### CHAPTER 2

### SPATIAL PATTERN ANALYSIS AS A FOCUS OF LANDSCAPE ECOLOGY TO SUPPORT EVALUATION OF HUMAN IMPACT ON LANDSCAPES AND DIVERSITY

### K.J. KOFFI<sup>1</sup>, V. DEBLAUWE<sup>1</sup>, S. SIBOMANA<sup>1,2</sup>, D.F.R. NEUBA<sup>3</sup>, D. CHAMPLUVIER<sup>4</sup>, C. DE CANNIERE<sup>5</sup>, N. BARBIER<sup>3</sup>, D. TRAORE<sup>6</sup>, B. HABONIMANA<sup>2</sup>, E. ROBBRECHT<sup>4</sup>, J. LEJOLY<sup>3</sup>, J. BOGAERT<sup>1</sup>

<sup>1</sup>Université libre de Bruxelles, Laboratoire d'Ecologie du Paysage, Bruxelles, Belgique ; <sup>2</sup>Université du Burundi, Faculté des Sciences Agronomiques, Bujumbura, Burundi ; <sup>3</sup>Université libre de Bruxelles, Service de Botanique Systématique et de Phytosociologie, Bruxelles, Belgique ; <sup>4</sup>Jardin Botanique National de Belgique, Meise, Belgique ; <sup>5</sup>Université libre de Bruxelles, Service de Lutte Biologique et d'Ecologie Spatiale, Bruxelles, Belgique ; <sup>6</sup>Université de Cocody-Abidjan, Laboratoire de Botanique, Abidjan, Côte d'Ivoire

Abstract. The relation between landscape patterns and ecological processes forms a central hypothesis of landscape ecology. Three types of pattern analysis to assess anthropogenic impacts on landscape ecosystems and biodiversity are presented in this chapter. Firstly, the results of an analysis of Acanthaceae data in Central Africa are presented and compared with phytogeographic theories. Phytogeography data reflect the spatial variability of plant diversity, and constitute therefore a major tool in conservation policy development. We investigated if it was possible to proxy the phytogeographic classifications by the spatial distribution of Acanthaceae only. When combined with a classic landscape pattern analysis, this type of study could provide complementary information for the definition of conservation priorities. Secondly, we present an analysis of periodic vegetations in the Sudan. It can be accepted that through an understanding of the underlying mechanisms of the formation of this unique pattern geometry, the knowledge with regard to the functioning and vulnerability of these ecosystems can be deepened. Using high-resolution remote sensing imagery and digital elevation models, the relation between pattern symmetry and slope gradient was explored. In particular, slope gradients that could

S.-K. Hong, N. Nakagoshi, B.J. Fu and Y. Morimoto (eds.), Landscape Ecological Applications in Man-Influenced Areas: Linking Man and Nature Systems, 7–32. © Springer Science+Business Media B.V. 2008

#### K.J. KOFFI ET AL.

condition the transition between spotted and tiger bush pattern types were focused. The influence of other sources of anisotropy was also considered. Finally, a complementary approach to the calculation of landscape metrics to analyse landscape pattern is described, using the spatial processes themselves causing landscape transformation. Landscape ecologists agree that there appears to be a limited number of common spatial configurations that can result from land transformation processes. Ten processes of landscape transformation are considered: aggregation, attrition, creation, deformation, dissection, enlargement, fragmentation, perforation, shift, and shrinkage. A decision tree is presented that enables definition of the transformation process involved using patch-based data. This technique can help landscape managers to refine their description of landscape dynamics and will assist them in identifying the drivers of landscape transformation

### 1. INTRODUCTION

'Landscape pattern' refers to features associated with the physical distribution or configuration of patches within a landscape (McGarigal and Marks, 1995). This spatial composition and configuration of landscape mosaics is dealt with in landscape ecology (Wiens, 2002), a branch of science developed to study ecological processes in their spatial context (Antrop, 2001). Changes in the spatial pattern of land use through time are considered to be crucial to the understanding of landscape dynamics and its ecological consequences (Turner and Ruscher, 1988). This central hypothesis of landscape ecology, i.e. that ecological patterns and processes are related (Turner, 1989), is known as the 'pattern/process paradigm' (Figure 1). Characteristic patterns of landscapes are supposed to be the result of the operation of ecological processes, that is, processes generate patterns and by analysing these patterns useful inferences about the underlying processes can be made (Coulson et al., 1999). This paradigm should also be applied in reverse order (Bogaert and Hong, 2003).

In order to investigate this link between pattern and process quantitatively, and to predict the effects of particular landscape patterns on processes (Levin, 1992), it is useful to characterize these patterns in quantifiable terms. Pattern maps provide unique information because they quantify biologically relevant information that is not necessarily evident from a simple land cover map (Riiters et al., 2000). This focus on pattern has lead to a large number of landscape metrics, of which many have been shown to be correlated (O'Neill et al., 1988) or to exhibit statistical interactions with each other (Li and Reynolds, 1994).

Landscape pattern analysis has consequently become a key activity of landscape ecologists. Nowadays, a variety of approaches are encountered in landscape ecology literature to deepen the knowledge on the functioning of landscape ecosystems and its influence on biodiversity. In this contribution, we present three examples of spatial pattern analysis in a landscape ecology perspective to illustrate the use of pattern analysis. Firstly, we present an analysis of the spatial pattern of Acanthaceae species, and link this information to classic theories of phytogeography. This type of analysis is useful when combined afterwards with a landscape pattern analysis (pattern of the abiotic environment or habitat), this to identify biodiversity conservation priorities. A second application of spatial pattern analysis involves the characterisation of unique landscape and vegetation patterns, such as tiger bush patterns in Africa. Through an understanding of the underlying mechanisms of the creation of this typical geometry, the functioning and vulnerability of these ecosystems can better be studied. Finally, a complementary approach to the calculation of landscape metrics to analyse landscape pattern is presented, using the spatial processes them causing landscape transformation. This technique can help landscape managers to refine their description of landscape dynamics and will assist them in analysing the drivers of landscape transformation.



Figure 1. Illustration of the pattern/process paradigm. (a) Ecological processes are influenced by landscape pattern, e.g., edge effects as a consequence of patch-matrix interactions in fragmented landscapes; (b) Patterns of landscapes are supposed to be the result of the operation of processes, e.g., habitat fragmentation transforms contiguous vegetations into isolated habitat patches.

### 2. THE SPATIAL DIMENSION OF SPECIES DIVERSITY: WHERE PHYTOGEOGRAPHY AND CONSERVATION MEET

### 2.1 Phytogeography and conservation

The most efficient method to gain understanding on the geographic distribution of plant species and on the ecological factors controlling this distribution is the analysis of spatial distribution maps of species (Lebrun, 2001). These maps enable the testing of hypotheses regarding the geographic origin of species, their speed of evolution, and their migration pathways. Moreover, a phytogeographic analysis enables to subdivide vast geographic units in smaller phytogeographic entities such as regions, districts, and sectors. When studied for multiple species or plant communities, these maps will reflect the spatial variation of plant (community) diversity, and consequently will be a useful tool in conservation policy development. For Central Africa – defined here as the geographic zone covered by the Democratic Republic of Congo, Burundi and Rwanda – three major phytogeographic theories have been proposed based on plant physiognomic arguments, bioclimatic data (precipitation, dry season length) and using the concept of endemism. This latter notion is central to the study of biogeography (Crisp et al., 2001). A taxon (e.g., a species) is considered endemic to a particular area if it occurs only in that area (Anderson, 1994). Ecologists are interested in areas of endemism because of their importance in conservation: narrowly endemic species are by definition rare, and therefore potentially threatened (Crisp et al., 2001).

Robyns (1948) divided Central Africa in 11 districts (Figure 2). White (1979, 1983) subdivided Africa and Madagascar in 20 regional entities, from which the Guineo-Congolian regional centre of endemism, the Zambezian regional centre of endemism, the Afromontane archipelago-like regional centre of endemism, the Guineo-Congolian/Zambezian regional transition zone and the Guineo-Congolian/Sudanian regional transition zone are found in Central Africa (Figure 3). Finally, Ndjele (1988) proposed a phytogeographic system subdividing the Democratic Republic of Congo in 13 sectors (Figure 4).



Figure 2. Subdivision of Central Africa in phytogeographic entities according to Robyns (1948). I: Coastal district; II: Mayumbe district; III: Lower Congo district; IV: Kasai district; V: Lower Katanga district; VI: Central Forest district; VII: Ubangi-Uele district VIII: Lake Albert district; IX: Lakes Edward and Kivu district; X: Ruanda-Urundi district; XI: Upper Katanga district.



Figure 3. Subdivision of Central Africa in phytogeographic entities according to White (1979, 1983). I: Guineo-Congolian regional centre of endemism (IB: Guinean sub-centre; IC: Congolian sub-centre);II: Zambezian regional centre of endemism; VIII: Afromontane archipelago-like regional centre of endemism; X: Guineo-Congolian/Zambezian regional transition zone; XI: Guineo-Congolian/Sudanian regional transition zone.



Figure 4. Subdivision of Central Africa in phytogeographic entities according to Ndjele (1988). I: Central Forest sector; II: Congolo-Sudanian transition sector; III: Congolo-Zambezian transition sector; IV: Mayumbe Forest sector; V: Lower Guineo/Zambezian transition sector; VI: Bemba sector; VII: Lualaba sector; VIII: Lunda sector; IX: Mountainous sector; X: Lake Mobutu sector; XI: Kivu Uplands sector; XII: Southern Sudania sector; XIII: Southern Atlantic sector of the Guinean coast.

The importance of these models should not be underestimated in the framework of species conservation. Phytogeography data reflect hotspots and spatial variability of plant diversity and constitute therefore a major tool in conservation policy development. Nevertheless, the present models can be

### K.J. KOFFI ET AL.

considered as rigid due to their complexity: many ecological and botanical parameters are considered to define the districts, centres of endemism, transition zones, mosaics and sectors. Therefore, we investigate in this contribution if it is possible to proxy the aforementioned phytogeographic classifications by the spatial distribution of one single family, i.e. the Acanthaceae. By analysis of the spatial distribution of Acanthaceae species relative to the phytogeographic subdivisions of Robyns (1948), White (1979, 1983) and Ndjele (1988), the indicator value of this family will be analysed.

# 2.2 The distribution of Acanthaceae in Central Africa: comparison with the phytogeographic theories of Robyns, White and Ndjele

A database composed of 9181 herbarium samples of the Acanthaceae family has been used in this study. Each herbarium sample contained, next to the species name, its taxonomic classification and a plant specimen, the geographical coordinates of the observation. These data were used to create spatial distribution maps using ArcView GIS 3.3 software.

The herbarium samples represented 48 genus, 310 species, and 6362 different geographical sites. The number of samples per species is quite variable. Nineteen species were represented by more than 100 samples, 35 species by a number of samples between 99 and 50, 141 species by a number of samples between 49 and 10, and 114 species by less than 10 samples. The samples have been collected by 417 scientists between 1888 and 2001 during expeditions financed by scientific institutes such as the Institut National pour l'Etude et la Recherche Agronomique au Congo, the Institut des Parcs Nationaux du Congo Belge, the Centre d'Etudes Médicales de l'Université libre de Bruxelles en Afrique Centrale and the Comité Spécial du Katanga.

Remarkable differences in the spatial presence of the species have been found (Figure 5). Certain species have been observed in almost every part of Central Africa, such as *Asystasia gangetica* subsp. *gangetica*. Others have been found to be associated with the hydrological network, such as *Justicia pynaertii*. The distribution of other species e.g. *Ruellia tuberosa* was related to its use by man. For *Justicia diclipteroides* subsp. *praetervisa*, an affiliation with the ecological conditions of the oriental mountainous region has been observed.

Firstly, a comparison of the spatial pattern of the Acanthaceae is made with the theory of Robyns (1948) (Figure 6). The Upper Katanga district contains the highest number of Acanthaceae species, and 52 among them are specific or characteristic for this district. In decreasing order follow the district of the Lakes Edward and Kivu and the district of the Central Forest, which contain 14, respectively 10 characteristic species. The Coastal, Lower Congo, and Ubangi-Uele districts contain only one single characteristic species, respectively *Barleria elegans, Ruellia togoensis* and *Lepidagathis peniculifera*. The Kasai district does not contain any species that is not found in another district also.



Figure 5. Spatial distribution of Acanthaceae species: examples. (a) Asystasia gangetica T. Anders. Subsp. micranta (Ness) Ensemu Kelbessa; (b) Justicia pynaertii De Wild.; (c) Ruellia tuberosa L.; (d) Justicia diclipteroides (Lindau) subsp. praetervisa (Lindau) Hedrén.

The presence of the Acanthaceae with regard to the zones defined by White (1979, 1983) is shown in Figure 7. Sixty-two characteristic species are found in the Zambezian regional centre of endemism, 34 are observed for the Afromontane archipelago-like regional centre of endemism, and 15 in the Guineo-Congolian regional centre of endemism. The Guineo-Congolian/Zambezian regional transition zone is characterised by *Barleria elegans* and *Justicia mendoncae*, while *Acanthus seretii*, *Lepidagathis peniculfera*, *Phaulopsis ciliata* and *P. savannicola* characterise the Guineo-Congolian/Sudanian regional transition zone.



Figure 6. Presence of Acanthaceae species in the phytogeographic entities of Robyns (1948). Y-axis indicates the number of species. The white proportion of each bar indicates the number of Acanthaceae species characteristic for the phytogeographic entity considered.

Of the sectors defined by Ndjele (1988), the most characterised by the presence of Acanthaceae species are the Bemba sector and the Central Forest sector, as well as the Mountain sector (Figure 8). The Mayumbe Forest sector, the Lower Guineo/Zambezian transition sector, the Southern Sudanian sector and the Southern Atlantic sector of the Guinean coast are characterized by one single species, respectively *Whitfieldia liebrechtsiana*, *Ruellia togoensis*, *Lepidagathis peniculfera*, and *Barleria elegans*. The Congolo-Sudanian transition sector and the Lualaba sector are not characterised by a species of the Acanthaceae family not occurring in another phytogeographic entity.

### 2.3 Discussion

Confrontation of the spatial pattern of the Acanthaceae species with the phytogeographic theories of Robyns (1948), White (1979, 1983) and Ndjele (1988) shows that the Zambezian regional centre of endemism, the Guineo-Congolian regional centre of endemism, and the Afromontane archipelago-like regional centre of endemism contain the highest number of herbarium samples. The flora of these zones is well known (Hepper, 1979) since they contain the main cities, research institutes, and universities, and since certain parts are characterized by a temperate climate. It should be emphasized that, outside these well-sampled zones, a large part of Central Africa is still unexplored. This observation has been confirmed for continental tropical Africa as a whole (Lebrun, 1973; Hepper, 1978; Kalanda, 1982; Lebrun and Stork, 1991; Lisowski, 1991). For some species however, a distribution

throughout the study zone is observed. Their ecological spectrum can consequently be considered as large. Other species are rather bound to particular geographic (ecological) regions, due to their smaller ecological spectrum. When a species is found in more than one single phytogeographic entity, it is considered a transition species. It should be noted that the regions of presence of particular species have been reduced considerably due to climatic changes when species were not able to respond properly to these dynamics (Schnell, 1971).

Species restricted to a small geographic region are considered prone to extinction. This is a key issue in conservation biology, where the vulnerability concept can be a more profound interpretation of phytogeographic observations. A wild (sensu not cultivated) plant species is considered vulnerable when it shows an increased extinction risk. The main criteria to evaluate this status are the population size and its phytogeography. According to the UICN (2001), a plant species shows an enhanced extinction risk when the population size is reduced by more than 50% during the last 10 years by reversible causes and by more than 30% by irreversible causes. To study vulnerability on a species base, a method is proposed using six parameters: zonation or altitude range, biotope, morphology, geography, diaspore type, and use by man (Betti, 2001). For each parameter, a score is assigned which increases with the risk of extinction. Finally, the average score is calculated which reflects the overall extinction risk or vulnerability of the species. A species is considered very vulnerable when it is bound to particular altitudinal limits, when it is associated with undisturbed of primary forests, when being a tree, shrub or liana species, when it is an endemic or Afromontane species, when disseminating by sarcochory or desmochory, and when it is used by man for construction or in traditional medicine practices.



Figure 7. Presence of Acanthaceae species in the phytogeographic entities of White (1979, 1983). Y-axis indicates the number of species. The white proportion of each bar indicates the number of Acanthaceae species characteristic for the phytogeographic entity considered.



Figure 8. Presence of Acanthaceae species in the phytogeographic entities of Ndjele (1988). Y-axis indicates the number of species. The white proportion of each bar indicates the number of Acanthaceae species characteristic for the phytogeographic entity considered.

The Zambezian region, denoted as the Upper Katanga district by Robyns (1948) and the Bemba sector by Ndjele (1988) represent the highest diversity of Acanthaceae, which confirms the existence of a centre of speciation of the African flora, more specifically in the Bangweolo-Katanga region (Lebrun, 1960, 1976; Ozanda, 1982), a region with a mineralised soil (deposition of copper) and characterized by climate types Aw and Cw of the Köppen classification (Bultot, 1950). Moreover, plateaus (1500-1700 m), open forests with *Brachystegia* and *Pseudoberlinia*, and typical herbal steppes are observed (Duvigneaud, 1958), next to dry dense forests (*Muhulu*), forest galleries, *Dembos* vegetations and typical plant communities associated with ore-containing sites. At the genus level, the Zambezian region is also the speciation centre of the *Thunbergia* and *Justicia* genus, the former being a principal genus of that region as observed by Ndjele (1988).

In the framework of conservation, it should be noted that the indicator value of the Acanthaceae is not constant throughout the study area considered. Certain phytogeographic entities are characterized by many species, while the presence or absence of one single species is characteristic to other zones. The use of a restricted number of species to substitute the more complex phytogeographic theories should therefore be executed with caution; nevertheless *Barleria elegans*, *Ruellia togoensis*  and *Lepidagathis peniculifera* seem to be species with discriminatory properties that can be used in a first approach to characterize regional gradients of plant diversity. For particular phytogeographic entities, no characteristic species have been found, which can indicate that the current approach has to be refined. Comparison with other families and confrontation with other phytogeographic theories and concepts should be effectuated before more profound conclusions can be drawn.

### 3. CHARACTERISING UNIQUE VEGETATION PATTERNS: ANALYSIS OF TIGER BUSH ORIENTATION USING FOURIER SPACE ANGULAR DISTRIBUTION AND REMOTE SENSING IMAGERY

### 3.1 Periodic vegetation patterns

In water-limited ecosystems, covering about one third of the Earth's surface (White, 1971; Schlesinger et al., 1990), the vegetation appears discontinuous and usually covers less than 60% of the landscape (Aguiar and Sala, 1999). In those regions between tropical savannah and desert, one can often observe particular vegetation mosaics in which the vegetation cover is not homogeneously or randomly distributed but is contracted into a "periodic" pattern. In the most famous case, the landscape is covered by bands of dense vegetation alternating with bands of bare soil or by strips covered by grass. This type of pattern is known as "tiger bush", by analogy to the tiger fur pattern. Another common vegetation mosaic consists of bare gaps regularly distributed within a dense matrix of vegetation. This kind of pattern, generally referred to as "spotted bush", is far less impressive on aerial photographs (Figure 9) and therefore attracted hardly attention of scientists. However, like tiger bush, spotted bush is spatially periodic (Couteron and Lejeune, 2001), i.e. the distance between two successive vegetated bands or a gap is relatively constant throughout the landscape. This distance is referred to as the "wavelength" of the pattern.

These periodic vegetation patterns are often not related to pre-existing substratum variability, though environmental factors can potentially distort the symmetry of the pattern. Although wind has often been considered (Ives, 1946; Aguiar and Sala, 1999; Leprun, 1999), a slope gradient is generally assumed to be the leading source of anisotropy in periodic vegetations. It has been observed that, when the slope gradient does not exceed a defined threshold (Valentin et al., 1999), isotropic spotted bush occur. On the other hand, a weak slope has been observed to generate a pattern with bands elongating orthogonally to the gradient (Greenwood, 1957; Boaler and Hodge, 1964; Mabbutt and Fanning, 1987; Montana et al., 1990).

This characteristic lead MacFadyen (1950), when he first described such patterns in Somaliland Republic, to propose their use as a slope aspect indicator on aerial photographs. This banded pattern, similar to contour lines on a map, lead to interpret the tiger bush pattern as a water harvesting strategy of vegetation. It was postulated





Figure 9. Spectral features computed from two typical 51 by 51 pixels sub-windows of (a) spotted and (b) banded vegetation. For visual purposes, both symmetric  $\theta$ -spectrum values are represented in order to cover all azimuth directions.

Mathematical implementations of vegetation pattern dynamics (Lefever and Lejeune, 1997; von Hardenberg et al., 2001; van de Koppel and Rietkerk, 2004) have lead to a complete review of our understanding of this phenomenon. By

considering the phytomass growth at any point in space as a function of aridity and of plant-plant or plant-resource interactions, models were able to reproduce the complete range of patterns encountered in the field and agreed on the prediction of a distinct succession of patterns along aridity gradients. Starting from wetter areas, one should invariably encounter continuous cover, spotted bush, bands with no preferred direction (sometimes called "labyrinthine" pattern), gaps consisting of bare soil periodically scattered with dense thickets, and finally desert without any vegetation. Inclusion of an external source of anisotropy in these models can lead to the formation of bands perpendicular to the gradient (Lefever and Lejeune, 1997), i.e. to tiger bush. Slope, and therefore sheet flow, can therefore be considered as a secondary driver in the pattern dynamics.

In this contribution, we used high-resolution remote sensing data combined with digital elevation models to explore the relation between pattern symmetry and slope gradient in the Kordofan province of the Sudan. In particular, we tried to evidence critical slope gradients that would condition the transition between spotted and tiger bush pattern types. Additionally, we analysed departure from the expected effect of slope anisotropy on the band orientation, in order to evidence the influence of other sources of anisotropy.

# 3.2 Quantitative pattern analysis of contracted vegetation in the Sudan using remotely sensed data

An area with periodic vegetation patterns was selected in the Western Kordofan state, ~700 km southwest of Khartoum (Sudan). This site was characterised by a sufficiently large wavelength to be detectable on satellite imagery of high resolution and covered a continuous area sufficiently wide to facilitate data handling. Our study area was located ~180 km south-east of the *Terminalia brownii* arcs and *Acacia mellifera* whorls described by Wickens and Collier (1971), which are currently strongly damaged (probably due to the high population density). In our site, the vegetation was intact and contracted either in bands – sometimes elongating over several kilometers – or in spotted patterns. The mean annual rainfall ranges from 510 to 590 mm and vegetation belongs to the Sudanian type (White, 1983).

Two panchromatic SPOT scenes covering the entire study area with a spatial resolution of 10 m were used. The scenes where taken in the middle of the dry season (December 22, 2001 and January 17, 2002). On panchromatic digital images, brightest pixels usually correspond to bare soil, intermediate gray-scale levels to continuous grass cover sites and darker pixels to woody vegetation. At first approximation, grey-scale levels can be considered a monotonically decreasing function of biomass. We used a SRTM digital elevation model with three arcs second spatial resolution (~90 m) to compute the topography features. Superposition of the digital elevation model with both SPOT scenes was achieved with an average error of less than 30 m in the field.

Slope can be considered theoretically as a vector; as such it is determined by intensity (gradient) and by direction (aspect). By convention, we defined the slope aspect as the direction of the steepest decrease of the altitude within the area

considered. It ranges from  $0^{\circ}$  to  $360^{\circ}$  ( $0^{\circ}$  being the north direction and values increasing clockwise).

Preliminary investigation of the images revealed vegetation bands lying on slope gradients of 0.2-1.5% and elongated perpendicularly to the slope (Figure 10). This typical tiger bush formation was characterized by a wavelength of 70-120 m. Another pattern was observed in his vicinity: wide areas of evenly spaced gaps in a continuous vegetation matrix. This spotted bush pattern showed a systematically smaller wavelength (40-60 m). A rectangular area of 2475 km<sup>2</sup> (10°57'-11°34'N; 28°11'-28°30'E) including the entire tiger bush area together with several wide areas of spotted bush were selected for further analysis. This study site was divided into non-overlapping square-shaped sub-windows of 510×510 m<sup>2</sup>. A zone covered by clouds as well as the border zone between both SPOT scenes was excluded for analysis so that a total of 8029 sub-windows were retained for pattern analysis.



Figure 10. Subset of the land cover map computed from K-means clustering. Contour lines were computed from the 3 arc second SRTM digital elevation model. Equidistance is 5 m. See text for the meaning of each class.

A two-dimensional Fourier transform and the associated computation of the twodimensional periodogram were applied. The use of the periodogram is recommended in the case of patterns showing spatial periodicity, since the amplitude values directly express the proportion of the image variance accounted for by periodic functions of explicit spatial frequencies and orientations. Pixel emissivity corrections are not needed since this proportion is invariant to linear grev scale level rescaling. This method has been successfully applied on digitalized aerial views of periodic (Couteron and Lejeune, 2001; Couteron, 2002) as well as non periodic (Couteron et al., 2005: Couteron et al., in press) vegetations. Two selected subwindows and their respective analysis are shown in Figure 9 to exemplify the method. Left side and right side graphs express the partitioning of image variance in typical banded and spotted vegetations respectively. A two-dimensional periodogram is a set of values, in Cartesian co-ordinates, each representing the portion of image variance  $\sigma^2$  in their particular direction and frequency. Pattern information relative to spatial frequency and to spatial orientation was separately captured by summing the periodogram values on either ring-shaped or wedgeshaped concentric frequency regions, in order to compute the r- and  $\theta$ -spectra respectively (Renshaw and Ford, 1984; Figure 9). These two spectra thus quantify the contributions of successive spatial frequencies (r-spectrum) and spatial orientation ( $\theta$ -spectrum) to the image variance. Due to sub-window size, the analysis was limited to the first 25 wave numbers in order to avoid aliasing effects. Nonhierarchical, unsupervised clustering using the K-means algorithm and the Euclidean distance (Legendre and Legendre, 1998) was performed on the r-spectra table after standardization to objectively classify the sub-windows into five coarseness-fineness classes.

The  $\theta$ -spectrum consisted of 36 orientations since we partitioned the 0°-180° range of the periodogram into classes of 5°. Due to their intrinsic nature we analyzed those angular data using circular statistics. The basic assumption of circular statistics is that a shift of 360° in data is meaningless. For example the mean direction between 5° and 355° should be 0° and not 180°. It should be emphasized that even when vegetation strips showed a certain orientation, a direction could not be assigned due to the absence of floristic field data indicating plant age or band dynamics. Therefore a shift of 180° in the band orientation was also meaningless. In this case the term "axial data" is used, as opposed to "vectorial data" such as slope orientation. Because each value of a  $\theta$ -spectrum could be considered as a vector with its direction and intensity, we characterised the pattern orientation as the weighted circular mean of the orientations of each sub-window. This mean orientation was computed as the vectorial sum of the  $\theta$ -spectra entries. Because these entries have a higher intensity when they express an orientation encompassing a high proportion of the image variance, this sum refers to the axis orthogonal to the maximal elongation of the pattern (i.e. the travelling wave direction).

### 3.3 Classification of land cover spatial pattern

The 8029 standardized *r*-spectra were submitted *K*-means clustering following Barbier et al. (in press). Five classes were considered appropriate to obtain a satisfactory separation between the observed landscape structures. The first three classes (C1 to C3) reflected a textural gradient associated with the relative importance of small versus large spatial frequencies in the spectrum (Figure 11). The first class (C1) gathered spectra dominated by very high spatial frequencies

#### K.J. KOFFI ET AL.

(>40 cycles/km) and was dominated by homogeneous savannas. Class C2 grouped sub-windows with spatial frequencies of similar importance all along the spectrum, although a small spike protruding at 17 cycles/km suggested that it contained mixed textures characteristic of classes C4 and C5. The third class (C3) was dominated by small spatial frequencies (<3 cycles/km) thereby corresponding to sub-windows marked by large landscape features, i.e. macroheterogeneity at sub-window scale, such as roads, croplands, hamlets, gallery forests or rocky escarpments. The two remaining classes (C4 and C5) were characterised by a strong pike associated with intermediate frequencies, corresponding to the spatial scales of the spotted and tiger bush respectively, as preliminarily identified.



Figure 11. Mean standardized r-spectrum of each class of land cover pattern (K-means clustering). See text for the meaning of each class.

## 3.4 Slope direction domain of periodic vegetation and dependency between slope and vegetation pattern orientations

The probability to find spotted bush (C4) was the highest on slope directions around  $270^{\circ}$ . Tiger bush (C5) exhibited a preferential direction between  $190^{\circ}$  and  $230^{\circ}$  (Figure 12). Slopes oriented between  $30^{\circ}$  and  $50^{\circ}$  seemed to be rarely covered by spatially periodic vegetation.



Figure 12. Rose diagram of slope direction. The number of sub-window classified as C4 (a) or C5 (b) in each angular bin were divided by the total number of sub-window in that particular direction. Length of pie chart accounts for proportion.

In order to quantify the dependency between each vegetation pattern orientation and the terrain slope direction on which they occur, a circular correlation test was performed. As expected, only the sub-windows classified as C5 (tiger bush) showed a clear correlation (Table 1) and the bands were on average elongated orthogonally to the slope (i.e. their travel direction was parallel to the slope). The V-Test (Fisher, 1993) showed that the shift between slope and pattern mean direction diverged consistently from a uniform distribution towards a distribution centred on zero degrees in the classes C2 and C5. It should be reminded that class C2 contained subwindows composed of a mixture of C4 and C5 classes. The strong dependency between vegetation and slope directions in class C5 was explored in detail. When the shift between the slope direction and C5 bands orientation was investigated, it was observed that its distribution was not uniform around the slope azimuthal circle (Figure 13). The bands were oriented orthogonally to the slope when oriented at 220° (e.g. south-west). From 220° to 340°, the shift increased progressively to reach a maximum at  $\sim 300^{\circ}$ . In this part of the azimuthal circle, the shift was negative, indicating that bands tended to rotate slightly counter clockwise with respect to the slope direction. Approaching 350°, the shift decreased and between 350° and 70°, the number of sub-windows classified as C5 was too low (<10) and their distribution insufficiently concentrated to compute the circular mean and its confidence interval. Near 100°, the shift reached a new maximum, on the positive direction this time, which suggested that bands tended to rotate slightly clockwise away from the slope direction. Afterwards, it diminished towards 220°.

### 3.5 Discussion

Using the Fourier space signature, we precisely mapped the different kinds of vegetation patterns observable on very high-resolution remotely sensed data for a study site in the Sudan. Each pattern class was characterised by a dominant peak in its frequency domain as characterised by the *r*-spectra. Therefore, due to their specific wavelengths, both periodic vegetations patterns, known as tiger bush and

spotted bush, were clearly separated from other landscape structures. Furthermore, the use of the  $\theta$ -spectrum allowed us to precisely determine band orientations of all sub-windows classified as tiger bush pattern.

Table 1. Dependency between slope and vegetation pattern orientation.  $\Pi_n$ : Circular rank correlation coefficient between the mean orientation of vegetation pattern and the direction of slope gradient; N: number of samples. Circular statistics were computed following Fisher (1993).

Class -	Circular rank correlation			<i>V</i> -Test (expected mean: 0°)	
	Ν	$\Pi_n$	Р	V	р
C1	899	0.011	< 0.005	-0.017	0.77
C2	2377	0.149	< 0.005	0.364	< 0.005
C3	1316	0.021	< 0.005	0.007	0.361
C4	1359	0.019	< 0.005	-0.018	0.829
C5	2078	0.535	< 0.005	0.803	< 0.005



Figure 13. Mean angular discrepancy between slope direction and C5 vegetation pattern orientation. Zero discrepancy indicates that bands of vegetation are orthogonal to the direction of slope. Positive and negative ones indicate a clock and counter-clock shift respectively of the vegetated bands. The mean shift (triangle) of every 20° bin is plotted between his 95% confidences bounds (diamonds).

It is commonly accepted that the tiger bush bands elongate orthogonally to the slope gradient so as to act as a rain gauge system (Valentin et al., 1999). Our results proved that such an assumption is exact, but only as a first approximation. Indeed, the band orientations were well correlated to the slope gradient and their discrepancy

rarely exceeded  $10^{\circ}$  in magnitude. Nevertheless, departure from orthogonality showed a systematic and significant structure as the band orientation turned slightly clockwise and counter clockwise on the slopes oriented southeast and northwest respectively. In between, when the slope orientation was southwest, the band travelling waves were orientated exactly in the same direction as the slope. On slopes oriented northeast, too few tiger bush are observed to precisely determine if there was a discrepancy. In some sense, the vegetated bands tended to rotate a little in order to face their upslope front with the northeast direction. Thereby they acted like if a weak anisotropy factor oriented northeast to southwest added his effect to the slope affect it. At our knowledge, only wind could have been responsible for this phenomenon. As observed for dune orientation in central Sudan as well as in the entire Sahelian band, two dominant winds are alternatively blowing in this orientation but in opposite direction: the Harmattan winds and the African monsoon winds.

Abiotic processes driven by wind and water include seed dispersion, and redistribution of fine soil particles, associated mineral nutrients and litter that is consequently concentrated underneath vegetated patches. Whether seeds or soil particle movements were involved in this case needs further field investigation. In this regard, the relative decrease of tiger bush presence observed on slopes oriented northeast could be interpreted in several ways. The opposition of slope and wind in the case of a weak slope gradient could lead to an isotropic environment. Therefore, bearing in mind that spotted bush (spots of bare soils periodically distributed in a vegetation matrix) are known to occur when the slope gradient does not exceed a certain threshold, we could expect to find an increasing proportion of this type of pattern when the slopes are oriented northeast. However, this was not the case, since the relative occurrence of spotted bush was the highest on westerly oriented slopes. Probably, another factor, i.e. the slope gradient, influenced pattern formation. In our study area, the mean slope was steeper when its direction was northeast to east (data not shown) reaching 0.65% versus 0.45% elsewhere. This could explain why there was so few-spotted bush on this slope direction. However, the reason why tiger bush did not appear remains unclear because it occurs on slope gradients as much as 1.5% on any direction.

In the light of our results, previous work mentioning periodic vegetation bands that are not aligned along the contour (Dunkerley and Brown, 2002) should be reinvestigated for wind and slope interaction. Consequently, the dichotomous distinction between bands and wind-induced anisotropy (d'Herbès et al., 2001) is likely to be tempered in favour of a continuum.

Analysis of remotely sensed data using the Fourier power spectrum enabled us to identify the periodic vegetation patterns and, for one of them called "tiger bush", to quantitatively test the dependence between the vegetation orientation and the anisotropic factors likely controlling them. It can be concluded that vegetation pattern orientation was mainly driven by slope and, to a lesser extent, by another factor that was assumed to be wind.

### 4. A TYPOLOGY FOR SPATIAL LANDSCAPE TRANSFORMATION PROCESSES

### 4.1 Spatial processes of land transformation

The conversion of native landscapes for human activities results in widespread changes in landscape spatial structure (Collinge, 1998). There appears to be a limited number of common spatial configurations that can result from land transformation processes (Franklin and Forman, 1987; Collinge and Forman, 1998). Based upon pattern geometry, eight processes have been described for landscapes composed of two classes, one representing the class of interest and the other one representing the underlying matrix: attrition, bisection, dissection, dissipation, fragmentation, incision, perforation, and shrinkage (Forman, 1995; Collinge, 1998; Collinge and Forman, 1998; Jaeger, 2000). These transformation processes described only land cover loss and were initially developed to assess the impact of pattern change on species diversity. A kind of hierarchical relationship between the processes was considered in Forman (1995) and Jaeger (2000). In Collinge (1998) and Forman and Collinge (1998), all processes were considered equivalent.

### 4.2 Identification of the spatial process involved in landscape pattern dynamics

A decision tree model (Figure 14) was presented to enable determination of the dominant land transformation process using area, boundary length and patch number statistics (Bogaert et al., 2004) of the class of interest. These characteristics were recognized as key elements for pattern description that would encompass most of the phenomena of observed patterns in a landscape (Giles and Trani, 1999). The aim was to provide environmental scientists with a quick protocol to determine the transformation process (es) present in the study area of interest (Bogaert et al., 2004).

The models includes processes associated with land cover increase, or with no change of the land cover extent, an evident novelty relative to Forman (1995), Collinge (1998), Collinge and Forman (1998), and Jaeger (2000). Some of the aforementioned processes were not retained because of their overlap with other ones, and every process was given an unequivocal definition. The following ten processes of landscape transformation were considered (Bogaert et al., 2004): aggregation (patch mergence), attrition (reduction of the number of patches), creation (formation of new patches), deformation (change of patch shape), dissection (subdivision of patches using equal-width lines), enlargement (patch size expansion), fragmentation (breaking up of patches into smaller parcels), perforation (gap formation), shift (patch repositioning), and shrinkage (reduction of patch size). For a geometrical illustration of the processes, the reader is referred to the seminal paper.



Figure 14. Flow chart based on the decision tree model (Bogaert et al., 2004) to identify spatial processes causing landscape pattern transformation. All decisions (diamond-shaped components) are based on either the area (a), the perimeter (p) or the number of patches (n) before  $(a_0, p_0, n_0)$  and after  $(a_1, p_1, n_1)$  the transformation of the landscape. Comparison of  $t_{obs}=a_1/a_0$  with a - by the user – predefined area loss ratio (t) enables distinction between fragmentation and dissection, which generate similar patterns.

Input data for the decision tree consists of the total class area (*a*), the total class perimeter or boundary length (*p*), and the number of patches (*n*) observed for the land cover class of interest before  $(a_0, p_0, n_0)$  and after  $(a_1, p_1, n_1)$  transformation. Since a binary landscape model was assumed, which was considered suitable for most applications, other key parameters mentioned by Giles and Trani (1999), such

as the proportion of the dominant class or the number of classes, were not considered. The decision tree algorithm leads to the identification of one single spatial process by comparing the values of  $a_0$ ,  $p_0$ ,  $n_0$  with  $a_1$ ,  $p_1$ ,  $n_1$  and is consequently based on equality, increase, or decrease of total land cover area, total perimeter length, and of the number of patches.

It should be noted that some processes in the decision tree algorithm are defined by less parameters than others. Aggregation, attrition, creation, dissection, enlargement and fragmentation are defined by two parameters only; while for deformation, perforation, shift and shrinkage three parameters are required. Use of all parameters for all processes could have refined the process identification, but would also have generated a more complex model, which could have countered the initial objective, i.e. designing a practical tool. An example for this case is the process of enlargement. It can be expected that perimeter increase coincide with enlargement. The absence of a parameter can also indicate redundancy of the parameter; this was the case for those transformation processes with  $n_1 > n_0$ ; the considered processes were all associated with perimeter increase, so that incorporation of this parameter would not have provided complementary information.

One weakness was nevertheless observed, which requires some flexibility by the user: patch attrition can dominate the analysis as a consequence of the design itself of the decision tree algorithm. The attrition or creation of one single patch can lead to completely different conclusions. In the case of the attrition of a single or a few patches (and assuming this being a marginal phenomenon in the landscape conversion considered), a methodological fix was suggested, i.e. to redo the analysis with omission of the decrease in number of patches (the user should consider  $n_1 = n_0$  instead of  $n_1 < n_0$ ).

Another particularity in the model is the difference between fragmentation and dissection, two processes which represent similar dynamics. In this case, a supplementary calculation was suggested, involving a comparison of the observed area loss ratio (defined as  $t_{obs}=a_1/a_0$ ) with a by the user predefined value (*t*). In this way, the user can make a distinction between landscape dissection (little area loss) and landscape fragmentation (considerable area conversion).

Next to the identification of the conversion process, which provides pattern information complementary to the detailed description of patterns using spatial statistics or metrics, two supplementary advantages of the decision tree model can be identified. Firstly, determination of the transformation process provides information on the causes or drivers of landscape transformation, since particular landscape conversions can be linked to particular initiators. Dissection is an evident example of this link, since it is associated with the construction of (rail) roads or similar linear structures (Forman, 1995), usually anthropogenic. Secondly, since the transformation process is determined for a well-defined time interval, sufficient temporal resolution of the data can reduce complex transformation scenarios to a sequence of individual processes. In this way, the well-known landscape dynamics in Cadiz Township (Wisconsin, USA, 1831-1950), which are generally simply denoted as fragmentation (Curtis, 1956), can be refined to fragmentation (1831-1882), and followed by attrition (1882-1935) and shrinkage (1935-1950) (Bogaert et al., 2004).

### 5. CONCLUDING REMARKS

Since the end of the 1930s, when the term "landscape ecology" was launched (Troll, 1939), many gigantic strides in theory, methodology, and applications have been made in this branch of science (Wu and Hobbs, 2002). The initial developments of landscape ecology took place mainly in Central and Eastern Europe, focusing on issues directly related to planning, management, conservation, and restoration of landscapes. This research emphasis on the interactions between human activities on one hand and resources (i.e., the landscape) on the other hand, initiated the development of holistic, interdisciplinary, and somewhat pragmatic views and approaches (Naveh, 2000; Wu and Hobbs, 2002). In contrast, landscape ecology began to develop in North America in the 1980s with an apparent emphasis on spatial heterogeneity and the concomitant effects on ecological processes where quantitative methods, such as spatial pattern analysis and modelling, prevailed (Wu and Hobbs, 2002). The development of landscape metrics and the ongoing polemic on their use (Bogaert et al., 2002) since the publication of the seminal paper of O'Neill et al. (1988) exemplify this development. The importance of the spatial character of problems and research is widely accepted (Bastian, 2001), but agreement likewise exists that spatial relations remain only one of the relevant foci of landscape ecology. Bridging this gap between landscape ecologists was considered an urgent need both for theoretical and practical reasons, this to enable the discipline to be really effective in terms of addressing world environmental and ecological problems (Farina, 1993).

Three types of spatial pattern analysis to assess anthropogenic impacts on landscape ecosystems and biodiversity are presented in this chapter. Firstly, the results of an analysis of the spatial distribution of Acanthaceae data in Central Africa are presented. Their spatial pattern is confronted with phytogeographic theories to test if it was possible to proxy the current phytogeographic classifications by the distribution of Acanthaceae only. Secondly, an analysis of periodic vegetations in the Sudan is presented. Using high-resolution remote sensing imagery and digital elevation models, the relation between pattern symmetry and slope gradient was explored. Finally, a complementary approach to the calculation of spatial metrics to analyse landscape pattern is described, using the spatial processes themselves causing landscape transformation. A decision tree is presented that enables definition of the transformation process involved using patch-based data.

### ACKNOWLEDGEMENTS

The authors acknowledge the Government of Ivory Coast for the doctoral fellowship of K.J. Koffi. V. Deblauwe is indebted to the FRIA for his doctoral fellowship. The research of S. Sibomana is supported by a CTB fellowship. We are grateful to the European OASIS project for providing us the remotely sensed data SPOT. Copyright –  $\bigcirc$  CNES (2001, 2002), distribution Spot Image S.A. The authors

acknowledge the Fonds voor Wetenschappelijk Onderzoek – Vlaanderen (G.0019.04), the Fonds National de la Recherche Scientifique (1.5.028.05), the Université libre de Bruxelles (Crédit extraordinaire de recherche), and the Politique Scientifique Fédérale (SR/00/045) for financial support.

#### REFERENCES

- Aguiar, M.R. and Sala, O.E. (1999). Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology & Evolution*, 14, 273-277.
- Anderson, S. (1994). Area and endemism. Quarterly Review of Biology, 69, 451-471.
- Antrop, M. (2001). The language of landscape ecologists and planners A comparative content analysis of concepts used in landscape ecology. *Landscape and Urban Planning*, 55, 163-173.
- Barbier, N., Couteron, P., Lejoly, J., Deblauwe, V. and Lejeune, O. Self-organised vegetation patterning as fingerprint of climate and human impact on semiarid ecosystems. *Journal of Ecology*, in press.
- Bastian, O. (2001). Landscape ecology: towards a unified discipline? Landscape Ecology, 16, 757-766.
- Betti, J.L. (2001). Vulnerabilité des plantes utilisées comme antipaludiques dans l'arrondissement de Mintom au Sud de la Réserve du Dja (Cameroun). Systematics and Geography of Plants, 71, 661-678.
- Boaler, S.B. and Hodge, C.A.H. (1964). Observations on vegetation arcs in the Northern region, Somali republic. *Journal of Ecology*, 52, 511-544.
- Bogaert, J., Ceulemans, R. and Salvador-Van Eysenrode, D. (2004). A decision tree algorithm for detection of spatial processes in landscape transformation. *Environmental Management*, 33, 62-73.
- Bogaert, J. and Hong, S.-K. (2004). Landscape ecology: monitoring landscape dynamics using spatial pattern metrics. In S.-K. Hong, J.A. Lee, B.-S. Ihm, A. Farina, Y. Son, E.-S. Kim and J.C. Choe (Eds.), *Ecological Issues in a Changing World* (pp. 109-131). Kluwer Academic Publishers, Dordrecht.
- Bogaert, J., Myneni, R.B. and Knyazikhin, Y. (2002). A mathematical comment on the formulae for the aggregation index and the shape index. *Landscape Ecology*, 17, 87-90.
- Bultot, F. (1950). Carte des Régions Climatiques du Congo Belge Etablie d'après les Critères de Köppen (Communication n°9 du Bureau Climatologique). Publication I.N.E.A.C.
- Collinge, S.K. (1998). Spatial arrangement of habitat patches and corridors: clues from ecological field experiments. *Landscape and Urban Planning*, 42, 157-168.
- Collinge, S.K. and Forman, R.T.T. (1998). A conceptual model of land conversion processes: predictions and evidence from a microlandscape experiment with grassland insects. *Oikos*, 82, 66-84.
- Coulson, R.N., Saarenmaa, H., Daugherty, W.C., Rykiel, E.J.Jr., Saunders, M.C. and Fitzgerald, J.W. (1999). A knowledge system environment for ecosystem management. In J.M. Klopatek and R.H. Gardner (Eds.), *Landscape Ecological Analysis – Issues and Applications* (pp. 57-79). Springer, New York.
- Couteron, P. (2002). Quantifying change in patterned semi-arid vegetation by Fourier analysis of digitized aerial photographs. *International Journal of Remote Sensing*, 23, 3407-3425.
- Couteron, P., Barbier, N. and Gautier, D. Textural ordination based on Fourier spectral decomposition: a method to analyze and compare landscape patterns. *Landscape Ecology*, in press.
- Couteron, P. and Lejeune, O. (2001). Periodic spotted patterns in semi-arid vegetation explained by a propagation-inhibition model. *Journal of Ecology*, 89, 616-628.
- Couteron, P., Pelissier, R., Nicolini, E.A. and Paget, D. (2005). Predicting tropical forest stand structure parameters from Fourier transform of very high-resolution remotely sensed canopy images. *Journal* of Applied Ecology, 42, 1121-1128.
- Crisp, M.D., Laffan, S., Linder, H.P. and Monro, A. (2001). Endemism in the Australian flora. *Journal of Biogeography*, 28, 183-198.
- Curtis, J.T. (1956). The modification of mid-latitude grasslands and forests by man. In W. L. Thomas (Ed.), Man's Role in Changing the Face of the Earth (pp. 721-736). University of Chicago Press, Chicago.
- d'Herbès, J.M., Valentin, C., Tongway, D.J. and Leprun, J.C. (2001). Banded vegetation patterns and related structures. In D.J. Tongway, C. Valentin, J.M. d'Herbès and J. Seghieri (Eds.), *Banded*

Vegetation Patterning in Arid and Semi-Arid Environments. Ecological Processes and Consequences for Management (pp. 1-19). Springer, New York.

- Dunkerley, D.L. and Brown, K.J. (2002). Oblique vegetation banding in the Australian arid zone: implications for theories of pattern evolution and maintenance. *Journal of Arid Environments*, 51, 163-181.
- Duvigneaud, P. (1958). La végétation du Katanga et de ses sols métallifères. Bulletin de la Société Royale Botanique de Belgique, 90, 127-286.
- Farina, A. (1993). From global to regional landscape ecology (editorial comment). *Landscape Ecology*, 8, 153-154.
- Fisher, N.I. (1993). Statistical Analysis of Circular Data. Cambridge University Press, Cambridge.
- Forman, R.T.T. (1995). Land Mosaics: The Ecology of Landscapes and Regions. Cambridge University Press, Cambridge.
- Franklin, J.F. and Forman, R.T.T. (1987). Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecology*, 1, 5-18.
- Giles, R.H.Jr. and Trani, M.K. (1999). Key elements of landscape pattern measures. *Environmental Management*, 23, 477-481.
- Greenwood, J.E.G.W. (1957). The development of vegetation patterns in Somaliland Protectorate. Geographical Journal, 123, 465-473.
- Hepper, N.F. (1978). The present stage of botanical exploration of tropical Africa. In I. Hedberg (Ed.) Systematic Botany, Plant Utilisation and Biosphere Conservation (pp. 41-46). I. Almqvist & Wiksell International, Stockholm.
- Hepper, N.F. (1979). Deuxième édition de la Carte du Degré d'Exploration Floristique de l'Afrique au Sud du Sahara. In G. Kunkel (Ed.), IXe Réunion plénière de l'AETFAT, Las Palmas.
- Ives, R.L. (1946). Desert ripples. American Journal of Science, 244, 492-501.
- Jaeger, J. (2000). Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. *Landscape Ecology*, 15, 115-130.
- Kalanda, K. (1982). Etude Taxonomique et Phytogéographique du Genre Vernonia Schreb. (Asteraceae) au Zaïre. Thèse doctorale, Université de Kisangani, Zaïre.
- Lebrun, J. (1960). Sur une méthode de délimitation des horizons et étages de végétation des montagnes du Congo Oriental. *Bulletin du Jardin Botanique de l'Etat*, 30, 75-94.
- Lebrun, J.P. (1973). Enumeration des Plantes Vasculaires du Sénégal. Etude botanique no. 2, Institut d'Elevage et de Médecine vétérinaire des Pays tropicaux, Maisons-Alfort.
- Lebrun, J.P. (1976). Richesse spécifique de la flore vasculaire des divers pays ou régions d'Afrique. *Candollea*, 31, 11-15.
- Lebrun, J.P. (2001). Introduction à la Flore d'Afrique. CIRAD. Ibis Press.
- Lebrun, J.P. and Stork, A.L. (1991). Énumération des Plantes à Fleurs D'Afrique Tropicale. Volume. 1. Généralités et Annonaceae à Euphorbiaceae et Pandanceae. Conservatoire et Jardin botaniques. Geneva.
- Lefever, R. and Lejeune, O. (1997). On the origin of tiger bush. *Bulletin of Mathematical Biology*, 59, 263-294.
- Legendre, P. and Legendre, L. (1998). Numerical ecology (2nd English ed.). Elsevier, Amsterdam.
- Leprun, J.C. (1999). The influences of ecological factors on tiger bush and dotted bush patterns along a gradient from Mali to northern Burkina Faso. *Catena*, 37, 25-44.
- Levin, S.A. (1992). The problem of pattern and scale in ecology. Ecology, 73, 1943-1976.
- Li, H. and Reynolds, J.F. (1994). A simulation experiment to quantify spatial heterogeneity in categorical maps. *Ecology*, 75, 2446-2455.
- Lisowski, S. (1991). Les Asteraceae dans la Flore D'Afrique Centrale. Fragmenta Floristica et Geobotanica 36(1 & 2). Polish Academy of Sciences, W. Szafer Institut.
- Mabbutt, J.A. and Fanning, P.C. (1987). Vegetation banding in arid Western Australia. Journal of Arid Environments, 12, 41-59.
- MacFadyen, W.A. (1950). Vegetation patterns in the semi-desert plains of British Somaliland. Geographical Journal, 116, 199-210.
- McGarigal, K. and Marks, B.J. (1995). FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure. Department of Agriculture, Pacific Northwest Research Station, PNW-GTR-351, Oregon.

- Montana, C., Lopez Portillo, J. and Mauchamp, A. (1990). The response of two woody species to the conditions created by a shifting ecotone in an arid ecosystem. *Journal of Ecology*, 78, 789-798.
- Naveh, Z. (2000). What is holistic landscape ecology? A conceptual introduction. Landscape and Urban Planning, 50, 7-26.
- Ndjele, M.B. (1988). Les Eléments Phytogéographiques Endémiques dans la Flore Vasculaire du Zaïre. Thèse doctorale, Faculté des Sciences, Université libre de Bruxelles, Belgique.
- O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, S.W., Dale, V. and Graham, R.L. (1988). Indices of landscape pattern. *Landscape Ecology*, 3, 153-162.
- Ozanda, P. (1982). Les Végétaux dans la Biosphère. Dion éditeurs, Paris.
- Renshaw, E. and Ford, E.D. (1984). The description of spatial pattern using two-dimensional spectral analysis. *Vegetatio*, 56, 75-85.
- Riitters, K., Wickham, J., O'Neill, R.V., Jones, B. and Smith, E. (2000). Global-scale patterns of forest fragmentation. *Conservation Ecology*, 4, www.consecol.org/vol4/iss2/art3.
- Robyns W. (1948). Les territoires phytogéographiques du Congo Belge et du Ruanda-Urundi. Atlas général du Congo Belge. Académie Royale des Sciences Coloniales, Bruxelles.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M. and Virginia, R.A. (1990). Biological feedbacks in global desertification. *Science*, 247, 1043-1048.
- Schnell, R. (1971). Introduction à la Phytogéographie des Pays Tropicaux. Volume II : Les Milieux. Les Groupements Végétaux. Editions Gauthier-Villars, Paris
- Troll, C. (1939). Luftbildplan und ökologische Bodemforschung. Zeitschrift der Gesellschaft für Erdkunde zu Berlin, 241-298.
- Turner, M.G. (1989). Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics, 20, 171-197.
- Turner, M.G. and Ruscher, C.L. (1988). Changes in landscape patterns in Georgia, USA. Landscape Ecology, 1, 241-251.
- UICN, (2001). Catégories et critères de l'UICN pour la Liste Rouge. UICN, Gland.
- Valentin, C., d'Herbes, J.M. and Poesen, J. (1999). Soil and water components of banded vegetation patterns. *Catena*, 37, 1-24.
- van de Koppel, J. and Rietkerk, M. (2004). Spatial interactions and resilience in arid ecosystems. *American Naturalist*, 163, 113-121.
- von Hardenberg, J., Meron, E., Shachak, M. and Zarmi, Y. (2001). Diversity of vegetation patterns and desertification. *Physical Review Letters*, 87, art-198101.
- White, F. (1979). The Guineo-Congolian region an its relationships to other phytochoria. Bulletin du Jardin Botanique National de Belgique, 49, 11-55.
- White, F. (1983). The Vegetation of Africa. A descriptive Memoire to Accompany the UNESCO/AETFAT Vegetation Map of Africa. UNESCO, Paris.
- White, L.P. (1971). Vegetation stripes on sheet wash surfaces. Journal of Ecology, 59, 615-622.
- Wickens, G.E. and Collier, F.W. (1971). Some vegetation patterns in the republic of the Sudan. Geoderma, 6, 43-59.
- Wiens, J.A. (2002). Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology*, 47, 501-515.
- Wu, J. and Hobbs, R. (2002). Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. *Landscape Ecology*, 17, 355-365.