Chapter 12 Forest Fragmentation: Causes, Ecological Impacts and Implications for Landscape Management

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Abstract

In order to enable the development of appropriate landscape management plans, the causes and impacts of fragmentation should be fully understood. A new definition, incorporating the key aspects cited in landscape ecological literature since the 1980s, is proposed in order to shed light on the matter of fragmentation. By means of two case studies in the Democratic Republic of the Congo (Oriental Province) and in North Benin, the key role of anthropogenic activities in landscape fragmentation is evidenced: the spatial dispersion of forest vegetation is linked to population density and land use change. The potential impact of fragmentation on biodiversity is shown by an analysis of forest diversity in Ivory Coast (Tanda region), and by a study of edge effects on two rodent species in the Democratic Republic of the Congo (Kisangani). The chapter is concluded by an study on how planned corridors, assuming a spatial regrouping of existing teak plantations, could contribute to the conservation and management of remaining natural forest patches in the Atlantic Department in Benin.

Keywords

Corridor, edge effect, forest degradation, fragmentation, land cover change, landscape connectivity, landscape metric, population density, transition matrix.

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12.1 Fragmentation: A plenitude of definitions

The process of forest fragmentation due to human activities such as logging or conversion of forests into agricultural areas and suburbanization (Forman 1995) has been identified as the most important factor contributing to the decline and loss of species diversity worldwide (Noss and Cooperrider 1994). Forest fragmentation occurs when a large region of forest is broken down, or fragmented, into a collection of smaller patches of forest habitat (Wilcove et al. 1986; Collingham and Huntley 2000; Fahrig 2003). The outcome of fragmentation can be considered as a 'binary landscape' in the sense that the resulting landscape is assumed to be composed of spatially dispersed forest fragments with a non-forest matrix between them (Franklin et al. 2002).

Defining fragmentation is crucial in evaluating its effects on species in the forest ecosystem and at the landscape level (Bogaert 2003; Lafortezza et al. 2008). A spectrum of definitions has been cited in landscape ecological literature since the 1980s, of which a representative sample is listed below:

Fragmentation ...

- ... is the process whereby a large, continuous area of habitat is reduced in area and divided into two or more fragments (Wilcove et al. 1986);
- ... is an alteration of the spatial configuration of habitats that involves external disturbance that alters the large patch so as to create isolated or tenuously connected patches of the original habitat (Wiens 1989);
- ... is an event that creates a greater number of habitat patches that are smaller in size than the original contiguous tract(s) of habitat (Bender et al. 1998);
- ... is habitat loss and isolation (Collinge 1996);
- ... refers to the patchiness of a landscape (De Santo and Smith 1993);
- ... produces a series of remnant vegetation patches surrounded by a matrix of different vegetation and/or land use (Saunders et al. 1991);
- ... is the process of breaking up continuous habitats, resulting in reduced area, increased edge, reduced interior area, increased isolation of patches and possibly increased number of patches and decreased average patch size (Davidson 1998); an increase in the total boundary length is also observed (Forman 1995);
- ... is the breaking up of a habitat, ecosystem or land use type into smaller parcels (Krebs 1994; Forman 1995); it is considered as a spatial process of land transformation (Forman 1995; Bogaert et al. 2004);
- ... is heterogeneity in its simplest form: the mixture of habitat and non-habitat (Franklin et al. 2002);
- ... refers to an increase of the number of patches in a landscape (Goodwin and Fahrig 2002);
- ... is the breaking up of extensive landscape features into disjunct, isolated or semi-isolated patches as a result of land use changes (Heywood and Watson 1995);

- ... is the breaking apart from habitat, and does not refer to habitat loss (Fahrig 2003; Yaacobi et al. 2007);
- ... is the disruption of continuity; when defined in this manner, the concept can be applied to any domain in which continuity is important to the functioning of ecosystems (Lord and Norton 1990);
- ... is a particular form of human-induced environmental degradation (Haila 2002);
- ... is a process of spatial landscape transformation, characterized by habitat loss, and an increase of the number of patches (Forman 1995; Jaeger 2000; Bogaert et al. 2004);
- ... is the complement of connectivity (Riitters et al. 2000);
- ... is both a state (or outcome) and a process; the process of habitat fragmentation is the set of mechanisms leading to a state of discontinuity of resources and conditions (Franklin et al. 2002);
- ... is conversion from natural vegetation to new land uses; the remaining habitat is inevitably divided into increasingly smaller parts (Groom and Schumaker 1993).

Although the limitations of the overview should be considered, four main features can be identified in these definitions:

- a continuum of habitat or vegetation is reduced to a discontinuum, composed of at least two ('more than one') patches;
- habitat destruction or loss is observed;
- spatial pattern is characterized by patch isolation due to the loss of the connecting habitat;
- habitat-matrix interactions are changed by an increase in cumulative patch perimeter, reducing total interior area (edge effect).

Taking these four key elements of fragmentation into account, a comprehensive definition could be proposed, i.e. *fragmentation is the process of breaking up continuous habitats and thereby causing habitat loss, patch isolation and edge effects* (Bogaert 2000). Some authors emphasize the distinction between the concepts of habitat loss and fragmentation (Franklin et al. 2002; Haila 2002; Fahrig 2003; Yaacobi et al. 2007), mainly due to the impact on diversity. Since many landscape ecologists accept both concepts to be inextricably related, we suggest to consider habitat loss as a component of fragmentation. For a more complete overview of existing definitions and views on fragmentation, and on its effects, the reader is referred to Haila (2002) and Fahrig (2003).

For Cadiz Township (WI, USA), the textbook example of fragmentation (Curtis 1956; Burgess and Sharpe 1981; Shafer 1990; Forman 1995) referring to land cover changes between 1831 and 1950 during the period of European settlement, the aforementioned four pattern features have been observed. Bo-gaert et al. (2004) confirmed this observation when the entire period was considered, but showed also that this sequence of land cover change could be disentangled into three distinct phases, in which only the first one (between

1831 and 1882) corresponded to fragmentation; the first subsequent phase (1882-1935) was characterized by patch attrition; patch shrinkage concluded the observed dynamics between 1935 and 1950.

In their overview of habitat fragmentation experiments, Debinski and Holt (2000) emphasize the wide range of species responses to fragmentation. Species can show highly disparate responses to fragmentation, including lack of response (Davies and Margules 1998). It should be noted that the aforementioned list of definitions only refers to nonspecific definitions of habitat or forest fragmentation, i.e. definitions independent of any particular species. This approach fits in with an aspiration to develop universal theories, applicable at the landscape as an entity and suitable for a variety of species, i.e. the entire landscape (eco)system (Bogaert 2000). This view is, however, considered also an ambiguity of the fragmentation concept (Haila 2002) contested by ecologists occupied by species-driven research (Franklin et al. 2002).

Within the emerging issue of landscape management and conservation, this contribution aims to explore forest fragmentation through the analysis of the main causes and ecological impacts. To achieve this objective, a deliberate choice is made for an approach based on case studies, referring to local or regional land cover dynamics in West and Central Africa (Benin, Ivory Coast, Democratic Republic of the Congo). This type of approach is justified by the variability of the ecosystems and landscapes subject to fragmentation worldwide, and by the ongoing discussion and controversy on the (ecological) consequences of habitat fragmentation (Bogaert 2003; Fahrig 2003; Ewers and Didham 2006; Yaacobi et al. 2007).

By means of simple fragmentation metrics such as the Monmonier index (Monmonier 1974), average patch size and the index of the largest patch (Mc-Garigal and Marks 1995), it is shown how fragmentation affects biodiversity and how anthropogenic pressure (measured directly by land cover change or indirectly by means of the population density) fragments natural land covers. The use of simple metrics, instead of a long series of complex and often correlated metrics, is also a deliberate choice, an issue still subject to debate in landscape ecological literature (Bogaert and Hong 2004; Li and Wu 2004; Bogaert and Mahamane 2005).

The first two case studies described in this chapter focus on the drivers of fragmentation. The first study investigates how population density leads to a lower presence of dense forests in the Oriental Province of the Democratic Republic of the Congo. An increasing degree of forest fragmentation is observed for increasing population densities. The second study deals with land cover change in North Benin, where agricultural development, cotton production in particular, has substituted the original forest and savannah vegetations.

After these two examples, the focus of the chapter is moved towards the impacts of fragmentation on biodiversity. The first study, situated in a forestsavannah transition zone in Ivory Coast (Tanda region), links the degree of landscape fragmentation to forest diversity itself and to the presence of heliophylic species; the latter species group is accepted to be an indicator of habitat disturbance and canopy openness. The second study, based on data collected in the Democratic Republic of the Congo (Kisangani), discusses the impact of edge habitats, a direct consequence of landscape patchiness, on the abundance of two rodent species.

Finally, a fifth case study is included in this chapter in order to illustrate how a fragmented landscape could be restored by means of planned, continuous corridors. The resources for these corridors, teak plantations, are actually already present but scattered throughout the landscape. A spatial regrouping of these patches in a network connecting valuable forests could contribute to a better management and conservation of the remaining diversity.

12.2 Demographic development and anthropogenic activity as drivers of fragmentation

In this section, two case studies illustrate the central role of anthropogenic activities and demographic pressure in land cover dynamics.

12.2.1 Forest fragmentation and population density in the Democratic Republic of the Congo (Oriental Province)

12.2.1.1 Context, data set and methods

In the tropical zone, forest cover is assumed to be a direct consequence of population density (Williams 2000). In Central Africa, for example, Bogaert et al. (2008) have explored this pattern and found a negative relationship between population density and forest cover. Other studies have considered the key role of the political and socio-economical context (e.g. land tenure system) in determining forest cover in the tropics (Hecht 1985; Angelsen and Kaimowitz 1999; Geist and Lambin 2001).

We investigated the relation between forest fragmentation and population density for a study area in the Oriental Province of the Democratic Republic of the Congo. The Congo Basin, the second largest forest area worldwide, is threatened by an increasing population density and agricultural development, mining industry, urbanisation and deforestation (PFBC 2006). The study area has been defined using a Landsat ETM+ scene (March 2001; path/row 176/060) covering a portion of $185 \times 185 \text{ km}^2$ of the Congo Basin. The central point of the study area is situated at 0°0′ N and 25°0′ E; the city of Kisangani (0°31′ N, 25°11′ E) is situated in the northern part of the scene. The scene has been divided in 266 grids of $10 \times 10 \text{ km}^2$. Population density has been calculated by means of the Africa Population Distribution Database (UNEP 2004) which consists of a population density grid-map of 2.5 km spatial resolution. An upper threshold of population density of 100 habitants/km² was applied in a grid to be included in this study; 246 grids corresponded to this criterion.

Forest pattern has been quantified using two fragmentation metrics: the number of patches, and patch dominance D_j also known as the index of the largest patch (McGarigal and Marks 1995); the latter was defined as the proportional area (%) taken by the largest patch $(a_{\max,j})$ in the patch type j with total area $a_{t,j}$:

$$D_j = \frac{a_{\max,j}}{a_{t,j}} \tag{12.1}$$

12.2.1.2 Results and discussion

Figs.12.1 and 12.2 show the correspondence between the fragmentation metrics (number of patches, index of the largest patch) and population density.



Fig. 12.1 Impact of population density on forest fragmentation in the Congo Basin (Oriental Province, Democratic Republic of the Congo). Fragmentation is measured by means of the number of forest patches. Data are presented on a grid base (grid size equal to $10 \times 10 \text{ km}^2$). Graph based on index averages for every population density.

A significant ($p < 0.01, R^2 = 0.48$) nonlinear relation is observed between the number of patches and population density, indicating that forest fragmentation is the highest for intermediate population densities. Patch number increases with population density up to ~60 inhabitants/km². Afterwards, patch number decreases again. This example underlines the complexity of landscape dynamics which are often characterized by a sequence of land transformation processes (Forman 1995; Bogaert et al. 2004) as already mentioned in section 12.1. The initial patch number increase can be interpreted as forest fragmentation; the second part of the curve corresponds to forest attrition, in which the initially created patches disappear.

The link between forest fragmentation and population density is confirmed by the index of the largest patch; this index decreases when population density increases $(p < 0.01, R^2 = 0.67)$: the higher the population density the lower the proportion taken by the largest patch, indicating that patches become smaller and are of comparable size when the number of inhabitants increases. Fragmentation and attrition lead to landscapes characterized by scattered land cover classes without dominant patches.

Both regression coefficients suggest that demographic factors play a principal role in changing forest cover pattern, which confirms the hypotheses of Williams (2000) and Bogaert et al. (2008). In the study area, this finding was expected due to the subsistence-type economy, in which people are often obliged to draw their daily needs from natural resources, leading to degradation of the forest resources (Bamba et al. 2008).



Fig. 12.2 Impact of population density on forest fragmentation in the Congo Basin (Oriental Province, Democratic Republic of the Congo). Fragmentation is measured by means of the index of the largest patch (D_j) . Data are presented on a grid base (grid size equal to $10 \times 10 \text{ km}^2$). Graph based on index averages for every population density.

12.2.2 Forest and savannah fragmentation as a consequence of cotton production in North Benin

12.2.2.1 Context, data set and methods

Since its introduction in Benin in 1946, cotton production (*Gossypium spp.*) has known a large expansion in the north of the country and has become the main source of income of its population (MAEP 2000). Cotton represents about 97% of the receipts of agricultural exportations (FAO 2004). As a consequence of cotton culture expansion, forest and savannah area have decreased and the concomitant ecosystems have been fragmented. This relationship between agricultural development, landscape dynamics and habitat fragmentation has been studied in detail for the Banikoara region, the principal zone of cotton production in Benin.

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In Banikoara, a study area of 192 km^2 has been chosen, with its centre situated at approximately $11^{\circ}13'$ N and $3^{\circ}54'$ E. Three Landsat TM/ETM+ images (1972, 1986 and 2006) have been classified into four main land cover classes: forest, savannah, agriculture (fallow/field complexes) and built-up. The complexes of fallow lands and fields were mosaics of old and new cotton fields. Image analysis (classification, class area analysis) was executed with ENVI 4.2 and ArcGis 9.2. Landscape dynamics was analyzed by a comparison of the area of each land cover class between the images. A transition matrix, revealing the area exchanges between the classes considered, was composed to understand the dynamics observed. Landscape fragmentation was measured by the average patch size per type (McGarigal and Marks 1995):

$$a_{av,j} = \frac{a_{t,j}}{n_j} \tag{12.2}$$

with $a_{av,j}$ the average patch size, $a_{t,j}$ the total class area and n_j the number of patches of the class considered. Increasing degrees of fragmentation will lead to lower values of $a_{av,j}$.

12.2.2.2 Results and discussion

The analysis of the land cover dynamics between 1972 and 1986, and between 1986 and 2006, showed that land use had shifted towards agriculture and that natural habitats (forest, savannah) decreased considerably in area (Table 12.1).

Table 12.1 Land cover (%) of the Banikora region in 1972, 1986 and 2006. Total study area equal to 192 $\rm km^2$

Land cover	1972	1986	2006
Forest	57.3	13.7	4.2
Savannah	34.4	39.8	16.2
Agriculture	8.1	45.1	75.4
Built-up	0.2	1.3	4.3

While forest and savannah dominated the landscape in 1972 (cumulative area 176 km²), their area decreased to 103 km² and 39 km² in respectively 1986 and 2006. Agricultural land use increased in the same period from 16 km² (1972) over 87 km² (1986) to 145 km² (2006). A landscape dominated by a forest matrix evolved hence in a 34-year period into an agricultural landscape. These observations coincide with those of Arouna et al. (2002) in North Benin between 1975 and 1998, where forest galleries, open forest and savannah vegetations have been ousted by a mosaic of fallow lands and fields, characterized by a regression of 41% of the forest area. In the centre of Benin, Oloukoi et al. (2006) have also recorded a dominance (61.2%) of agricultural fields over forests. An increase of the importance of the built-up class was also noted, likely due to an increase of the population density. The observed substitution of forest and savannah by agricultural fields and fallow lands is evidenced by the transition matrix between 1972 and 2006 (Table 12.2). It shows that only a small fraction of the original forest area (3.95%) was not subject to change, and that the forest was mainly transformed into agricultural land use (83.32%) over time. The savannah vegetation was more resistant to land use change (27.23%), nevertheless a large part is also used for agricultural production (65.08%). Agricultural land cover was the most stable patch type (76.85%), and its conversions to forest (2.95%) and savannah (12.10%) can be linked to shifting agriculture (Bogaert et al. 2008). Built-up was the second most stable class (47.46%). The conversion of builtup to savannah (32.43%) is explained by land abandonment and demographic shifts. The initial villages are abandoned for new ones more closely situated to more productive lands. The transition of built-up to agriculture can be explained by the recuperation of formerly inhabited zones by immigrants.

Table 12.2 Land cover dynamics in the Banikoara region between 1972 and 2006. All land cover fractions are expressed as a percentage of the 1972 class area. Total study area equal to 192 km^2 .

		2006				
		Forest	Savannah	Agriculture	Built-up	
1972	Forest	3.95	8.03	83.32	4.70	
	Savannah	4.85	27.23	65.08	2.84	
	Agriculture	2.95	12.10	76.85	8.10	
	Built-up	0.80	32.43	19.31	47.46	

The land cover dynamics described in Tables 12.1 and 12.2 have had profound impacts on the landscape configuration (Fig. 12.3).



Fig. 12.3 Evolution of the average patch area for each land cover class in the Banikoara region between 1972 and 2006.

Increased levels of fragmentation were observed for the classes representing natural land covers, as quantified by the average patch size, which dropped considerably for the forest and savannah land cover classes, especially between 1972 and 1986, and which increased remarkably for the agricultural land cover in the same period. The built-up land cover class had the highest increase within the period between 1986 and 2006.

The aforementioned tendencies reflect an anthropisation of the Banikoara region between 1972 and 2006, reflected by a substitution of the forest landscape matrix by cotton fields, and by an increase of the population of about 46% between 1992 and 2003 (INSAE 2003). This type of agricultural development, where natural land covers are replaced by anthropogenic ones, leading to a more fragmented status of the natural habitats, was earlier confirmed in Benin by Codjia and Gnagna (1993), Tenté (2000) and Orékan (2007), and for the Democratic Republic of the Congo by Bamba et al. (2008) and Bogaert et al. (2008).

12.3 Empirical evidences of the impact of fragmentation on biodiversity

In this section, the effect of habitat fragmentation on biodiversity is shown by means of two case studies.

12.3.1 Fragmentation alters forest diversity in a forest-savannah transition zone (Tanda region, Ivory Coast)

12.3.1.1 Context, data set and methods

Many studies have reported rapid land cover changes in the tropics (Skole and Tucker 1993); landscape fragmentation as an expression of anthropogenic activities has been considered one of the dominant drivers of landscape dynamics (Bucini and Lambin 2002). Forests situated at forest-savannah contact zones are considered to be more vulnerable to this type of degradation because of the high frequency of edges and of the heterogeneity of the landscape matrix itself (Hennenberg et al. 2008). The forest-savannah contact zones situated in the eastern part of Ivory Coast are accepted as the physical expression of the expanding savannah vegetations nearby (Barima et al. 2009). For the Tanda region, characterized by such transition zones, the impact of fragmentation on forest species diversity was studied in order to quantify the consequences of anthropogenic landscape degradation.

The study area is situated in the mesophylic sector of the Guinean domain; its principal climax vegetation is the humid semi-deciduous dense forest. Three vegetation types dominate the land cover: secondary forest, wooded savannah and tree savannah (Guillaumet and Adjanohoun 1971). By means of Landsat ETM+ imagery of 2002, forest landscapes were identified (Barima et al. 2009) and 50 sites of each 1 km² were defined based on a randomized stratification strategy. For every site, the number of forest patches (N) and the total forested area (A, expressed as the number of pixels) were determined using ArcGis 9.2. Patches were defined considering four neighbouring positions for every pixel. The degree of forest fragmentation (F, Monmonier 1974) was consequently calculated:

$$F = \frac{N-1}{A-1}$$
(12.3)

High values of the fragmentation index correspond to a high degree of fragmentation. A forest inventory was executed in one patch per site; species with DBH>10 cm were included. Species names were based on Lebrun and Stork (1991-1997). Species were classified as heliophylic or non-heliophylic according to Hawthorne (1996), Molino and Sabatier (2001) and Bakayoko (2005). The presence of heliophylic species is accepted as characteristic for open, disturbed vegetations. The diversity of every site has been quantified using the Shannon index (H', Magurran 2004), which integrates, in one single metric, both richness and evenness of the sample:

$$H' = -\sum_{i=1}^{S} p_i \log p_i$$
 (12.4)

with S the number of species in the sample and p_i the proportional abundance of the *i*-th species. A high value of H' reflects the presence of many species and/or the absence of dominating species in the sample. Poor, dominated samples will be characterized by low values of H'. The relationship between forest fragmentation, the percentage of heliophylic species and forest diversity was investigated by linear regression.

12.3.1.2 Results and discussion

Forest diversity was found to be determined by forest fragmentation (Fig. 12.4, $R^2 = 0.41, p < 0.001$). Also the presence of heliophylic species was influenced by the patchiness of the landscape ($R^2 = 0.33, p < 0.001$). Forest diversity diminished when forest fragmentation increased, which suggests that communities in degraded landscapes contained less species, or that they were dominated by one or a few species, or a combination of both. At the same time, a shift towards communities with more heliophylic species was observed with increasing fragmentation.

Fragmentation creates more open forest canopies (Uhl et al. 1997), which favours the proliferation of these species developing in direct sunlight. This observation, which links fragmentation to canopy openness and hence to tree density, suggests a key role in degradation for selective forest logging. The higher numbers of large heliophylic species or pioneers in logged forest, shown here and elsewhere (Bischoff et al. 2005; Berry et al. 2008), suggest that these

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Fig. 12.4 The impact of anthropogenic forest fragmentation on forest diversity in the Tanda region (Ivory Coast), measured by the Shannon diversity index and by the presence of heliophylic species. Fragmentation was measured by the Monmonier fragmentation index (Monmonier 1974).

species were more likely to survive in logged forest or became established in greater numbers soon after disturbance (Whitmore 1984). The empirically shown impacts of anthropogenic patchiness on forest diversity and vegetation composition confirm earlier observations by Benítez-Malvido and Martínez-Ramos (2003) and by Berry et al. (2008).

12.3.2 Edge effects and rodent abundance in Kisangani (Democratic Republic of the Congo)

12.3.2.1 Context, data set and methods

Habitat fragmentation leads to an increased frequency of patch edges (Bogaert 2000). Edge effects are observed when two different land cover types are adjacent and when both types are sufficiently different in structure (Forman 1995; Farina 2000a). Due to the contact with a contrasting land cover, the peripherical zones of both land covers are altered with regard to their microclimates; as a consequence of the strong link between ecological conditions and biodiversity, differences in species composition are observed between the central unaltered parts of a patch and the area along its perimeter (Forman 1995; Kolasa and Zalewski 1995; Bogaert et al. in press). Measuring these edge effects is appealing to improve understanding of anthropogenic effects on landscapes (Bogaert et al. in press). Consequently, empirical data should be collected *in situ* to enable more realistic estimates of edge effects and their ecological consequences (Chen et al. 2008).

The influence of edge effects on rodent diversity was assessed by means of the presence of two rodent species, *Hybomys univittatus* and *Praomys* cf. *jack*- soni, in the Masako Forest Reserve (MFR, $0^{\circ}36'$ N et $25^{\circ}13'$ E) in the Democratic Republic of the Congo (Iyongo Waya Mongo 2008). MFR, with an area equal to 2,105 ha, is situated at about 15 km of Kisangani and is characterized by an equatorial-continental climate type denoted as "Af" according to Koppen (Dudu 1991). MRF is mainly composed of primary forests of *Gilbertio-dendron dewevrei* (Caesalpiniaceae), next to secondary forests, swamp forests and fallow lands (Makana 1986; Kahindo 1988; Mabay 1994). A heterogeneous (*sensu* mixed or transitional) edge zone of about 40 m situated in between a secondary forest and a fallow land has been selected to assess edge effects on the presence of the two aforementioned rodent species.

Four capture zones have been installed covering both adjacent land cover types and the transition zone in between; each capture zone was composed of four parallel transects of 350 m situated 10 m apart. The distance between two traps inside a transect was 7 m (50 traps per transect) and *Elaeis* guineensis pulp was used as bait. Individuals have been captured by means of classic "Lucifer" rat traps between November 2007 and January 2008, a period characterized by one rainy month followed by two dry months. Captures have been pooled for every habitat type involved and compared between the habitats by means of the Kruskal-Wallis and Mann-Whitney statistical tests. Species have been identified by phylogenetic sequence analysis (cytochrome of mitochondrial DNA) using a data base of DNA sequences (Terryn et al. 2007) at the Royal Belgian Institute of Natural Sciences (Vertebrate department).

12.3.2.2 Results and discussion

Three hundred and ninety-nine individuals have been captured of which 110 of Hybomys univittatus and 289 of Praomys cf. jacksoni. Comparison of the average number of individuals captured per trap and per habitat showed a significant effect of the habitat type for both Hybomys univitatus and Praomys cf. jacksoni (Fig.12.5), suggesting a causality between the ecological characteristics of each habitat and the abundance of the species. These results were confirmed by the Mann-Whitney test. For Hybory's univitatus, a significant difference between the abundance in the fallow land and the secondary forest was observed (H = 13.40, p < 0.01; U = 17, p < 0.05). Between the abundance recorded in the fallow land and in the edge zone (H = 13.40, p > 0.05; U =40, p > 0.05), and between the abundance recorded in the secondary forest habitat and in the edge zone (H = 13.40, p > 0.05; U = 91, p > 0.05), no significant differences were detected. For *Praomys* cf. *jacksoni*, the abundance observed varied differently: while no significant difference was recorded for the comparison of the abundance between the fallow land and the secondary forest habitat (H = 28.19, p > 0.05; U = 96, p > 0.05), the abundance of the edge zone and the fallow land habitat (H = 28.19, p < 0.001; U = 14, p < 0.001)were found significantly different; the same conclusion was made for the comparison of the abundance between the edge zone and the forest habitat (H = 28.19, p < 0.001; U = 4, p < 0.001).





Fig. 12.5 Edge effect on rodent abundance in the Masako Forest Reserve (Democratic Republic of the Congo). Average number of individuals captured per trap in fallow land, edge and secondary forest habitat for *Hybomys univittatus* (left) and *Praomys* cf. *jacksoni* (right) are given together with their standard errors. Significant differences are indicated by different characters.

For both species the expression of the edge effect was clearly different, since the distribution of the number of individuals among the habitat types was not similar. For *Hybomys univittatus*, an intermediate abundance is observed for the edge zone, relative to the adjacent fallow and forest cover types, which corresponds to a classic edge effect of gradual change across a boundary between two different land cover types (Iyongo Waya Mongo 2008; Bogaert et al. in press). According to the capture data, Hybomys univitatus preferred the fallow habitat type to the secondary forest habitat, which should be interpreted with caution, since this observation is inconsistent with Dudu (1991), who signalled a higher presence of Hybomys univitatus in secondary forest habitats. This contradiction should be verified; it could, however, be explained as a seasonal variability of species abundance due to seasonal changes in precipitation influencing insect and fruit availability in the habitats concerned (Nicolas and Colyn 2003). Praomys cf. jacksoni seemed to avoid the edge zone, and to prefer either the forest habitat or the fallow habitat, which confirmed the observations of Dudu (1991), who noted likewise quasi equal abundance for this species in both fallow and secondary forest vegetations.

For both species, an undeniable edge effect has been observed, as shown by the significant differences in abundance between the three habitats considered, which corresponds to one type of edge effect as described by Murcia (1995), who also mentioned changes of the physical environment (e.g. increased temperatures in the edge zone) and changes of the interaction between species (e.g. altered predation patterns) as types of edge effects. Comparison of both species emphasizes that edge effects can take different forms in nature; the edge zone constitutes a distinct habitat, preferred or avoided by species, or simply considered as a transitional zone between more and less favourable habitat types. A classification of species according to their type of response to land cover transitions, as presented for rodents in Iyongo Waya Mongo (2008), is therefore indispensable for fully understanding the impact of fragmentation and the concomitant edge effects on diversity. Due to the direct link between land cover pattern, microclimate and diversity, edge effects can be considered as a typical example or application of the pattern/process paradigm, a central theme of landscape ecology, which links landscape pattern to its ecological consequences (Turner 1989; Coulson et al. 1999).

12.4 Implications for landscape management — conclusions

The four case studies previously discussed provide tangible examples of the main causes and ecological impacts of forest fragmentation. Landscape planners should consider this type of information in their landscape-scale design proposals (Brown et al. 2007; Corry et al. 2008).

To mitigate the negative effects of fragmentation on diversity and ecosystem function, landscape corridors could be created in order to compensate for lower diversity due to edge effects or small patches (Farina 2000b). An example is therefore presented in which anthropogenic, scattered landscape elements are spatially rearranged to create corridors between existing, valuable ecosystems.

12.4.1 Creation of a teak (*Tectona grandis* L. f.) corridor network in the Atlantic Department (Benin) to remediate forest isolation

12.4.1.1 Context, data set and methods

Vast areas of forest are destroyed every year in Benin as a consequence of agricultural development or timber extraction (FAO 2005). This deforestation has not spared the natural forests of the municipality of Zè, situated in the oriental part of the Atlantic Department where it has led to considerable patch isolation. Nevertheless, a fraction of the lost forest area has been compensated for by forest plantations, especially teak (*Tectona grandis* L. f.) (Ganglo et al. 1999). In the municipality of Zè, more than 618 patches of teak covering a cumulative area of about 1000 ha have been registered (Toyi 2007). These plantations are primarily considered as wood production units although an important ecological function could also be attributed to these landscape elements if their spatial pattern should be taken into account: a spatial aggregation of the areas of the teak plantations could establish planned continuous (*sensu* Hilty et al. 2006) corridors between the isolated natural forests. Landscape corridors constitute key elements for the conservation and restoration

of biodiversity since they offer supplementary habitats and increase habitat connectivity (Paillat and Butet 1994; Hilty et al. 2006). Designing a network of connectivity across a landscape benefits directly humans, as well as biodiversity (Hilty et al. 2006). This consideration of a second function of teak plantations, next to purely wood production, corresponds to the notion of the multiple ecosystem services (Costanza et al. 1997); corridors can provide free ecosystem services (Hilty et al. 2006). In this contribution, different scenarios of corridor creation using teak plantations for the municipality of Zè are analysed in order to illustrate the concept and to evidence its potential for landscape planning based upon ecological and economical grounds.

Five natural forest patches have been chosen in the aforementioned municipality (Fig.12.6): Djigbé-Agué ($6^{\circ}52'48''$ N, $2^{\circ}23'6''$ E; 18.57 ha), Djigbé-Aguudji ($6^{\circ}52'03''$ N, $2^{\circ}23'15''$ E; 28.11 ha), Ouovinou ($6^{\circ}52'57''$ N, $2^{\circ}24'18''$ E; 48.55 ha), Aglangouin ($6^{\circ}52'48''$ N, $2^{\circ}24'54''$ E; 129.68 ha) and Sèdjè ($6^{\circ}47'42''$ N, $2^{\circ}24'00''$ E; 329.57 ha). These forests are isolated and situated in a zone not appropriate for shifting agriculture; anthropogenic pressure on these forests is consequently negligible, which emphasizes their importance for diversity conservation. The maximum distance between the teak plantations and the forest patches to determine the plantations to be included in the study was set to 5 km. The dislocation of plantations with area superior to 20 ha was avoided. One hundred and fifteen patches of teak were considered in this analysis, with total area equal to 305 ha, which constitutes the upper limit of the total corridor area to be established. A corridor width of 100 m has been chosen.

Five scenarios are considered to define the corridor networks: (A) a minimum number of links between the forests, with minimal cumulative corridor distance; (B) a closed peripherical corridor loop in which every forest is linked to two other forests; (C) the same scenario as B completed with one extra link (the shortest); (D) a corridor network in which every forest is connected to every other forest and in which crossing points are not considered as network nodes; (E) a corridor network in which every forest is connected to every other forest and in which crossing points are considered as network nodes.

To quantify the proposed corridor network architecture, the gamma and alpha index are used (Forman and Godron 1986). The gamma index (γ) , measuring connectivity, is the ratio of the number of links in a network (L) to the maximum possible number of links in that network which is determined by the number of network nodes (V) present, i.e.,

$$\gamma = \frac{L}{3(V-2)} \tag{12.5}$$

The gamma index varies from zero (none of the nodes is linked) to 1 (every node is linked to every other possible node). A second network index, the alpha index (α), is a measure of circuitry, the degree to which "circuits" that connect nodes in a network are present. The alpha index is the ratio



Fig. 12.6 Forest fragments selected in the municipality of Zè. Existing teak plantations could be used for creating ecological corridors in this landscape.

of the actual number of circuits in the network to the maximum number of possible circuits, and is calculated by

$$\alpha = \frac{L - V + 1}{2V - 5} \tag{12.6}$$

and α ranges from zero, for a circuit-less network, to 1 for a network with the maximum possible number of loops present. Together, connectivity and circuitry, indicate the degree of network complexity (Forman and Godron 1986).

12.4.1.2 Results and discussion

Fig.12.7 shows the five diagrams of the corridor networks proposed. In E, the crossing points of the corridors are considered as secondary nodes since, in practice, at these points animals can change of corridor. The secondary nodes are certainly not equivalent to the main nodes of the network, i.e. the forests in the municipality of Zè, representing a larger area and biodiversity. Table 12.3 shows the results of the network complexity analysis for the five scenarios proposed.

Three of the proposed networks (A, B and C) do not utilise all the resources available for corridor creation; scenario A is the most simple to realize, due to its short distance. Nevertheless, this network is not characterized by good connectivity and circuitry values, which undermine its effectiveness in conservation and to enhance interactions between individuals of the isolated forests. 290 Chapter 12 Forest Fragmentation: Causes and Impacts



Fig. 12.7 Diagrammatic representation of the five corridor network scenarios considered for the municipality of Zè. Black filled circles represent the five forests to be connected by the network. Small open circles are secondary nodes situated at the crossing of corridors.

Table 12.3 Network complexity statistics of the five corridor network scenarios. A corridor width of 100 m is assumed. D is the total network length. R is the ratio of the network area to the cumulative area of teak plantations (305 ha). Network complexity is determined by the number of links (L) and the number of nodes (V). γ quantifies network connectivity; α quantifies network circuitry.

	Network scenario							
	А	В	С	D	Е			
$D(\mathrm{km})$	13.05	21.60	24.48	39.18	39.18			
R	0.43	0.71	0.80	1.28	1.28			
L	4	5	6	10	18			
V	5	5	5	5	10			
γ	0.44	0.56	0.67	1.00	0.75			
α	0.00	0.20	0.40	1.00	0.60			

Scenarios B and C are characterized by higher values for γ and α , which indicates that they should lead to better results with regard to conservation. Scenario C could be preferred over B because its connectivity is higher and more circuits are available for the species using the corridor network. Its relatively short length is expected to provide increased connectivity than longer corridors (Hilty et al. 2006), a characteristic not quantified by γ and α . Scenario D is to be preferred based upon γ and α , but cannot be realized *in situ*, since the resources needed exceed the total teak area available for spatial rearrangement by 28%. When the crossing points of the corridors are considered as secondary nodes, the connectivity and circuitry indices indicate lower values, due to a potential number of links that could theoretically still be created with these secondary nodes. It should be noted that corridor width, in this study set to 100 m, remains subject to debate (Hilty et al. 2006) and should be considered with regard to the species considered. Nevertheless, the chosen value lies inside the range described in other studies (Hilty et al. 2006).

Relating the composition and structure of landscapes to the ecosystems they provide is a challenge for landscape ecologists (Crow 2008). Connectivity is one of the landscape characteristics that can compensate for diversity loss due to edge effects, and that can show that a landscape contains a higher species number than predicted by island biogeography theory (Farina 2000b). Maintaining or restoring landscape connectivity is currently a central concern in ecology and land conservation planning (Saura and Torné 2009).

For the municipality of Zè, five corridor networks have been analyzed to link five existing forests. Three of the scenarios can be realized, of which one should be preferred based upon its architecture and length. This exercise underlines the potential of landscape planning in biodiversity management at the landscape scale. As an application of the "pattern/process paradigm", landscape configuration could be used to have a beneficial effect on landscape biodiversity, a concept which has led recently to the development of a software package (Conefor Sensinode 2.2) quantifying the importance of habitat patches for landscape connectivity (Saura and Torné 2009).

By rearranging the existing plantations, a network can be created that mitigates the negative effects of forest fragmentation such as population isolation and edge effects. In this way, timber production could contribute to a better functioning of the ecosystems by linking them; in this way, economical and ecological objectives are integrated. Nevertheless, this type of theoretical consideration should be validated by long-term experiments; the empirical understanding of corridor effects on community structure and diversity is still in its infancy (Haddad and Tewksbury 2006).

12.4.2 Summary and concluding remarks

In order to enable landscape managers to manage fragmented landscapes adequately, the causes and ecological consequences of habitat fragmentation have to be fully understood. Field data should guide landscape ecologists in this more comprehensive understanding and their interpretation should constitute a main occupation of landscape ecologists (Chen et al. 2008).

In this chapter, two case studies are presented illustrating the main drivers of fragmentation in the Democratic Republic of the Congo (Oriental Province) and in North Benin. Anthropogenic pressure and population density caused forest degradation leading to the dissipation of forest habitats. Two case studies quantifying the impacts of fragmentation on biodiversity are discussed; decreasing levels of forest diversity in fragmented forests were detected in the Tanda Region of Ivory Coast; edge effects on two rodent species were observed in Kisangani (Democratic Republic of the Congo). The fifth case study considered the possibility to remediate fragmented landscapes by a spatial planning of teak plantations in the Atlantic Department in Benin. All five studies were based on field data analysis and provide additional clues on the process of forest fragmentation, observed in different forms and associated with divergent consequences.

Although these studies give a limited perspective on the possible causes and consequences of fragmentation, they contribute to the ongoing debate on landscape management and conservation at multiple scales. A more comprehensive view on fragmentation as well as more efficient landscape management plans are needed, avoiding dispersion of valuable natural resources in the future and mitigating the impact of less favourable spatial patterns on diversity.

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References

- Angelsen A, Kaimowitz D (1999) Rethinking the causes of deforestation: Lessons from economic models. World Bank Res Obser 14: 73-98.
- Arouna O, Sinsin B, Houndagba CJ (2002) L'exploitation des Ressources Biologiques et la Dynamique de la Forêt Classée de l'Alibori Supérieur au Bénin. Notes du Laboratoire d'Ecologie Appliquée, Université d'Abomey-Calavi, Bénin.
- Bakayoko A (2005) Influence de la Fragmentation Forestière sur la Composition Floristique et la Structure Végétale dans le Sud-ouest de la Côte d'Ivoire. Thèse de doctorat, Université de Cocody-Abidjan, Abidjan.
- Bamba I, Mama A, Neuba DFR et al. (2008) Influence des actions anthropiques sur la dynamique spatio-temporelle de l'occupation du sol dans la province du Congo central (R.D. Congo). Sciences & Nature 5: 49-60.
- Barima YSS, Barbier N, Bamba I et al. (2009) Dynamique paysagère en milieu de transition forêt-savane ivoirienne. Bois For Trop 299: 15-25.
- Bender DJ, Contreras TA, Fahrig L (1998) Habitat loss and population decline: A meta-analysis of the patch size effect. Ecology 79: 517-533.
- Benítez-Malvido J, Martínez-Ramos M (2003) Impact of forest fragmentation on understory plant species richness in Amazonia. Conserv Biol 17: 389-400.
- Berry NJ, Phillips OL, Ong RC et al. (2008) Impacts of selective logging on tree diversity across a rainforest landscape: The importance of spatial scale. Landscape Ecol 23: 915-929.
- Bischoff W, Newbery DM, Lingenfelder M et al. (2005) Secondary succession and dipterocarp recruitment in Bornean rain forest after logging. Forest Ecol Manag 218: 174-192.
- Bogaert J (2000) Quantifying habitat fragmentation as a spatial process in a patchcorridor-matrix landscape model. PhD dissertation, University of Antwerp, Antwerp.
- Bogaert J (2003) Lack of agreement on fragmentation metrics blurs correspondence between fragmentation experiments and predicted effects. Conserv Ecol 7(1) (URL: www.consecol.org/vol7/iss1/resp6).
- Bogaert J, Ceulemans R, Salvador-Van Eysenrode D (2004) Decision tree algorithm for detection of spatial processes in landscape transformation. Environ Manage 33: 62-73.

- Bogaert J, Hong SK (2004) Landscape ecology: Monitoring landscape dynamics using spatial pattern metrics. In: Hong SK, Lee JA, Ihm BS et al (eds) Ecological Issues in a Changing World. Status, Response and Strategy. Kluwer Academic Publishers, Dordrecht.
- Bogaert J, Mahamane A (2005) Ecologie du paysage: Cibler la configuration et l'échelle spatiale. Ann Sci Agron Bénin 7: 1-15.
- Bogaert J, Bamba I, Koffi KJ et al. (2008) Fragmentation of forest landscapes in Central Africa: Causes, consequences and management. In: Lafortezza R, Chen J, Sanesi G et al. (eds) Patterns and Processes in Forest Landscapes. Springer Science+Business Media B.V., New York.
- Bogaert J, Barima YSS, Ji J et al. (in press). A methodological framework to quantify anthropogenic effects on landscape pattern. In: Hong SK, Wu J, Kim JE et al. (eds) Ecology of Asian Cultural Landscapes. Springer Verlag, New York.
- Brown RD, Lafortezza R, Corry RC et al. (2007) Cultural patterns as a component of environmental planning and design. In: Hong SK, Nakagoshi N, Fu B et al. (eds) Landscape Ecological Applications in Man-influenced Areas: Linking Man and Nature Systems. Springer Science+Business Media B.V., New York.
- Bucini G, Lambin EF (2002) Fire impacts on vegetation in Central Africa: A remote sensing-based statistical analysis. Appl Geogr 22: 27-48.
- Burgess RL, Sharpe DM (1981) Introduction. In: Burgess RL, Sharpe DM (eds) Forest Island Dynamics in Man-dominated Landscapes. Springer-Verlag, New York.
- Chen J, Brosofske KD, Lafortezza R (2008) Ecology and management of forest landscapes. In: Lafortezza R, Chen J, Sanesi G et al (eds) Patterns and Processes in Forest Landscapes. Springer Science+Business Media B.V., New York.
- Codjia C, Gnagna P (1993) Dynamique des paysages des forêts classées de Toui et de Kilibo. Mémoire, Université Nationale du Bénin, Abomey-Calavi.
- Collinge SK (1996) Ecological consequences of habitat fragmentation: Implications for landscape architecture and planning. Landscape Urban Plan 36: 59-77.
- Collingham YC, Huntley B (2000) Impacts of habitat fragmentation and patch size upon migration rates. Ecol Appl 10: 131-144.
- Corry RC, Lafortezza R, Brown RD et al. (2008) Using landscape context to guide ecological restoration: An approach for pits and quarries in Ontario. Ecol Rest 26: 120-127.
- Costanza R, d'Arge R, de Groot R et al. (1997) The value of the world's ecosystem services and natural capital. Nature 387: 253-260.
- Coulson RN, Saarenmaa H, Daugherty WC et al. (1999) A knowledge system environment for ecosystem management. In: Klopatek JM, Gardner RH (eds) Landscape Ecological Analysis: Issues and Applications. Springer, Berlin Heidelberg New York.
- Crow TR (2008) Managing forest landscapes for climate change. In: Lafortezza R, Chen J, Sanesi G et al. (eds) Patterns and Processes in Forest Landscapes. Springer Science+Business Media B.V., New York.
- Curtis JT (1956) The modification of mid-latitude grasslands and forests by Man. In: Thomas WL (ed) Man's Role in Changing the Face of the Earth. University of Chicago Press, Chicago.
- Davidson C (1998) Issues in measuring landscape fragmentation. Wildlife Soc B 26: 32-37.
- Davies KF, Margules CR (1998) Effects of habitat fragmentation on carabid beetles: Experimental evidence. J Animal Ecol 67: 460-471.
- Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. Conserv Biol 14: 342-355.

- 294 Chapter 12 Forest Fragmentation: Causes and Impacts
- De Santo RS, Smith DG (1993) An introduction to issues of habitat fragmentation relative to transportation corridors with special reference to High-Speed Rail (HSR). Environ Manage 17: 111-114.
- Dudu AM (1991) Etude du peuplement d'insectivores et de rongeurs de la forêt ombrophile de basse altitude du Zaïre (Kisangani, Masako). Thèse de doctorat, Université d'Anvers, Anvers.
- Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81: 117-142.
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol S 34: 487-515.
- FAO (2004) Etude de la situation et de l'évolution des systèmes de vulgarisation et d'animation forestière en Afrique sahélienne. FAO, Rome.
- FAO (2005) Evaluation des ressources forestières mondiales. Rapport national 144 Bénin. FAO, Rome.
- Farina A (2000a) Principles and Methods in Landscape Ecology. Kluwer Academic Publishers, Dordrecht.
- Farina A. (2000b) Landscape Ecology in Action. Kluwer Academic Publishers, Dordrecht.
- Forman RTT, Godron M (1986) Landscape Ecology. John Wiley & Sons, New York.
- Forman RTT (1995) Land Mosaics: The Ecology of Landscapes and Regions. Cambridge University Press, Cambridge.
- Franklin AB, Noon BR, Luke George T (2002) What is habitat fragmentation. Stud Avian Biol 25: 20-29.
- Ganglo CJ, Lejoly J, Pipar T (1999) Le teck (*Tectona grandis* L. f.) au Bénin, gestion et perspectives. Bois For Trop 261: 17-27.
- Geist HJ, Lambin EF (2001) What drives tropical deforestation? A meta-analysis of proximate and underlying causes of deforestation based on subnational scale case study evidence. LUCC Report Series No. 4, Louvain-la-Neuve.
- Goodwin BJ, Fahrig L (2002) How does landscape structure influence landscape connectivity? Oikos 99: 552-570.
- Groom M, Schumaker NH (1993) Evaluating landscape change: Patterns of worldwide deforestation and local fragmentation. In: Kareiva PM, Kingsolver JG, Huey RB et al. (eds) Biotic Interactions and Global Change. Sinauer Associates Inc., Sunderland.
- Guillaumet JL, Adjanohoun E (1971) La végétation de la Côte d'Ivoire. In: Avenard JM, Edlin M, Girard G (eds) Le Milieu Naturel de la Côte d'Ivoire. Mémoires de l'Orstom, Paris.
- Haddad NM, Tewksbury JJ (2006) Impacts of corridors on populations and communities. In: Crooks KR, Sanjayan M (eds) Connectivity Conservation. Cambridge University Press, Cambridge.
- Haila Y (2002) A conceptual genealogy of fragmentation research: From island biogeography to landscape ecology. Ecol Appl 12: 321-334.
- Hawthorne WD (1996) Holes and the sums of parts in Ghanaian forest regeneration, scale and sustainable use. P Roy Soc Edinb 104: 74-176.
- Hecht SB (1985) Environment, development, and politics: Capital accumulation and the livestock sector in Amazonia. World Dev 13: 663-684.
- Hennenberg KJ, Orthmann B, Steinke I et al. (2008) Core area analysis at semideciduous forest islands in the Comoé National Park, NE Ivory Coast. Biodivers Conserv 17: 2787-2797.
- Heywood VH, Watson RT (eds) (1995) Global Biodiversity Assessment. Cambridge University Press, Cambridge.
- Hilty JA, Lidecker WZJr, Merenlender AM (2006) Corridor Ecology. The Science and Practice of Linking Landscapes for Biodiversity Conservation. Island Press,

Washington.

- INSAE (2003) Troisième Recensement Général de la Population et de l'habitat. Institut National de la Statistique et de l'Analyse Economique, Cotonou.
- Iyongo Waya Mongo L (2008) Etude des Effets de Lisière sur les Populations des Rongeurs dans la Réserve Forestière de Masako (Kisangani, R.D. Congo). Mémoire de DEA, Université libre de Bruxelles, Bruxelles.
- Jaeger J (2000) Landscape division, splitting index, and effective mesh size: New measures of landscape fragmentation. Landscape Ecol 15: 115-130.
- Kahindo M (1988) Contribution à l'étude floristique et phytosociologique de la Réserve Forestière de Masako (Haut-Zaïre). Mémoire, Université de Kisangani, Kisangani.
- Kolasa J, Zalewski M (1995) Notes on ecotone attributes and functions. Hydrobiologia 303: 1-7.
- Krebs CJ (1994) Ecology: The Experimental Analysis of Distribution and Abundance. Harper Collins College Publishers, New York.
- Lafortezza R, Corry R, Sanesi G et al. (2008) Cultural determinants of spatial heterogeneity in forest landscapes. In: Lafortezza R, Chen J, Sanesi G et al. (eds) Patterns and Processes in Forest Landscapes. Springer Science+Business Media B.V., New York.
- Lebrun JP, Stork AL (1991-1997). Enumération des Plantes à Fleurs d'Afrique Tropicale. Conservatoire et Jardin Botanique de la ville de Genève, Genève.
- Li H, Wu J (2004) Use and misuse of landscape indices. Landscape Ecol 19: 389-399.
- Lord JM, Norton DA (1990) Scale and the spatial concept of fragmentation. Conserv Biol 4: 197-202.
- Mabay K (1994) Contribution à l'étude structurale des forêts primaire et secondaire de la Réserve de Masako. Mémoire, Université de Kisangani, Kisangani.
- MAEP (2000) Rapport annuel. Ministère de l'Agriculture, de l'Elevage et de la Pêche, Cotonou.
- Magurran AE (2004) Measuring Biological Diversity. Blackwell Publishing, Oxford.
- Makana M (1986) Contribution à l'étude floristique et écologique de la forêt à *Gilbertiodendron dewevrei* (De Wild) J. Léonard de Masako (Kisangani). Mémoire, Université de Kisangani, Kisangani.
- McGarigal K, Marks BJ (1995) Fragstats: Spatial pattern analysis program for quantifying structure. PNW-GTR-351, Oregon.
- Molino JF, Sabatier D (2001) Tree diversity in tropical rain forests: A validation of the intermediate disturbance hypothesis. Science 294: 1072-1074.
- Monmonier MS (1974) Measures of pattern complexity for choroplethic maps. Am Cartographer 1: 159-169.
- Murcia C (1995) Edge effects in fragmented forests: Implications for conservation. Trends Ecol Evol 10: 58-62.
- Nicolas V, Colyn M (2003) Seasonal variations in population and community structure of small rodents in a tropical forest of Gabon. Can J Zoolog 6: 1034-1046.
- Noss RF, Cooperrider AY (1994) Saving Nature's Legacy: Protecting and Restoring Biodiversity. Island Press, Washington DC.
- Oloukoi J, Mama VJ, Agbo FB (2006) Modélisation de la dynamique de l'occupation des terres dans le département des Collines au Bénin. Télédetection 6: 305-323.
- Orékan VA (2007) Implémentation du modèle local CLUE-s aux transformations spatiales dans le Centre Bénin aux moyens de données socio-économiques et de télédétection. Thèse de doctorat, Université de Bonn, Bonn.

Paillat G, Butet A (1994) Fragmentation et connectivité dans les paysages: Importances des habitats corridors pour les petits mammifères. Laboratoire d'Evolution des Systèmes Naturelles et Modifiés, Université de Rennes, Rennes.

PFBC (2006) Les forêts du bassin du Congo: état des forêts 2006. Partenariat pour

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les Forêts du Bassin du Congo, Paris.

- Riitters KH, Wickham JD, Vogelmann JE et al. (2000) National land cover pattern data (Ecology 81: 604). Ecol Arch E081-004.
- Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: A review. Conserv Biol 5: 18-32.
- Saura S, Torné J (2009) Conefor Sensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. Environ Modell Softw 24: 135-139.
- Shafer CL (1990) Nature Reserves. Smithsonian Institution Press, Washington.
- Skole D, Tucker CJ (1993) Tropical deforestation and habitat fragmentation in the Amazon: Satellite data from 1978 to 1988. Science 260: 1905-1910.
- Tenté B (2000) Dynamique actuelle de l'occupation du sol dans le massif de l'Atacora: étude du secteur Perma-Toukountouna. Mémoire de DEA, Université Nationale du Bénin, Abomey-Calavi.
- Terryn L, Wendelen W, Leirs H et al. (2007) African Rodentia. (URL: http://projects.biodiversity.be/africanrodentia).
- Toyi M (2007) Etude de la structure spatiale des teckeraies privées dans la Commune de Zè au sud du Bénin. Mémoire de DESS/AGRN, Université d'Abomey-Calavi, Abomey-Calavi.
- Turner MG (1989) Landscape ecology: The effect of pattern on process. Annu Rev Ecol Syst 20: 171-197.
- Uhl C, Barreto P, Veríssimo A et al. (1997) Natural resource management in the Brazilian Amazon. Bioscience 47: 160-168.
- UNEP (2004) Africa Population Distribution Database. United Nations Environment Programme GRID Sioux Falls Dataset (URL: http://na.unep.net/datasets /datalist.php).
- Whitmore TC (1984) Tropical Rain Forests of the Far East. Clarendon Press, Oxford.
- Wilcove DS, McLellan CH, Dobson AP (1986) Habitat fragmentation in the temperate zone. In: Soulé ME (ed) Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates Inc., Sunderland.
- Wiens JA (1989) The Ecology of Birds Communities. Cambridge University Press, Cambridge.
- Williams M (2000) Dark ages and dark areas: Global deforestation in the deep past. J Hist Geogr 26: 28-46.
- Yaacobi G, Yaron Z, Rosenzweig ML (2007) Habitat fragmentation may not matter to species diversity. P R Soc B 274: 2409-2412.