area $\mathbf{R}$ as a spatial point pattern (Diggle 1983). Each point where elephants were observed is called an event. We calculated the first- order intensity function $\lambda(x)$ for the elephant point map to give an expected number of events per unit area (Fotheringham*, et al.* 2000):

$$\lambda(x) = \lim_{r=0} \frac{E(N(C(x,r),X))}{\pi r^2} \tag{1}$$

where **E(N)** is the expected number of events in the study area considered and $C(x,r)$ a circular sub-region of **R** located at x with a radius r. A kernel function was used in this study with r equal to 3000 m based on the approximate distance (3000 m) that is used to separate transects in wildlife surveys (Cumming 1997b). We then normalised $\lambda(x)$ by dividing it by the expected number of events in **R** to produce a normalised or probability function $\lambda_n(x)$ (Fotheringham*, et al.* 2000):

$$\boldsymbol{\lambda n(x) = \frac{\lambda(x)}{E(N(R,X))}} \tag{2}$$

We used $\lambda_n(x)$ to estimate the spatial distribution of elephants in the study area during the 1980s and 1990s. This method was used because it is spatially explicit and gives weight to elephant location rather than absolute numbers: the aim was to determine whether spatial heterogeneity affects the presence of at least a single elephant and since three elephant survey data sets were combined, adding the total number of observed elephants of the three years would give a false impression about absolute elephant abundance.

2.1.3 Remote sensing data

The amount of vegetation cover was estimated from NDVI derived from the readily available TM images of 19 October 1984 and the one of 16 April 1992:

$$NDVI = \frac{(NIR - R)}{(NIR + R)} \tag{3}$$

where NIR and R are respective spectral reflectance values in the near infrared and the red. Data were normalised to the range of 0 to 255 in order to facilitate data handing in image processing software. Relative radiometric correction of the two images was done using the regression method based on pseudo variant objects such as water bodies, airstrips and roads (fig. 4). This was done to minimise atmospheric effects in the analysis of spatial heterogeneity from NDVI images of the two dates. Fig. 5 shows the NDVI images of the 61 km x 61 km study area. NDVI was used because it is an established index for estimating vegetation quantity (Walsh *et al.* 1997, Walsh *et al.* 2001). Also, NDVI have been shown to provide an effective measure of photosynthetically active biomass (Tucker and Sellers 1986, Los. 1998, Turner*, et al.* 1999, Birky 2001, Hill and Donald 2003) and it is an index of total vegetation biomass (Goward and Dye 1987). Also, NDVI is also strongly related to the extent of vegetation cover and therefore, can be used to detect land cover changes (e.g. woodland replacement with agriculture) and can also be used as an indicator of spatial heterogeneity in the landscape (Kerr and Ostrovysky 2003). Dry season imagery was used in this study because elephant data was collected in the dry season. In addition, it is easier to distinguish between fallow agricultural fields and natural vegetation using NDVI in the dry season than in the wet season, i.e. high NDVI values are expected for natural vegetation and lower NDVI values are expected for fallow agricultural fields (fig. 5).

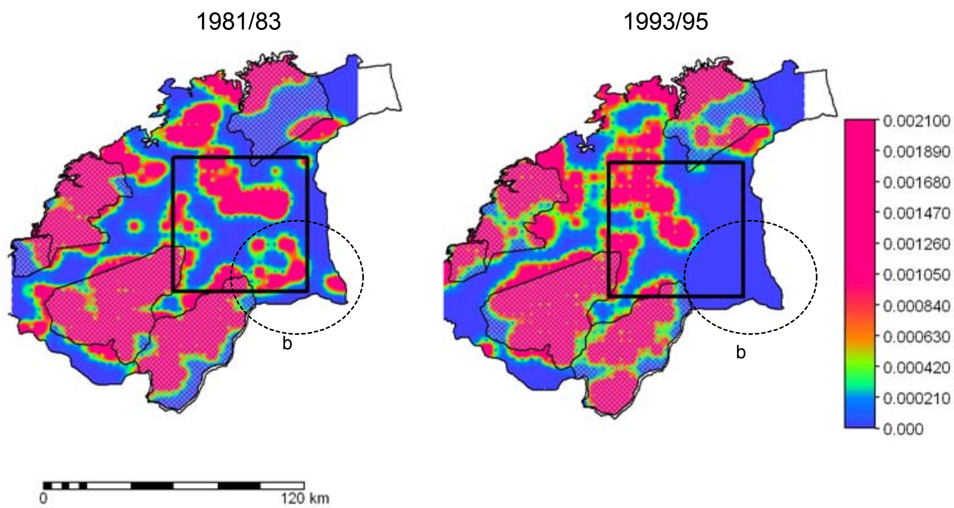


Fig. 3 Maps of the probability of elephant presence in the study area in 1981/83 and 1993/95 and the 61 km by 61 km square box selected for this study. The ellipse (b) illustrates an area where there was a major noticeable decrease in the probability of elephant presence between 1981/83 and 1993/95.

Thus, it is apparent in fig. 5 that areas with low NDVI mainly coincide with agricultural fields. It was assumed that the time differences between the dates of the wildlife surveys and the satellite images was close enough and therefore, had negligible negative effects on the analysis.

Several advantages were envisaged in using Landsat TM imagery to characterise the spatial heterogeneity for the study of elephant distribution. Most importantly, the spatial resolution or grain of Landsat TM, i.e. 30 m by 30 m was deemed detailed enough to enable the quantification of spatial heterogeneity that is relevant for analysing elephant distribution; generally, the grain should be several magnitudes smaller than the total range of the organism (Sparrow 1999). Since elephants in the Sebungwe region have an estimated range of 83 km^2 to 263 km^2, approximating a horizontal length scale (horizontal dimension) of 9.1 km and 16.2 km, respectively (Guy 1976a, Dunham 1986), the grain of 30 m makes it a million times smaller than the minimum range of the elephant.

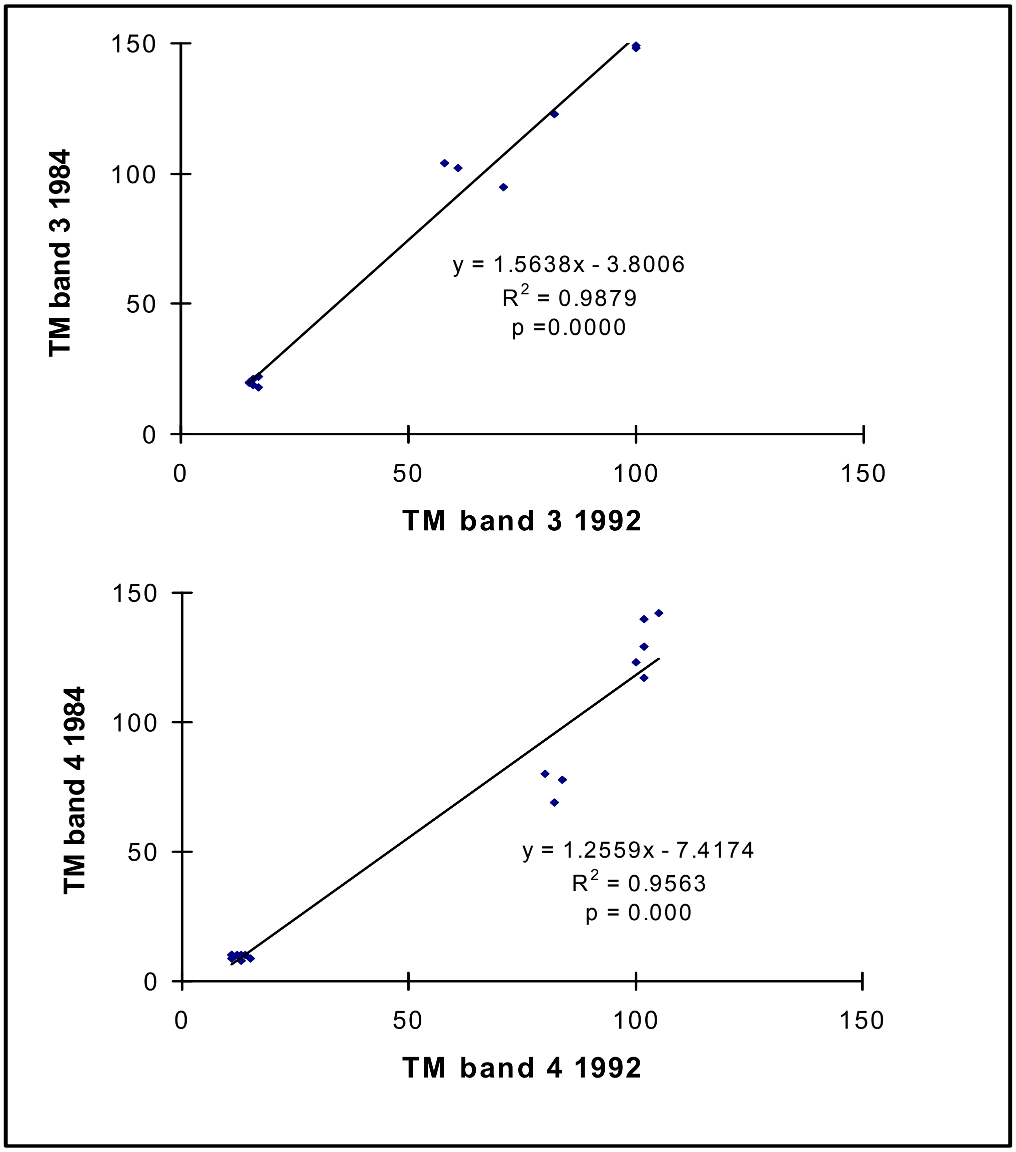


Fig. 4 Relationship between the DN values of sampled pseudo variant objects between the Landsat TM images of 19 October 1984 and 16 April 1992.

2.2 Methods

2.2.1 Characterising spatial heterogeneity using wavelets

Wavelet energy (Bruce and Hong-Ye. 1996) was used to quantify dominant scale and intensity of spatial heterogeneity in the NDVI images of 1984 and 1992. The determination of wavelet energy begins with a wavelet transform (in this study a Haar wavelet was used), which is defined as the convolution of two wavelet functions, i.e. the *smooth* $\phi(x, y)$ and *detail* $\varphi(x, y)$ functions, and an NDVI image $f(x, y)$ at successive bases, (2^j), i.e. $= 0,1,2.$ in the vertical, diagonal and horizontal directions for the 2-dimensional data. A wavelet transform results in a set of coefficients where each coefficient is associated with a base level, $= 0,1,2.$, a direction and a particular location.

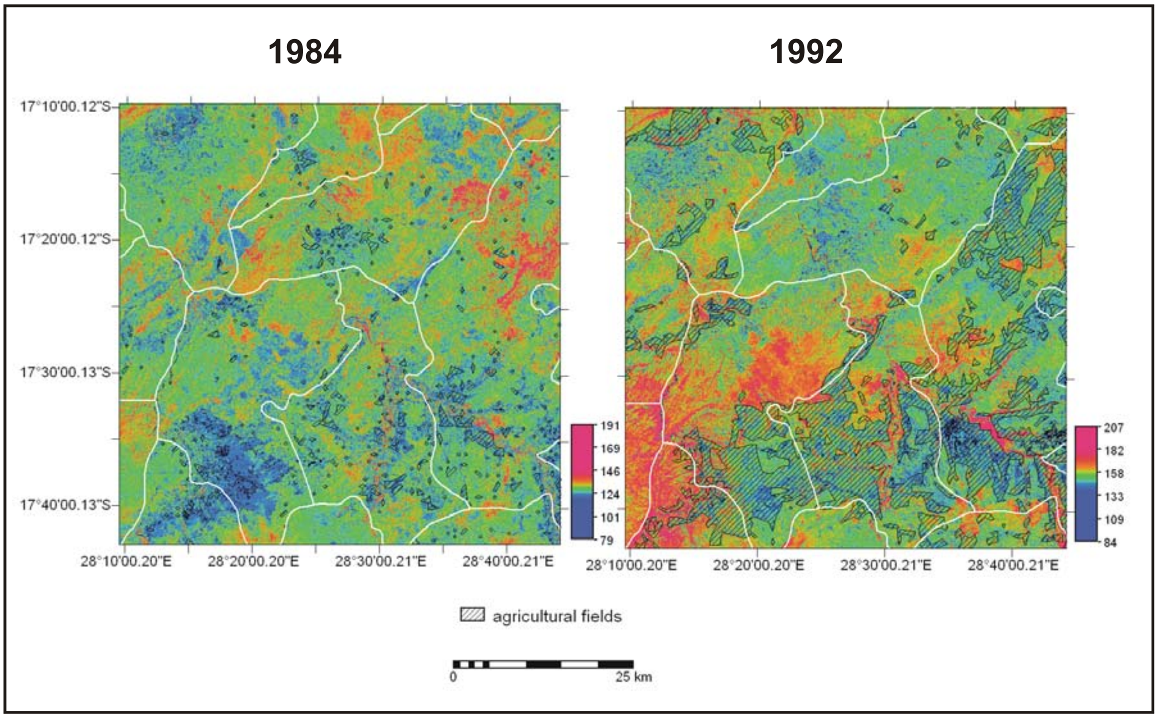


Fig. 4 Map showing the 1984 and 1992 NDVI maps of the 61 km by 61 km square box overlaid with layers of ward boundaries and agricultural fields. The NDVI values were stretched the same way for display to make them comparable but the NDVI ranges were different for 1984 and 1992.

The wavelet approximation $\hat{f}(x, y)$ of the original 2-dimensional function $f(x, y)$ is a sum of the smooths and the detail functions at different bases:

$$\hat{f}(x, y) = S_J(x, y) + \sum_{j=1}^{J} \sum_{dir} D_j^{dir}(x, y) \tag{4}$$

S_J represents the smooth coefficients and D_j^{dir} are the directional (i.e. vertical, horizontal and diagonal) detail coefficients. By convention, the smallest grain of $f(x, y)$ is equals to $j = 0$. Therefore, each scale level j corresponds to a grain equals $2^j * s$ where s is the size of the original grain at which $f(x, y)$ is mapped (in this case 30 m, the spatial resolution of Landsat TM). The decision on the magnitude of J (i.e. the broadest base or window of focus) is made in advance and depends on how much detail is required in the analysis and also on the size of the image. In this study we selected J equals 7, an equivalent of a spatial dimension of 3840 m, slightly larger than the separation distance of flight lines used in wildlife surveys, i.e. 3000 m (Cumming 1997b). Note that the theory and formal treatment of wavelets has been covered exhaustively elsewhere (Mallat 1989, Ogden 1997) and is beyond the scope of this study.

Wavelet coefficients can be positive or negative but the absolute coefficient value measures the magnitude of contrast in $f(x, y)$ at a specific location with a base of 2^j. Wavelet energy was calculated as a second moment of the wavelet transform defined as the sum of squares of the coefficients at base 2^j, divided by the sum of squares of all the coefficients in $\hat{f}(x, y)$:

$$E_j^{\,d} = \frac{1}{E}\sum_{k=1}^{n/2^j} d^2{}_{j(x,y)}, j = 1.,\ldots.J \quad , \tag{5}$$

where $d_{j(x,y)}$ are the detail wavelet coefficients at j and position (x, y), E is the total sum of squares of $\hat{f}(x, y)$ and $n/2^j$ is the number of coefficients at level j. Then, wavelet energy values were plotted against scale and the highest local maxima in the wavelet energy function represented the intensity of spatial heterogeneity while the corresponding scale value represent the dominant scale of spatial heterogeneity (Murwira and Skidmore. 2003). The detail functions rather than the smooth approximations were used in the analysis because they are scale specific. For example, details at j = 1 capture vegetation patches that have a size between 30 m and 60 m. In contrast, smooth coefficients can only capture scales that are equal or greater than 2^j, thus they are not scale specific.

2.2.2 Relating the probability of elephant presence to spatial heterogeneity

The analysis of the relationship between the probability of elephant presence and the dominant scale and intensity of spatial heterogeneity was conducted based on the 61 km x 61 km study area, i.e. in the communal lands of the Sebungwe. The individual units of analysis were defined to be the intersection of the ward boundaries and vegetation class boundaries, thereby incorporating variation due to management and ecological factors respectively. The analysis units were obtained by crossing the ward and vegetation class maps in a Geographical Information system (GIS). The floristic-physiognomic vegetation class map (fig. 2) describes the potential vegetation species, and is therefore constituted by floristic units that are considered stable over time (Timberlake, *et al.* 1993). All in all, 22 units of analysis were used in this study.

Before the probability of elephant presence was related to the dominant scale and intensity of spatial heterogeneity, the wavelet functions for separate wards, as well as physiognomic-floristic vegetation classes (Miombo, Mopane, Miombo-Mopane and Setaria) were plotted and the dominant scale and intensity information was determined each unit of analysis. The Faidherbia vegetation class was excluded in the analysis because it covers a very small part of the study area such that not enough coefficients are included in the Faidherbia unit. Then, the probability of elephant presence in each analysis unit was determined by crossing the map of the probability of elephant presence (fig. 3) and the map of analysis units defined by wards and vegetation classes and calculating the average probability of elephant presence. The mean probability of elephant presence for each unit of analysis was used as a measure of elephant presence in regression analysis.

Next, regression analysis was used to relate the probability of elephant presence to the dominant scale and intensity of spatial heterogeneity respectively using both the 1980s and 1990s data. In addition, the probability of elephant presence was analysed as a function of both the dominant scale and intensity of spatial heterogeneity plus the interaction between the two. Use of data from two dates enabled us to check whether elephant presence was consistently related with the dominant scale and intensity of spatial heterogeneity irrespective of time. The final regression analysis attempted to determine whether there was a relationship between the spatial changes in both dominant scale and intensity of spatial heterogeneity between 1984 and 1992 and the spatial changes in the probability of elephant presence between 1981-83 and 1993-95. To accomplish this, the intensity and dominant scale values of 1984 were subtracted from the respective values of 1992 such that positive values would represent an increase in each respective factor while negative values would represent a decrease in each respective factor between the two periods.

3. Results

3.1 Spatial heterogeneity in Sebungwe in 1984 and 1992

Fig. 6 shows selected wavelet energy functions illustrating changes in dominant scale and intensity of spatial heterogeneity in the study area between 1984 and 1992. Generally, the wavelet energy functions in 1992 had higher values than in 1984. For example, the Setaria typifies changes in both the dominant scale of spatial heterogeneity and intensity of spatial heterogeneity between the two dates. In 1984 the Setaria had larger dominant scales of spatial heterogeneity than in 1992, whereas the intensity of spatial heterogeneity in 1984 and was smaller than in 1992.

Fig. 7 shows a multiscale wavelet coefficient representation of NDVI in the study area in 1984 and 1992. It can be observed that there was a decrease in the dominant scales of spatial heterogeneity in the selected Setaria analysis units from 1920 m and 960 m in 1984 to 240 m and 480 m in 1992 respectively in Nenyunka and Madzivazvido. In contrast, it can be observed that there was no change in the dominant scale of spatial heterogeneity for the selected Miombo-Mopane analysis unit in Madzivazvido between 1984 and 1992.

3.2. Relationship between elephant presence and spatial heterogeneity: 1980s and 1990s

Fig. 8 shows that there were significant ($p < 0.01$) quadratic relationships between the probability of elephant presence and the intensity of spatial heterogeneity both in 1980s and 1990s. It can be observed that as the intensity of spatial heterogeneity increases, there is a concomitant increase in the probability of elephant presence until a certain level and then the probability of elephant presence begins to saturate (fig. 8a) or even decrease (fig. 8b). It can also be observed that the lowest intensity of spatial heterogeneity was recorded in Setaria in 1984 in Simchembo ward (fig. 7a and fig. 1) and in Miombo-Mopane and Miombo both in Nemangwe 5 ward in 1992 (fig. 8b and fig. 1). The regression functions for 1980s and 1990s explain 61 % and 71 % of the variance in the probability of elephant presence respectively.

Fig. 9 shows that there were significant ($p < 0.01$) quadratic relationships between the probability of elephant presence and dominant scale of spatial heterogeneity in 1980s and 1990s. This relationship is such that there is an initial increase in the probability of elephant presence with increasing dominant scale until a certain level after which it can be observed that as the dominant scale of spatial heterogeneity continues to increase, the probability of elephant presence declines. It can also be observed that the largest dominant scale of spatial heterogeneity was recorded in Setaria in Simchembo ward and Miombo in Nabusenga ward in 1984 (fig. 9a) while in 1992 the largest dominant scale was recorded in Miombo and Mopane in Nemangwe 5 and Miombo in Chireya 1 (fig. 9b and fig. 1). The regression functions for 1980s and 1990s explain 65 % and 68 % of the variance in the probability of elephant presence respectively.

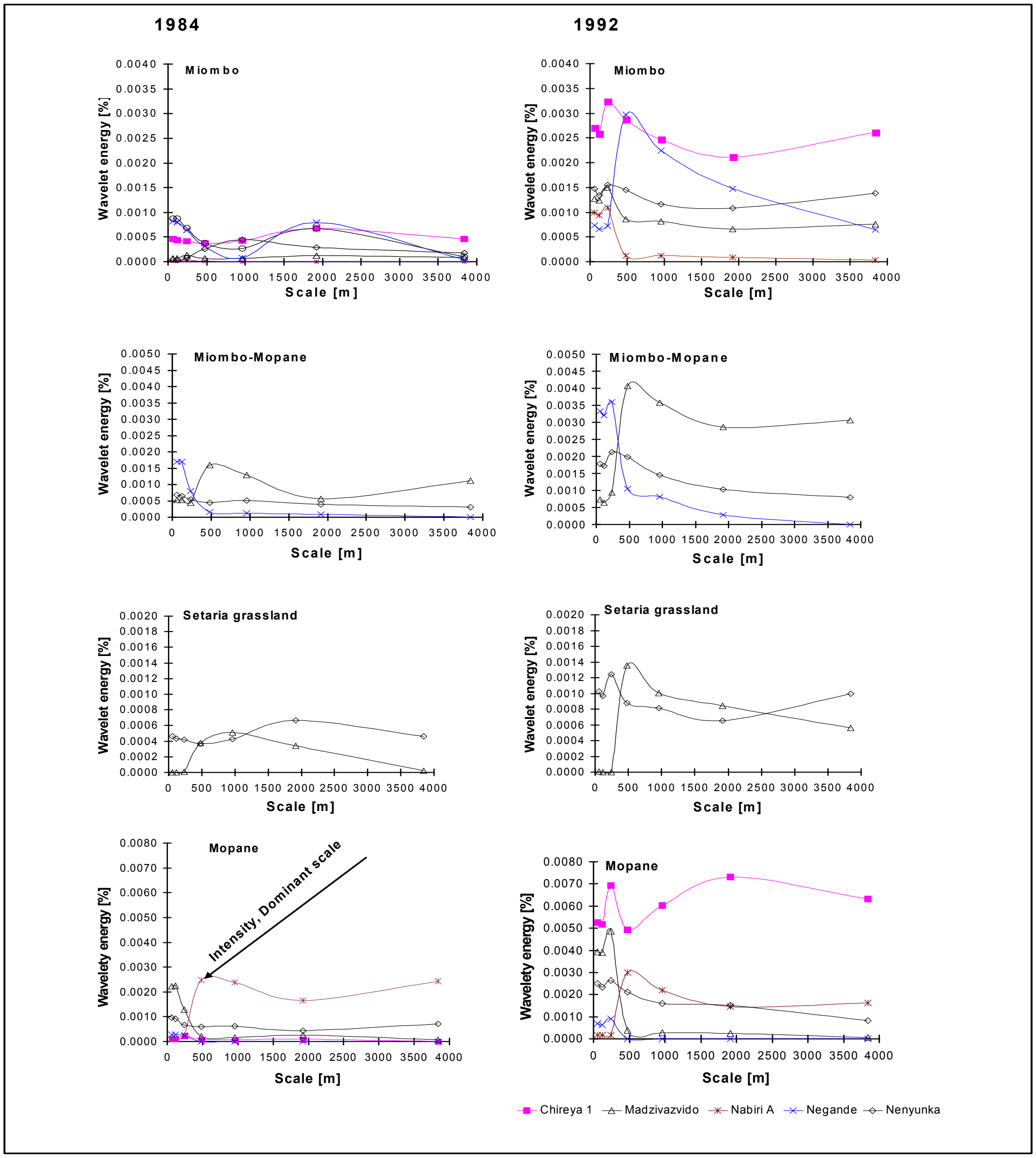


Fig 6. Selected wavelet energy functions illustrating variations in intensity and dominant scale in different wards and vegetation classes in 1984 and 1992. The arrow shows an example of the determination of the intensity and dominant scale of spatial heterogeneity from a wavelet energy function.

Fig. 10 shows that there were significant ($p < 0.01$) relationships between the probability of elephant presence and the interaction between the dominant scale of spatial heterogeneity and the intensity of spatial heterogeneity in 1980s and 1990s. It can be observed that a combination of low intensity of spatial heterogeneity and large dominant scales of spatial heterogeneity is associated with a low probability of elephant presence.

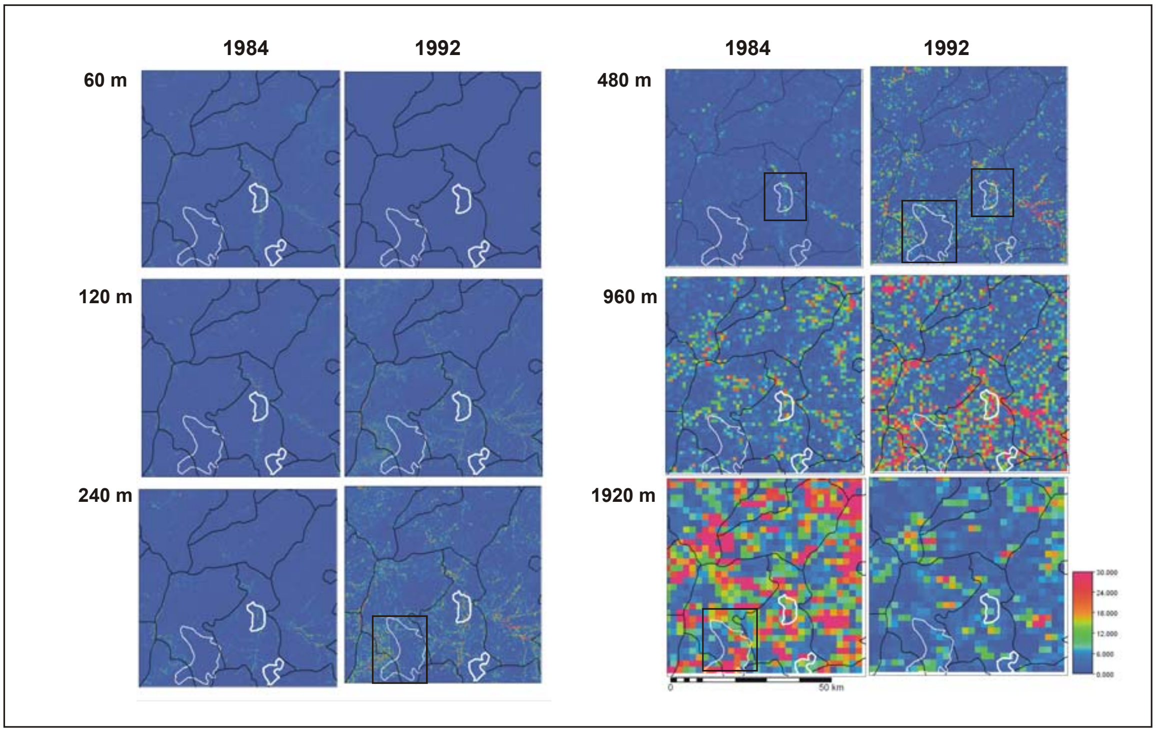


Fig. 7 The spatial distribution of total wavelet energy per pixel at different scales (wavelet spans) across different wards in 1984 and 1992, as well as in selected vegetation class polygons (The total wavelet energy for the image was divided by 1000000 to enhance the wavelet energy for visual presentation). The polygon contained in a larger box depicts Setaria predominantly in Nenyunka ward while the polygon contained in the smaller box is Miombo-Mopane vegetation class in Madzivazvido ward.

For example, it can be observed the Setaria vegetation class in Simchembo ward, had a combined low intensity and large dominant scale in the 1980s and it was associated with a low probability of elephant presence (fig 10a). In addition, it can be observed that the Miombo vegetation class in Nemangwe 5 ward had a combined low intensity and large dominant scale in the 1990s that was associated with a low probability of elephant presence (fig 10b). It can also be observed that agricultural fields covered most of Nemangwe 5 in 1992 (fig. 5). Next, it can be observed that the probability of elephant presence is high in situations where the intensity of spatial heterogeneity is high and dominant scale of spatial heterogeneity is large. For example, it can be observed that the Miombo-Mopane vegetation class in Madzivazvido has a large dominant scale of spatial heterogeneity and a high intensity of spatial heterogeneity that are associated with a high probability of elephant presence (fig. 10).

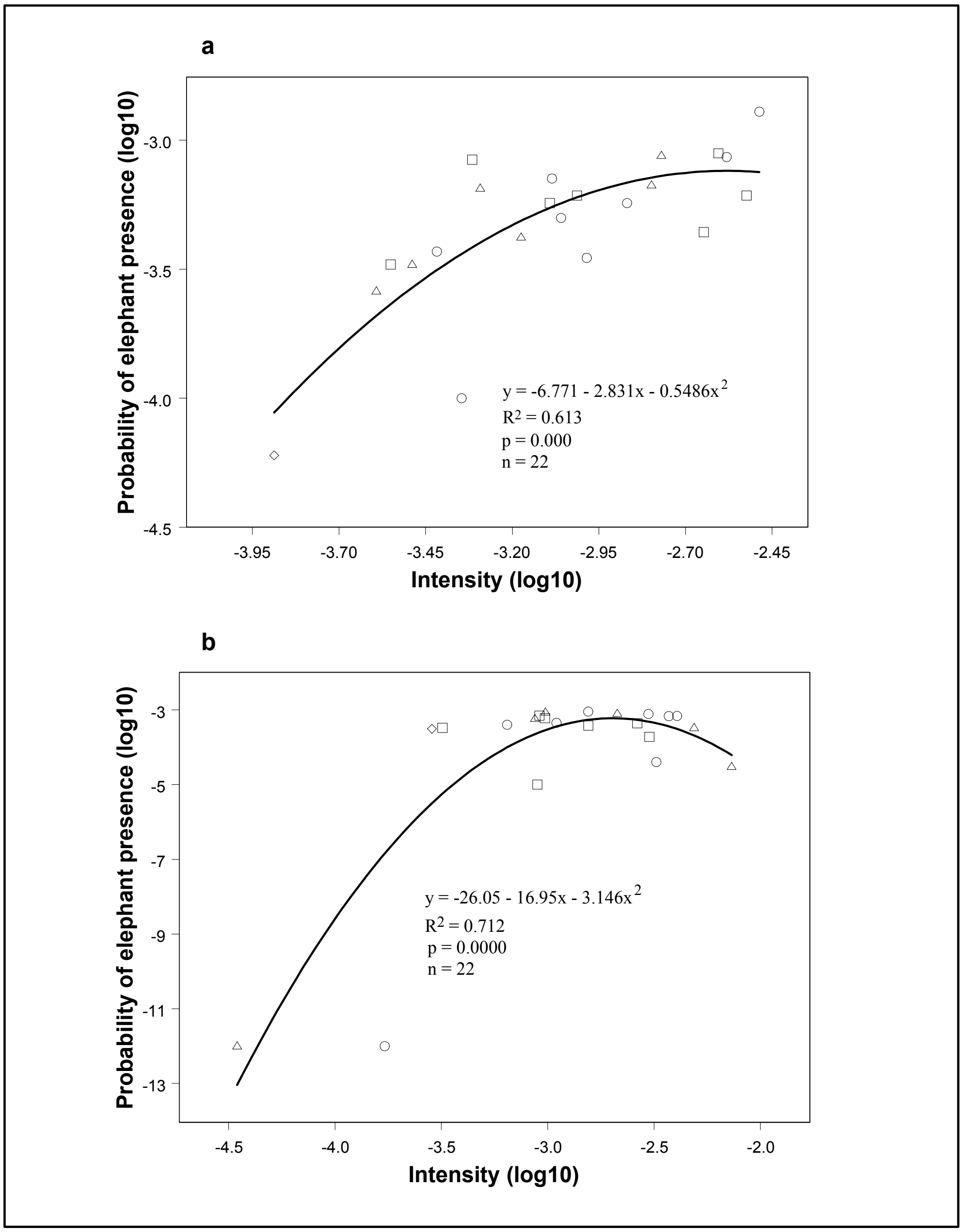


Fig. 8 A significant ($p < 0.01$) relationship between the probability of elephant presence and the intensity of spatial heterogeneity (intensity) in the study area in the (a) 1980s and (b) 1990s in (○) Miombo, (□) Mopane, (◇) Setaria and (△) Miombo-Mopane floristic-physiognomic vegetation classes.

A general observation based on fig. 10 is that an increase in the intensity of spatial heterogeneity is associated with a moderate increase in the probability of elephant presence at small dominant scales of spatial heterogeneity while it leads to a higher increase in the probability of elephant presence at larger dominant scales of spatial heterogeneity in (fig. 10). All in all, the regression functions of the 1980s and the 1990s explain 80 % and 93 % of the variance in the probability of elephant presence respectively (fig. 10).

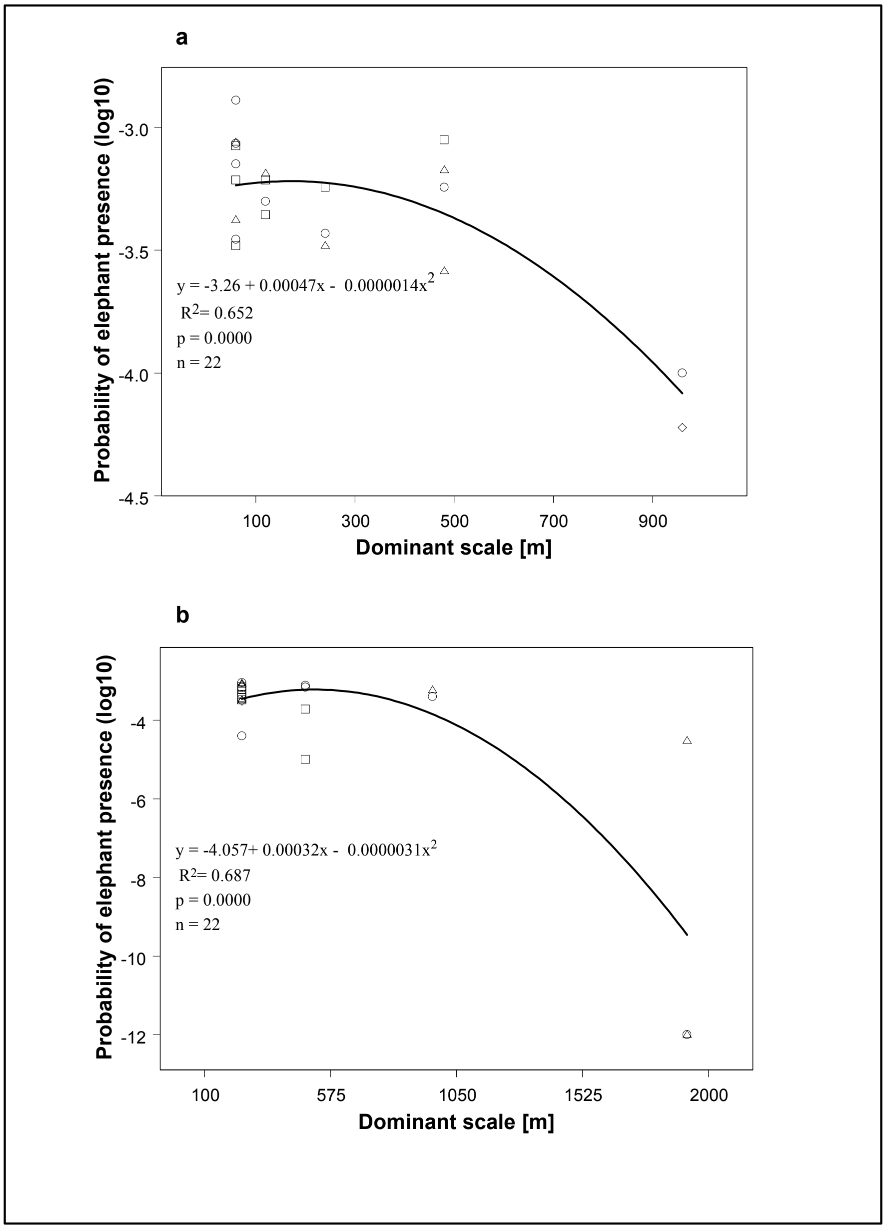


Fig. 9 A significant ($p < 0.01$) relationship between the probability of elephant presence and the dominant scale of spatial heterogeneity (dominant scale) in the study area in the (a) 1980s and (b) 1990s in (❍) Miombo, (☐) Mopane, (◇) Setaria and (△) Miombo-Mopane floristic-physiognomic vegetation classes.

3.2. Relationship between change in elephant presence and change in spatial heterogeneity

When the spatial changes in the probability of elephant presence between 1983 and 1995 were related with spatial changes in dominant scale and intensity of spatial heterogeneity between 1984 and 1992, the results showed a statistically significant ($p < 0.01$) relationship (fig. 11). It can be observed that a combination of an increase in intensity of spatial heterogeneity and a decrease in the dominant scale of spatial heterogeneity were associated with a decrease in the probability of elephant presence in the study area. On the other hand, a decrease in the intensity of spatial heterogeneity in combination with an increase in the dominant scale of spatial heterogeneity is also associated with the decrease in the probability of elephant presence.

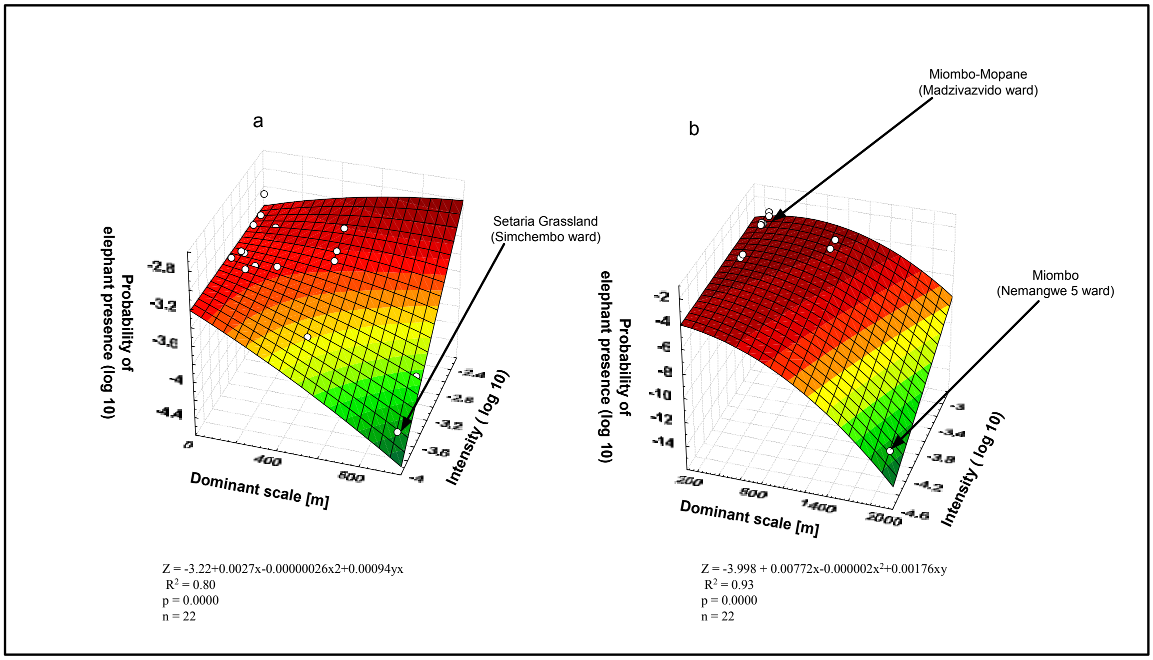
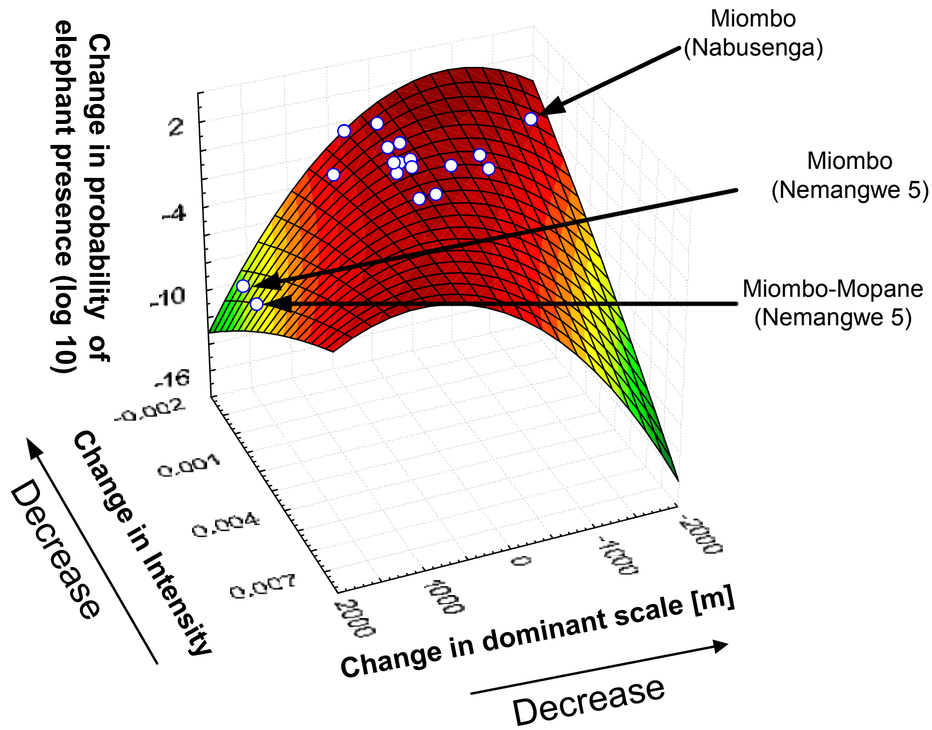


Fig. 10 A significant (p < 0.01) relationship between the probability of elephant presence and the intensity and dominant scale of spatial heterogeneity plus their interaction in the (a) 1980s and (b) 1990s.

For example, a combination of the decrease in the dominant scale of spatial heterogeneity and the increase in intensity of spatial heterogeneity in Setaria in Nenyunka ward were associated with a decrease in the probability of elephant presence (fig. 6, fig. 7 and fig 11). Concurrently, an increase in agricultural fields in the same land unit between 1984 and 1992 can be observed (fig. 5).

In addition, a combination of the increase in dominant scale of spatial heterogeneity and the decrease in intensity of spatial heterogeneity in the Mopane vegetation class in Nemangwe 5 ward was associated with a decrease in the probability of elephant presence (fig. 6, fig. 7 and fig 11). Also, a concurrent increase in agricultural fields in the same land unit between 1984 and 1992 (fig. 5) can be observed.

In contrast, it is apparent (fig. 11) that a combined increase in the intensity of spatial heterogeneity and dominant scale of spatial heterogeneity was associated with an increase in the probability of elephant presence up to a certain level and then it decreases. For example an increase in the intensity and dominant scale of spatial heterogeneity in the Miombo vegetation class in Nabusenga was associated with an increase in the probability of elephant presence (fig. 11) The regression function explained 89 % of the variance of the change in probability of elephant presence between the 1980s and 1990s.



$Z = 0.567 - 0.0019x - 0.0000018x^2 - 59.69y + 25374.9y^2 + 0.707xy$
$R^2 = 0.89$
$p = 0.000$

Fig. 11 A significant (p < 0.01) relationship between change in the probability of elephant presence and changes in the intensity and dominant scale of spatial heterogeneity between the 1980s and 1990s.

4. Discussion

The intensity and the dominant scale of spatial heterogeneity reliably predicted the spatial distribution of elephants in the human dominated savanna landscapes of the Sebungwe. In addition, the changes in both intensity and dominant scale of spatial heterogeneity in the landscape could also reliably predicted changes in the spatial distribution of the elephant between the early 1980s and the early 1990s. Where our findings differ significantly from those based on the direct image approach (Oindo and Skidmore 2001) and patch mosaic approach (Osborn and Parker 2003) is in the comprehensive way we characterised spatial heterogeneity (based on the intensity and dominant scale approach). Using the intensity and the dominant scale as inseparable properties of spatial heterogeneity, we were not only able to characterise the variability that is emphasized by the direct image approach by using the intensity of spatial heterogeneity, but we were also able to characterise the patch size that the patch mosaic approach emphasizes by using the dominant scale. Furthermore, using wavelet transform, which treats a landscape property such as vegetation cover as a continuum, we incorporated the gradient that characterises patch boundaries in the savanna landscape, thereby avoiding the crisp boundary approach based on image classification (Murwira and Skidmore (2003).

The probability of elephant presence in the Sebungwe is significantly related to the individual properties of spatial heterogeneity (intensity and dominant scale) (fig. 8 and fig. 9). With regards to the relationship with the intensity of spatial heterogeneity, the results imply that elephants in the Sebungwe prefer areas with relatively high amounts vegetation compared with areas with low amounts of vegetation (fig. 5, fig. 8). This result is supported by Guy, (1976b) who reported that elephants in the Sebungwe associate with areas of high vegetation density to maximise their chances of finding food. Elephants also prefer high vegetation density for temperature regulation (Guy 1976a), as well as to maximise chances of cover from human harassment including hunting during the official hunting season (i.e. in the dry season). However, the fact that this relationship either saturates or even decrease at high intensity values imply that as the amount of vegetation increases beyond a certain level, it either no longer has an effect on elephant presence or it even results in a negative trend (fig. 8) just like in the species richness-productivity relationship (Said 2003). But it may as well be due to the related influence of the dominant scale of spatial heterogeneity, i.e. the patch size at which the intensity is manifested. This is because the quadratic relationship between the probability of elephant presence and dominant scale of spatial heterogeneity means that elephants avoid very small and very large dominant scales of spatial heterogeneity, but prefer intermediate dominant scales of spatial heterogeneity (fig. 9). We know that relatively large dominant scales of spatial heterogeneity indicate the domination of landscape by large patch sizes while relatively small dominant scales of spatial heterogeneity indicate the domination of the landscape by small patch sizes.

Earlier (in the introduction) we demonstrated that the intensity and dominant scale of spatial heterogeneity are inseparable properties of a continuous landscape property such as vegetation cover. Our findings indicated that the spatial distribution of elephants responds to a combined effect of both intensity of spatial heterogeneity and the dominant scale of spatial heterogeneity. The findings indicate that elephants avoid two main environments. Firstly, the results indicated that elephants avoid areas with low quantities of vegetation that occur at large patch sizes, i.e. by showing that a combination of low intensity of spatial heterogeneity occurring at large dominant scales that is characteristic of landscapes with low amounts of vegetation cover such as grasslands (fig.4 and fig. 10a) and agricultural fields (fig. 5 and fig. 10b) in the Sebungwe are associated with a low probability of elephant presence. In an agricultural area within a savanna landscape such as the Sebungwe, it is known that there will never arise a situation where a complete tree cover results in low intensity of spatial heterogeneity at a large dominant scale situation. Therefore, low intensity at large dominant scales is always associated with grassland or agriculture. Secondly, the results indicate that elephants also avoid environments dominated by small patches of both high vegetation cover (e.g. remnants of woodland) and low vegetation cover, (e.g. patches of bare ground, grassland or agricultural fields), i.e. elephants avoid environments that have either high or low intensity that occur at the small dominant scales of spatial heterogeneity. In contrast, our findings indicate that elephants prefer environments characterised by large patch sizes of high vegetation cover and fewer agricultural fields, i.e. there is a high probability of elephant presence in environments with high intensity of spatial heterogeneity and medium to large dominant scales of spatial heterogeneity. However, we do not expect an infinite increase in the probability of elephant presence with increases in the intensity and the dominant scale of spatial heterogeneity because at very large dominant scales elephant presence tends to decline. This phenomenon is probably because very high intensity values and very large dominant scales can indicate the existence of both very low vegetation cover (e.g. agricultural fields and bare ground) and very high vegetation cover (e.g. of remnants of woodland) that both occur in very large patches. In this scenario, it is the hostile patches (agricultural fields or bare ground) that drive the elephants away. Overall, we can deduce that intensity and the dominant scale of spatial heterogeneity act together to influence the degree of elephant presence in the agricultural landscapes of the Sebungwe.

Elephants leave locations where an increase in the intensity of spatial heterogeneity occurs together with a decrease in dominant scale of spatial heterogeneity, suggesting that elephants avoid areas that are increasingly being dominated by small patches with predominantly low vegetation cover. This phenomenon is equivalent to an area being increasingly dominated by small patch sizes of agricultural fields or bare ground. In addition, the increase in agricultural fields in parts of the study area such as in Chireya 1 that was associated with a decline in the intensity of spatial heterogeneity and an increase in the dominant scale of spatial heterogeneity resulted in a decline in the probability of elephant presence. In contrast, elephant presence increased with increases in both intensity and the dominant scale of spatial heterogeneity, suggesting that elephants prefer environments that are changing into having large patches with high vegetation cover and fewer agricultural fields. However, we do expect only a finite increase in elephant presence being associated with increases in both the intensity and dominant scale of spatial heterogeneity because at very large dominant scales, elephant presence tends to decline. Consequently, we deduce that a combined change in the intensity and dominant scale of spatial heterogeneity had a significant effect on the probability of elephant presence in the communal lands of the Sebungwe region between the 1980s and 1990s.

Our findings indicate that humans and elephants can coexist in the agricultural landscapes of the Sebungwe when appropriate levels of spatial heterogeneity, i.e. appropriate levels of intensity of spatial heterogeneity occurring at appropriate dominant scales of vegetation cover are maintained in the landscape. In other words, our findings indicate that CAMPFIRE can work if the response of the spatial distribution of elephants, among other wildlife species, to the intensity and the dominant scale of spatial heterogeneity in space and the response of the spatial distribution of elephants to changes in the intensity and the dominant scale of spatial heterogeneity over time is understood.

5. Conclusions

In this study, two hypotheses were tested. Firstly, we tested whether and how elephants were related to the intensity and dominant scale of spatial heterogeneity in the agricultural landscape of the Sebungwe. Secondly, we tested whether and how spatial changes in elephant presence were related to changes in the intensity and dominant scale of spatial heterogeneity agricultural landscape of the Sebungwe between the early 1980s and the early 1990s. Consequently, some conclusions and management recommendations can be drawn from the results:

- The intensity and dominant scale of spatial heterogeneity can reliably predict elephant distribution in an agricultural landscape.

- Changes in the intensity and dominant scale of spatial heterogeneity can also reliably predict changes in elephant distribution.
- In managing the Sebungwe landscape to enhance wildlife species presence for the benefit of CAMPFIRE, management decisions should take into consideration the factor of spatial heterogeneity when planning the amount and spatial arrangements of agricultural fields.
- Considering the dominant scale and intensity factors improves the characterisation of spatial heterogeneity from remote sensing that can be useful in predicting other ecological patterns such as the distribution of different wildlife species.

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