Elephant response to spatial heterogeneity in a savanna landscape of northern Tanzania

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Landscape heterogeneity, namely the variation of a landscape property across space and time, can influence the distribution of a species and its abundance. Quantifying landscape heterogeneity is important for the management of semi-natural areas through predicting species response to landscape changes, such as habitat fragmentation. In this paper, we tested whether the change in spatial heterogeneity of the vegetation cover due to farming expansion affected the distribution of the African elephant in the Tarangire-Manyara ecosystem, northern Tanzania. Spatial heterogeneity (based on the normalized difference vegetation index) was characterized at multiple spatial scales using the wavelet transform and the intensity-dominant scale method. Elephant distribution was estimated from time-series aerial surveys using a kernel density function. The intensity, which relates to the contrast in vegetation cover, quantified the maximum variation in NDVI across multiple spatial scales, whereas the dominant scale, which represents the scale at which this maximum variation occurs, identified the dominant inter-patches distance, i.e. the size of dominant landscape features. We related the dominant scale of spatial heterogeneity to the probability of elephant occurrence in order to identify: 1) the scale that maximizes elephant occurrence, and 2) its change between 1988 and 2001. Neither the dominant scale and intensity of spatial heterogeneity, nor the probability of the elephant occurrence changed significantly between 1988 and 2001. The spatial scale maximizing elephant occurrence remained constant at 7000 to 8000 m during each wet season. Compared to the findings of a recent, similar study in Zimbabwe, our results suggest that the change in the dominant scale was relatively small in Tarangire-Manyara ecosystem and well within the critical threshold for elephant persistence. The method is a useful tool for monitoring ecosystems and their properties.
difference vegetation index (NDVI). For the intensity-dominant scale method, the intensity refers to the maximum contrast or variance in vegetation cover (e.g. in NDVI) measured at successively increasing window sizes (e.g. at multiple scales). The dominant scale represents the window size (e.g. scale) at which this maximum variance occurs. In other words, the intensity quantifies the maximum change in the vegetation cover across multiple spatial scales, whereas the dominant scale quantifies the ‘dominant’ inter-patches distance, i.e. the size of dominant landscape features. Consequently, the dominant scale directly relates to the level of patchiness (or fragmentation) of a landscape (Murwira and Skidmore 2006). Importantly, as shown by Pittiglio et al. (2011), this method is robust when used with different pixel sizes, such as Orthophoto (1 m pixel size), Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER, 15 m) and Landsat Enhanced Thematic Mapper Plus (ETM+, 30 m) – in other words the Murwira–Skidmore method is grain independent, for features equal or larger than the original pixel size (Pittiglio et al. 2011).

Murwira and Skidmore (2005) applied the intensity-dominant scale method to quantify change in landscape heterogeneity (and fragmentation) and its relation to the distribution of the African elephant *Loxodonta africana* in an agriculture-dominated savanna landscape in Zimbabwe. That study showed that the decline in elephant population between the early 1980s and early 1990s was correlated to a decrease in the dominant scale of landscape heterogeneity from about 750 to 450 m (i.e. an increase in patchiness and consequently in habitat fragmentation), caused through farm expansion (Murwira et al. 2010). The same study revealed that elephants disappeared from the ecosystem when the dominant scale decreased to <400 m, meaning that the landscape became too fragmented for the elephant persistence (Murwira and Skidmore 2005).

In this paper we used the intensity-dominant scale method based on wavelet transform to test whether a change in spatial heterogeneity of vegetation cover due to farming expansion affected the wet season distribution of the African elephant between 1988 and 2001 in the Tarangire-Manyara ecosystem, northern Tanzania. Our focus was the African elephant between 1988 and 2001 in the Tarangire-Manyara ecosystem, northern Tanzania. The research area includes protected (Tarangire and Lake Manyara National Parks), semi-protected (Manyara Ranch, Lolkisale and Mkungunero Game Controlled Areas) and unprotected areas (Fig. 2). The Tarangire-Manyara ecosystem is predominantly formed by a gently undulating plateau with elevations and dominant scale method – Murwira and Skidmore (2005)) can affect elephant occurrence, with specific reference to the Tanzanian and Zimbabwean case studies. Gradient landscapes in Fig. 1a, comprising semi-natural savanna, are characterized by a variation in vegetation cover. The dominant scale of spatial heterogeneity is large, representing (and matching) large dominant patches of relatively homogeneous vegetation (Fig. 1a, $t_1$). As farming expands in savanna ecosystems, the patches of natural vegetation become increasingly fragmented and smaller; consequently, the dominant scale is reduced (Fig. 1a, $t_2$). Eventually, the landscape becomes characterized by large blocks of farms and small patches of natural vegetation and the dominant scale is large (Fig. 1a, $t_3$). In savanna ecosystems the grass (including crops) is brighter than trees in the wet season. At the beginning of the conversion process ($t_1$), the intensity (which is directly related to the brightness of the satellite image and to NDVI) is low, because of the relatively homogeneous brightness of natural vegetation (Pittiglio et al. 2011). At $t_2$, the intensity increases because the NDVI variation (and reflectance) between crops and natural vegetation is higher and the boundary between these patches is crisp. The highest intensity occurs at $t_3$, because the reflectance of crops is at a maximum, and higher than grass and trees in the wet season.

The probability of elephant occurrence remains high and relatively stable in semi-natural savanna, while only small changes in the dominant scale occur (determined by small and sparse arable fields, Fig. 1b, point A). Then the probability of elephant occurrence slowly decreases in response to habitat fragmentation (and consequently smaller dominant scales) (Fig. 1b). However, as observed in Zimbabwe by Murwira and Skidmore (2005), when the patches of natural vegetation become increasingly fragmented and the size of the dominant scale reaches a certain threshold, the probability of elephant occurrence drops sharply, disappearing from the ecosystem (Fig. 1b, point B). Because the elephant population of the Tarangire-Manyara ecosystem remained stable during the study period, we hypothesized that: a) the dominant scale of spatial heterogeneity that maximizes elephant occurrence was large, representing large patches of natural vegetation (see point A, Fig. 1b); b) compared to the findings in Zimbabwe, the change in the dominant scale was expected to be relatively small in Tarangire-Manyara ecosystem and not approaching the critical threshold (point B) of elephant persistence.

**Methods**

**Study area**

The Tarangire-Manyara ecosystem (between 3°36’S and 4°7’S, and 35°82’E and 36°74’E) is part of the Maasai steppe and hosts the largest population of elephant *Loxodonta africana* in northern Tanzania. The research area includes protected (Tarangire and Lake Manyara National Parks), semi-protected (Manyara Ranch, Lolkisale and Mkungunero Game Controlled Areas) and unprotected areas (Fig. 2). The Tarangire-Manyara ecosystem is predominantly formed by a gently undulating plateau with elevations...
between 1000 and 2000 m a.s.l. The annual average rainfall is 450–650 mm (Prins and Loth 1988). The rainfall pattern is bimodal with short rains occurring from November to December and long rains from February to May. Two types of open savanna are found in the Tarangire-Manyara ecosystem: microphyllous savanna on the riverine areas dominated by *Acacia tortilis* trees, and broad-leaf deciduous savanna on the ridges and upper slopes dominated by *Combretum* and *Commiphora* species (Lamprey 1963). Vegetation descriptions have been given by Lamprey (1963), Loth and Prins (1986), and Kahurananga (1979) for different parts of the Tarangire-Manyara ecosystem. Seasonal distribution of elephant and its determinants can be found in Pittiglio et al. (2012).

**Locations and estimation of elephant occurrence**

Elephant distribution was studied by point pattern analysis of the GPS locations (grid cell centroids) obtained by the Systematic Reconnaissance Flight method – SRF (Norton-Griffiths 1978, TAWIRI 2001) in May 1988 and May 2001, during the wet season. SRF data consisted of a 5 by 5 km grid (totally 587 cells), covering an area of 14 675 km². For each grid cell the elephant density per km² is reported. The elephants were recorded in 458 grid cells in May 1988 and 507 grid cells in May 2001. Although the elephant is highly detectable in the open vegetation (Prins and Douglas-Hamilton 1990), it is also vagile and inhabits heavily wooded as well as narrow riverine forest areas. Because these characteristics may affect the accuracy of distribution models based on point data (McPherson and Jetz 2007) and because SRF data are seasonal population samples (Norton-Griffiths 1978), we estimated the elephant distribution using a kernel density function, as described by Pittiglio et al. (2012). The standard bivariate normal kernel density function (Silverman 1986) was used to estimate the probability of elephant occurrence in both
years, weighted by the elephant density per location (Horne and Garton 2006) and normalized between 0 and 1. Hence, locations with higher elephant density had a higher probability of elephant occurrence. A threshold of 95% of the probability volume contour (Kernohan et al. 2001) defined the area of occupancy by elephants. To avoid over- or under-smoothing the data, the smoothing parameter $h$ was selected using the likelihood cross validation (CVh) method (Horne and Garton 2006). In 2001 the total counts aerial survey (Norton-Griffiths 1978) and the SRF survey were both flown in May (the wet season), but a few days apart (TAWIRI 2001). Because these surveys produced a different estimation of elephant occurrence in southern Tarangire-Manyara ecosystem, the two data sets were integrated. In particular, the probability of the elephant occurrence generated separately for each survey were added together and normalized between 0 and 1. To calculate the elephant CVh yr$^{-1}$, we used Animal Space Use 1.3. beta (Horne and Garton 2009). The Kernel analysis was performed using Hawth’s analysis tools 3.27 (Beyer 2004).

The wavelet transform analysis

The wavelet transform is a convolution of the wavelet function with the satellite image data. Generally speaking, it can be thought of as a cross-correlation of the image with a set of wavelets with various ‘widths’ (Addison 2002). By moving the wavelet along the image, the transform quantifies the local match of the wavelet with the image at different locations and scales, thereby identifying coherent features related to a specific scale in the image (Addison 2002). The Haar wavelet detects edges, boundary and abrupt discontinuity in the data such as, changes and gaps in the canopy cover (Bradshaw and Spies 1992). We used the Haar two-dimensional Discrete Wavelet Transform (2D DWT) and multi-resolution analysis to quantify the intensity and the dominant scale of NDVI-derived landscape heterogeneity from remotely sensed data (Murwira and Skidmore 2006, Pittiglio et al. 2011). The DWT decomposes the image with orthogonal wavelets (the smooth and the detail function), which act like low- and
high-pass filters at successive bases \((2^j, j = 0,1,2,...,J)\) in the vertical (north to south), diagonal (north-east to south-west and south-east to north-west), and horizontal (east to west) direction. At each level of decomposition (which follows a sequence of the power of 2), the transform produces 4 outputs: the ‘smooth’ (which is an averaged south-west and south-east to north-west), and horizontal in the vertical (north to south), diagonal (north-east to south-west and south-east to north-west), and ‘horizontal’ details (Bruce and Gao 1996). The details express the deviations from the average value of the image at each direction and scale (Bruce and Gao 1996). Each output contains a set of coefficients (called crystal or subband; Daubechies 1992, Bruce and Gao 1996): high absolute values represent a good match between the wavelet and the data (i.e. a change in vegetation cover); small or zero values a lack of match. Each coefficient is associated with a base level (scale \(j = 1,2,...,J\)), a direction and a particular location. By iteratively decomposing the image, the transform estimates the underlying smooth version of the original image, the ‘vertical’, the ‘diagonal’, and the ‘horizontal’ details (Bruce and Gao 1996). The amount of vegetation cover was estimated from the energy calculation (Donoho and Johnstone 1995). The wavelet energy was used to determine the intensity and dominant scale of landscape heterogeneity. The composite wavelet energy (i.e. the sum of the wavelet energy in the different directions at each level \(j\); Murwira and Skidmore (2006) was plotted against scale to obtain the wavelet energy curve. Then the maximum intensity and the dominant scale across all levels of decomposition \((j)\) were determined by selecting the highest wavelet energy value (i.e. maximum intensity) of the curve (Pittiglio et al. 2011). Only the composite wavelet energy function of the detail coefficients was used because detail functions are scale specific (Murwira and Skidmore 2006). The wavelet energy curve is similar to a scalogram, which plots the average wavelet variance against scale (Dale and Mah 1998).

To efficiently analyze the study area with the wavelet transform, the images were split into 20 contiguous quadrants of \(30720 \times 30720\) m (i.e. \(1024 \times 1024\) pixels in TM and ETM+), and \(2048 \times 2048\) pixels in ASTER), and each quadrant was decomposed from the finest to the coarsest scale along intervals of the power of 2. Contiguous quadrats is a recommended technique in spatial ecology to study patterns on gradients (Dale 1999). Only quadrants included in the SRF survey area were considered for the analysis \((n = 14;\text{ total area } = 13,212 \text{ km}^2;\text{ Fig. 2})\). The intensity and dominant scale of each image were calculated for each quadrant and the results between years were compared within the common scale range of 60 to 15,360 m, at intervals of the power of 2. The size of the quadrants was chosen according to the average home range extent of the elephants in this area (average linear dimension = 30 km; Galanti et al. 2000). The quadrants represent the sampling units for the statistical analysis (Dale 1999).

The wavelet transform was performed in IDL 6.4.1 (ITT), using a revised version of the available Haar 2D DWT script, which is based on Mallat’s algorithm (Mallat 1989) and Press et al. (1992). The SURE thresholding was performed in R (R Development Core Team), using the Waveslim package (ver. 1.6.4; Whitcher 2010).

### Estimating the amount of vegetation cover and farming expansion from satellite images

The amount of vegetation cover was estimated from the NDVI using the near-infrared and red bands of the satellite images (Walsh et al. 1997) acquired at the time of the elephant surveys. NDVI is a measure of the amount of canopy ‘greenness’ (Glenn et al. 2008), and can be considered an indicator of the vegetation cover, specifically the green vegetation cover (Roderick et al. 1999). NDVI has been successfully used to explain the distribution of herbivores (Petorelli et al. 2005) including the elephant (Murwira and Skidmore 2005). As most of the images acquired in the wet season were affected by high cloud cover (between 20 and 90%), only six images (Table 1) could be selected for our analysis: two adjacent TM images from 17 October 1988 (path/row: 168/62 and
168/63; 0% cloud cover), two ETM+ images from 21 February 2000 (path/row: 168/62 and 168/63; 0% cloud cover), one ETM+ image from 28 April 2001 (path/row: 168/63; 12% cloud cover), and one ETM+ image from 2 June 2002 (path/row: 168/63; 17% cloud cover). Drought significantly affects the green vegetation cover and consequently the dominant scale. The ETM+ 2000 image was characterized by a prolonged dry season (TWCM 2000). Hence only 8 quadrants of the ETM+ images (showing cultivation in 2000 or cloudless in 2001–2002) could be considered for the analysis (Table 1). Because a recent study by Pittiglio et al. (2011) demonstrated that the dominant scale of spatial heterogeneity in semi-natural areas is not affected by pixel size (e.g. ETM+ versus ASTER), we used nine adjacent ASTER cloudless images (EOS, 15 m) from 27 January and 5 February 2006 for the remaining quadrants. The wavelet energy curves from the NDVI of the ASTER 2006 were compared with those obtained from the NDVI of the ETM+ 2000, 2001 and 2002 for each shared quadrant. The dominant scale was obtained from the ASTER images if these curves were similar, and from the ETM+ images otherwise. A detailed description of the satellite data processing can be found in the Supplementary material Appendix 1.

To quantify farming expansion, a shapefile of crop farming in 1988 and 2000 (OIKOS 2002) was updated for the study area by digitizing new farms from the satellite images acquired for the wavelet analysis. The amount of cultivation was calculated for each quadrant and related to the dominant scale of landscape heterogeneity for both 1988 and 2001.

### Table 1. Comparison between the dominant scale of NDVI-derived landscape heterogeneity from ETM+ 2000, 2001, 2002 and ASTER 2006 images for each quadrant and the assigned dominant scale for the analysis.

<table>
<thead>
<tr>
<th>Quadrant</th>
<th>ETM+ 2000 dominant scale</th>
<th>ETM+ 2001 dominant scale</th>
<th>ETM+ 2002 dominant scale</th>
<th>ASTER 2006 dominant scale</th>
<th>Assigned dominant scale</th>
</tr>
</thead>
<tbody>
<tr>
<td>000_000</td>
<td>15 360</td>
<td>15 360</td>
<td>15 360</td>
<td>15 360</td>
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<td>15 360</td>
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<td>15 360</td>
</tr>
</tbody>
</table>

Relating the probability of elephant occurrence to landscape heterogeneity

To test whether elephant distribution and landscape heterogeneity changed significantly between 1988 and 2000, we calculated the average probability of elephant occurrence, the dominant scale and the intensity of NDVI-derived landscape heterogeneity for each quadrant of 30'720 by 30'720 m (n = 14) and for each year. The variables were square root transformed to approximate a normal distribution prior to performing the statistical analysis. The difference between the average probability of elephant occurrence between 1988 and 2001 was tested using a t test for paired samples. This test was also applied to compare the average dominant scale of NDVI-derived landscape heterogeneity (hereafter named dominant scale of landscape heterogeneity) between the same periods. The non-normality of the average intensities of NDVI-derived landscape heterogeneity (hereafter named intensity) could not be removed by any transformation. The nonparametric Wilcoxon signed-rank test was therefore applied to test for the difference in median intensity between 1988 and 2001. To quantify the spatial scale maximizing elephant occurrence, the probability of elephant occurrence was regressed for each quadrant against the dominant scale of landscape heterogeneity. A quadratic function was chosen, following the method by Murwira and Skidmore (2005). Only the quadrants within the kernel contours (average normalized probability of elephant occurrence > 0.002) were analyzed (n = 9). The predictors were centered (i.e. the average was subtracted from each value) to reduce collinearity (Allison 1999) in the quadratic regression (Quinn and Keough 2002). Data and residuals of the regression analysis were tested for spatial autocorrelation using the Moran’s I test (Carl et al. 2008). To test whether the change in the dominant scale of landscape heterogeneity affected the elephant distribution, the difference in the probability of elephant occurrence was linearly regressed against the difference in dominant scale of landscape heterogeneity between 1988 and 2001. A linear regression was chosen because the elephant population was known to be relatively stable during the study period and a zero slope was expected. Statistical analysis was performed in SPSS 16.0.1.

### Results

Figure 3 shows the NDVI wavelet energy curves obtained from the TM 1988, ETM+ 2000, 2001 and 2002 and
The average dominant scale of landscape heterogeneity in 1988 (mean = 89.03; 95% CI = 67.03–111.03; back transformed mean = 7900 m) did not significantly differ from 2000 (mean = 98.76, 95% CI = 86.88–110.66; back transformed mean = 9700 m; \( t = -0.97, p = 0.35, \text{DF} = 13 \)). The median intensity of landscape heterogeneity in 1988 (median = 0.18, range = 0.21, n = 14) was not significantly different from 2000 (median = 0.22, range = 0.15, n = 14; \( z = -1.1, p = 0.27, n = 14 \)). Minor changes in the dominant scale were observed in five quadrants (Fig. 3). In Q002_000 and Q004_001 the dominant scale obtained from the ETM+ 2001 was used for further analysis, while for the other quadrants the dominant scales obtained from the ASTER 2006 images (which were not significantly different to the ETM+ images) were used (Table 1).

Figure 3. Wavelet energy curves, dominant scale and maximum intensity from TM 1988, ETM+ 2000, 2001, 2002, and ASTER 2006 images for each quadrant.
elephant occurrence was found at a dominant scale of 7000 m (this value is derived by back transforming the variable, Fig. 5). In 2001 this relationship was weaker (adjusted $R^2 = 0.44; p = 0.07, n = 9$) (Table 2) and the dominant scale occurred at 8300 m (Fig. 5). Lower probabilities of elephant occurrence were related to both larger and smaller dominant scales of landscape heterogeneity (see Fig. 4a–b for reference). The largest dominant scale captured blocks of cultivated fields (e.g. in Q003_000 and Q004_000) as well as substantial portions of herbaceous and wooded savanna on the eastern side of the study area (e.g. in Q003_002). Small dominant scales represented patterns of highly heterogeneous land cover types such as the mosaic of open-trees and open-shrubs in flooded areas in Q002_002 and closed-trees and shrubs in Q004_002.

No relation was found between the change in elephant occurrence and the change in dominant scale of landscape heterogeneity for the two periods ($p > 0.05$). The results of the spatial autocorrelation analysis were not significant ($p > 0.05$).

The cultivated area was 750 km$^2$ in 1988 and 1140 km$^2$ in 2000. The increase in cultivation (between 50 and 150 km$^2$) decreased from 15360 to 7680 m, while in Q001_001, Q002_002 and Q002_003 the dominant scale increased from 1920 to 7680 m (Fig. 3).

The smoothing parameters $b$ were set at 7400 m for the SRF data and at 4708 m for the total counts. Visual inspection of the kernels confirmed that the CVh method did neither over-smooth nor under-smooth the data (Fig. 4a–b).

The average probability of elephant occurrence in 1988 (mean = 0.15; 95% CI = 0.05–0.24) was not significantly different from the probability in 2001 (mean = 0.18; 95% CI = 0.08–0.29; $t = 0.63$, $p = 0.54$, DF = 13). The spatial distribution of the probability of elephant occurrence (as depicted by 95% of the probability volume contours) slightly changed from 1988 to 2001. Specifically, in 2001 the elephant distribution in northern Tarangire National Park expanded in and outside the protected area, towards the south and east (Fig. 4a–b).

In 1988 the average probability of elephant occurrence was significantly related to the dominant scale of landscape heterogeneity (adjusted $R^2 = 0.82; p = 0.002, n = 9$) by a quadratic function (Table 2). The highest probability of elephant occurrence was found at a dominant scale of 7000 m (this value is derived by back transforming the variable, Fig. 5). In 2001 this relationship was weaker (adjusted $R^2 = 0.44; p = 0.07, n = 9$) (Table 2) and the dominant scale occurred at 8300 m (Fig. 5). Lower probabilities of elephant occurrence were related to both larger and smaller dominant scales of landscape heterogeneity (see Fig. 4a–b for reference). The largest dominant scale captured blocks of cultivated fields (e.g. in Q003_000 and Q004_000) as well as substantial portions of herbaceous and wooded savanna on the eastern side of the study area (e.g. in Q003_002). Small dominant scales represented patterns of highly heterogeneous land cover types such as the mosaic of open-trees and open-shrubs in flooded areas in Q002_002 and closed-trees and shrubs in Q004_002.

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The cultivated area was 750 km$^2$ in 1988 and 1140 km$^2$ in 2000. The increase in cultivation (between 50 and 150 km$^2$)

Table 2. Regression coefficients, standard errors (SE), $t$ and $p$ values of the quadratic relations between the probability of elephant occurrence and the dominant scale of landscape heterogeneity in 1988 and 2001.

<table>
<thead>
<tr>
<th></th>
<th>1988 (n = 9)</th>
<th></th>
<th>2001 (n = 9)</th>
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<tr>
<td></td>
<td>Coefficient</td>
<td>SE</td>
<td>t-value</td>
</tr>
<tr>
<td>Dominant scale</td>
<td>-0.002</td>
<td>0.001</td>
<td>-2.91</td>
</tr>
<tr>
<td>Dominant scale$^2$</td>
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<td>0.000</td>
<td>-5.52</td>
</tr>
<tr>
<td>Constant</td>
<td>0.445</td>
<td>0.042</td>
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Figure 4. The probability of elephant occurrence in 1988 (a) and 2001 (b) generated with the kernel density function. Crop fields are shown in white both in 1988 and 2000.
At increasing scales of decomposition (hence at coarser resolutions) the method captures the inter-patch distance of dominant vegetation. For instance, at a scale of about 960 m, the patch size between open-shrubs and open-trees, as well as between agriculture and semi-natural vegetation become obvious (see the circles in Fig. 6e). The dominant scale of about 7680 m identifies the boundary between homogeneous natural vegetation inside the park and the agricultural area outside the park. Moreover, it identifies the size of the forest (in the mountain) at the lowest left corner of the map (Fig. 6f). Figure 6g shows that at a scale of 15 360 m the highest contrast in NDVI occurs between forest and agriculture at the lower left corner of the map.

Discussion

This study did not find any substantial change in dominant scale and intensity of NDVI-derived landscape heterogeneity in the wet season between 1988 and 2000. On average, the dominant scale was large in both years, representing large patches of natural vegetation (e.g. in Q003_002) as well as large blocks of farms (e.g. in Q003_000). These findings support our first hypothesis as illustrated in the inset of Fig. 6c–d). At increasing scales of decomposition (hence at coarser resolutions) the method captures the inter-patch distance of dominant vegetation. For instance, at a scale of about 960 m, the patch size between open-shrubs and open-trees, as well as between agriculture and semi-natural vegetation become obvious (see the circles in Fig. 6e). The dominant scale of about 7680 m identifies the boundary between homogeneous natural vegetation inside the park and the agricultural area outside the park. Moreover, it identifies the size of the forest (in the mountain) at the lowest left corner of the map (Fig. 6f). Figure 6g shows that at a scale of 15 360 m the highest contrast in NDVI occurs between forest and agriculture at the lower left corner of the map.

Table 3. Regression coefficients, standard errors (SE), t and p values of the logarithmic relations between the dominant scale of landscape heterogeneity and cultivation in 1988 and 2000.

<table>
<thead>
<tr>
<th></th>
<th>1988 (n = 8)</th>
<th></th>
<th>2000 (n = 8)</th>
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<td></td>
<td>Coefficient</td>
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<td>t-value</td>
<td>p-value</td>
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</tr>
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<td>0.05</td>
<td>4843</td>
</tr>
<tr>
<td>Constant</td>
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<td>10 767</td>
<td>−1.4</td>
<td>0.2</td>
<td>−12 520</td>
</tr>
</tbody>
</table>

Figure 5. The quadratic relation between the probability of elephant occurrence and the dominant scale of landscape heterogeneity in 1988 (gray dash-dot line) and 2001 (black dotted line). The dominant scales of 7000 and 8300 m sustain the highest probability of elephant occurrence in 1988 and 2001 respectively.
Figure 6. Wavelet results for the quadrant Q002_000: (a) Africover; (b) NDVI of ETM+ 2000; (c) wavelet coefficients at scale 240 m; the arrow shows a swamplike area; the rectangular includes high wavelet coefficients, which capture the contrast between crop fields and natural vegetation (see inset (d); source: ETM+ 2000); (e) wavelet coefficients at scale 960 m; the circles show the contrast between swamplike areas and open shrubs (on the right) and crop fields and closed trees (on the left); (f) wavelet coefficients at scale 7680 m (dominant scale); (g) wavelet coefficients at scale 15 360 m; (h) wavelet energy curve of Q002_000 showing one dominant scale at 7680 m. The boundary of agricultural areas is shown in white. TNP (Tarangire National Park).

Fig. 1a–b. The probability of elephant occurrence in the Tarangire-Manyara ecosystem in the wet season did not show any change between 1988 and 2001, confirming the results for elephant trends obtained by SRF in the wet season for the same period (TAWIRI 2001). The dominant scale of landscape heterogeneity was significantly correlated with the probability of elephant occurrence, leading to the conclusion that elephants respond to an inter-patch
distance of 7000–8000 m in the Tarangire-Manyara ecosystem during the wet season. These patches are about 10 times larger than those observed by Murwira and Skidmore (2005) in a heavily human impacted savanna landscape in Zimbabwe. In that study, the dominant scale maximizing elephant occurrence was about 750 m in early 1980s, and reduced to 450 m in early 1990s, due to agricultural expansion. The Zimbabwean study further showed that elephant numbers not only declined between the 1980s and the 1990s, but disappeared from the ecosystem if the dominant scale decreased to < 400 m (Murwira and Skidmore 2005). A highly fragmented landscape, with a threshold of 30–40% of land being converted to agriculture, was earlier identified in Zimbabwe as the tipping point for elephant persistence (Hoare and Toit 1999). Our results suggest that the vegetation structure and cover of the Tarangire-Manyara ecosystem has not been modified by human activity (including agriculture) to the extent that it causes a decrease in the density of large body sized generalist herbivores, such as the elephant. Indeed, large vegetation patches and thus different forage options over large units may provide a wider selection for elephants (Laca 2008). These findings further support our hypothesis that in Tarangire-Manyara ecosystem the dominant scale of NDVI-derived landscape heterogeneity does not approach the critical threshold of elephant persistence (see point A in Fig. 1b).

The results of this study revealed that the spatial distribution of elephants has slightly changed in the Tarangire-Manyara ecosystem between 1988 and 2001 during the wet season. The ranging patterns of elephants was severely affected by illegal hunting, human disturbance and harassment (Osborn 2004). In the 1980s a poachers’ campsite was located in both the Lolkisale and the Mkungunero Game Controlled Area (Prins unpubl.), thus limiting elephant distribution to the Tarangire National Park. As the risk of poaching outside Tarangire National Park decreased after the international ban on ivory trade in 1989, elephants roamed over larger unprotected areas. As shown in Fig. 4a–b, the elephant range expanded in semi-protected (Lolkisale Game Controlled Area) and unprotected areas at the north-eastern and south-eastern side of the study area. Because of the existence of large blocks of cultivated land in the western part of the study area (20–30% of the quadrants), the elephants may have utilised the less cultivated areas in the north-eastern and south-eastern part of the study area. Therefore, we believe that agriculture may have contributed to reshaping the spatial distribution of elephants in the Tarangire-Manyara ecosystem during the wet season, without affecting the total population. This further corroborates the initial hypotheses illustrated in Fig. 1b.

Farming covered 6% of the total study area in 1988 (about 750 km²) and 9% in 2000 (1140 km²), indicating that only a small portion of land was converted to agriculture (about 35 km² yr⁻¹ or a 5% annual increase). On the contrary, in the Zimbabwean study, cultivation increased from 8% of the total study area in 1884 (about 294 km²) to 44% in 1992 (1651 km²; Murwira et al. 2010), determining a significant change in the landscape structure (about 170 km² yr⁻¹ or a 58% annual increase). As shown in Supplementary material Appendix 2, Fig. A1, the dominant scale of landscape heterogeneity was significantly related to the area of cultivation by quadrant for both years. The relationship was not significant if we included quadrants with arable land < 25 km². The results suggest that these patches did not substantially modify the landscape structure, as they are not clustered in large cultivated blocks. The quadrants with largest cultivated areas were located in the western and north-eastern part of our study area (see quadrants Q000_001, Q002_000, Q003_000, Q004_000 in Fig. 4a) and predate 1988 (OIKOS 2002). We found that the dominant scale reaches an asymptote for areas of cultivation > 100–150 km² by quadrant. This is related to the size of the quadrants (about 30 × 30 km), which determine the number of the wavelet decompositions and therefore the largest dominant scale of 15 360 m. In our study, the largest cultivated area by quadrant was about 260 km² (see Q004_000 in 2000 in Fig. 4b), which relates to a linear dimension of about 16 000 m. Hence, the largest dominant scale of 15 360 m (and therefore the size of the quadrant) was effective in capturing the largest linear dimension of cultivated land (about 16 000 m) in our study area. In other words, our method was able to pick up large changes that may pose a risk to the elephant persistence.

A challenge for elephant persistence may be the expansion of agriculture on their migration routes (Bornert 1985). The elephant routes from Tarangire National Park to the dispersal areas on the western side of the park were seriously threatened by agriculture in the 1980s (Bornert 1985). Current migratory routes for elephants connect Tarangire National Park to the northern, north-eastern, southern and south-eastern dispersal areas outside the park (Galanti et al. 2006, Pittigli et al. 2012). According to our analysis, no substantial changes occurred in the dominant scale of landscape heterogeneity along these migration routes between 1988 and 2006, except for two quadrants. In quadrant Q001_001 (including Lolkisale Game Controlled Area and Lolkisale village, Fig. 2), the dominant scale increased from 1920 m in 1988 to 7680 m in 2001, but then decreased to 480 m in 2006 (after the period of the SRF surveys). In quadrant Q004_001 (including the Mkungunero Game Controlled Area) the dominant scale decreased from about 15 360 m in 1988 to 7680 m in 2006. In both quadrants agriculture has increased over the past 30 yr (OIKOS 2002); continued agricultural expansion may obstruct the migratory routes of elephants towards the dispersal areas outside the park.

Our study reveals a few shortcomings of the intensity-dominant scale method proposed by Murwira and Skidmore (2005) that require further clarification. The size of the quadrant is an important parameter and should be chosen in relation to the environmental conditions, area of cultivation (or landscape feature of interest), and species home range. Therefore quadrants of 30 × 30 km may not be large enough for agriculture-dominated savanna landscapes. The risk of missing a coarse dominant scale may not be excluded. We performed the Haar 2D DWT at once on the TM 1988 image using the largest workable extent (a resized area of 4096 × 4096 pixels, about 120 × 120 km). This area, which is 4 times larger than the quadrant size
and for testing ecological hypotheses. A useful tool for monitoring ecosystems and their properties presented here is robust, easy and fast to implement. It forms a climatic and environmental conditions. The method for quantifying landscape heterogeneity under different vegetation has not yet reached the maximum productivity wet seasons (late October and early February), when the images acquired at the beginning of the short and long study this problem was limited by deriving the NDVI from variation in areas with high vegetation biomass. In our may prevent the wavelet transform from capturing the distribution of small body-sized and sedentary species (e.g. the impala). Furthermore, NDVI is known to saturate the distribution of small body-sized and sedentary species. (e.g. the impala). Furthermore, NDVI is known to saturate for high vegetation biomass values (Hobbs 1995). This may prevent the wavelet transform from capturing the variation in areas with high vegetation biomass. In our study this problem was limited by deriving the NDVI from images acquired at the beginning of the short and long wet seasons (late October and early February), when the vegetation has not yet reached the maximum productivity and biomass. However, more robust vegetation indices, such as the enhanced vegetation index (EVI), may be needed for quantifying landscape heterogeneity under different climatic and environmental conditions. The method presented here is robust, easy and fast to implement. It forms a useful tool for monitoring ecosystems and their properties and for testing ecological hypotheses.

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References


