Available online at http://ajol.info/index.php/ijbcs

Int. J. Biol. Chem. Sci. 6(4): 1467-1479, August 2012

International Journal of Biological and Chemical Sciences

ISSN 1991-8631

Original Paper

http://indexmedicus.afro.who.int

Influence of forest degradation on tree diversity in a forest-savannah transition in Eastern Ivory Coast

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ABSTRACT

This study aimed at determining forest degradation impact on tree diversity in a forest-savannah transition zone in Ivory Coast. Structures of forest patches were given from the comparison of their number, area and index of fragmentation on basis of two land cover maps. Two forest types were identified according to their degradation. Results showed that landscape and forest disturbance, characterized by a forest canopy opening up, led to an increase of light-tolerant species and their richness in degraded forests. Thus, if diversity is summarized to species richness, forest degradation does not lead to a reduction of diversity. In contrast, species in degraded forests are less evenly distributed than those in non-degraded forests. Species abundance distribution in degraded forests indicates that only a few species dominate this zone due essentially to anthropogenic disturbances. In non-degraded forests, abundance distribution shows a relatively stable community in which individuals are more evenly distributed among species. Considering species abundance distribution and evenness index, non-degraded forest has a greater diversity than degraded forest.

Keywords: Landscape fragmentation, forest degradation, diversity index, species abundance distribution, light-demanding species.

INTRODUCTION

Habitat fragmentation is a dynamic process whose impact varies according to species, landscape type, spatial scale and geographical region considered (Bogaert and Barima, 2008; Bogaert et al., 2011). During this process, habitat area reduction and isolation are observed. This change in landscape pattern is often accompanied by a reduction in habitat quality, which limits long-term chance of species (or taxa) survival in any given fragment (Benitez-Malvido and Martinez-Ramos, 2003). Tropical forest fragmentation has therefore been described as one of the main threats to biodiversity (Bogaert et al., 2011). In particular, taxa with

DOI : http://dx.doi.org/10.4314/ijbcs.v6i4.6

highly specific requirements according to their environment, such as those which are dependent on habitats close to their natural state, can be specially endangered (Herbener et al., 2012).

Landscapes in Eastern Ivory Coast, where forest and savannah meet, have been subjected to fragmentation (Goetze et al., 2006). This phenomenon is now amplified in this region, from forest-savannah transition that divides the country into two parts, northern savannah and southern forested landscapes (Barima et al., 2010b). This area represents a front of anthropogenic disturbance from savannah zone to forest and leads to a change in landscape composition and configuration (Goetze et al., 2006; Barima et al., 2010b). Drivers of this disturbance are mainly timber exploitation (industrial and artisanal), slash-and-burn agriculture and forest or wildfire (Barima et al., 2010a). These activities increase forest stands vulnerability of this region, particularly due to creation of new edge areas which cause changes in local diversity (Hamilton, 2005).

Quantifying this diversity is one of the principal aims of biological conservation, and there are numerous articles discussing the best way to perform it (Ludwig and Reynolds, 1988; Hubbell, 2001; Hamilton, 2005) Several indices have been developed for measuring biodiversity (species richness, Shannon’s index, Simpson’s index, Hill’s index, etc.). Species richness or number of species is currently used. This determination is quick and easy. It gives specific information on observed or potential species number in a plant community (Ludwig and Reynolds, 1988). Biodiversity richness component is also a characteristic of plant community related to its stability, productivity, trophic structure and species migration (Hamilton, 2005). Species proportional abundance in a community is another component of biodiversity (Hurlbert, 1971; Dunstan et al., 2012). It can be measured by means of an evenness index, such as Pielou's index. But describing species diversity by a single value can compromise a large part of community structure detail (Hamilton, 2005). For this reason the use of species abundance distribution models is recommended as they provide independent and complementary information on community structure like tropical forest stand (Magurran and Henderson, 2003). Various mathematical functions have been used to model the distributions observed; the most used are log-normal, broken-stick and log-series distributions (Hubbell, 2001). Their interpretation provides indications of ecological processes (disturbance, regeneration, etc.) that have led to community composition observed (Yin et al., 2005). Therefore, in a relatively stable forest, where various species are frequent, log-normal distribution of species abundance would be expected (Masharabu et al., 2010). When these species share equally an ecological factor, log-series distribution is observed (Hubbell, 2001). In a perturbed community where rare species are encountered, abundance distribution would correspond to broken-stick distribution (Magurran and Henderson, 2003).

The present study aims to assess the relationship between forest structure (number of patches, forest area) disturbances and tree diversity in forest-savannah transition zone. Assuming that forest structural degradation leads to a decreasing of tree diversity, this study attempted to show whether forest species richness could only allow to describe forest diversity in a disturbed forest-savannah contact zone. It also showed the role of evenness and abundance species distribution in diversity description of forests stands.

MATERIALS AND METHODS

Study area

Study area is located in forest-savannah transition zone of Tanda’s Department (Eastern Ivory Coast) (Figure 1). This region is situated in West African intertropical zone where dense, humid, semi-deciduous forests meet guinea savannahs. Its climate is tropical with a mean annual rainfall of 1019 mm and an average temperature of 26.2°C. Forests of study zone have undergone significant disturbance due to slash-and-burn agriculture, timber exploitation, and wildfire (Barima et al., 2010a).

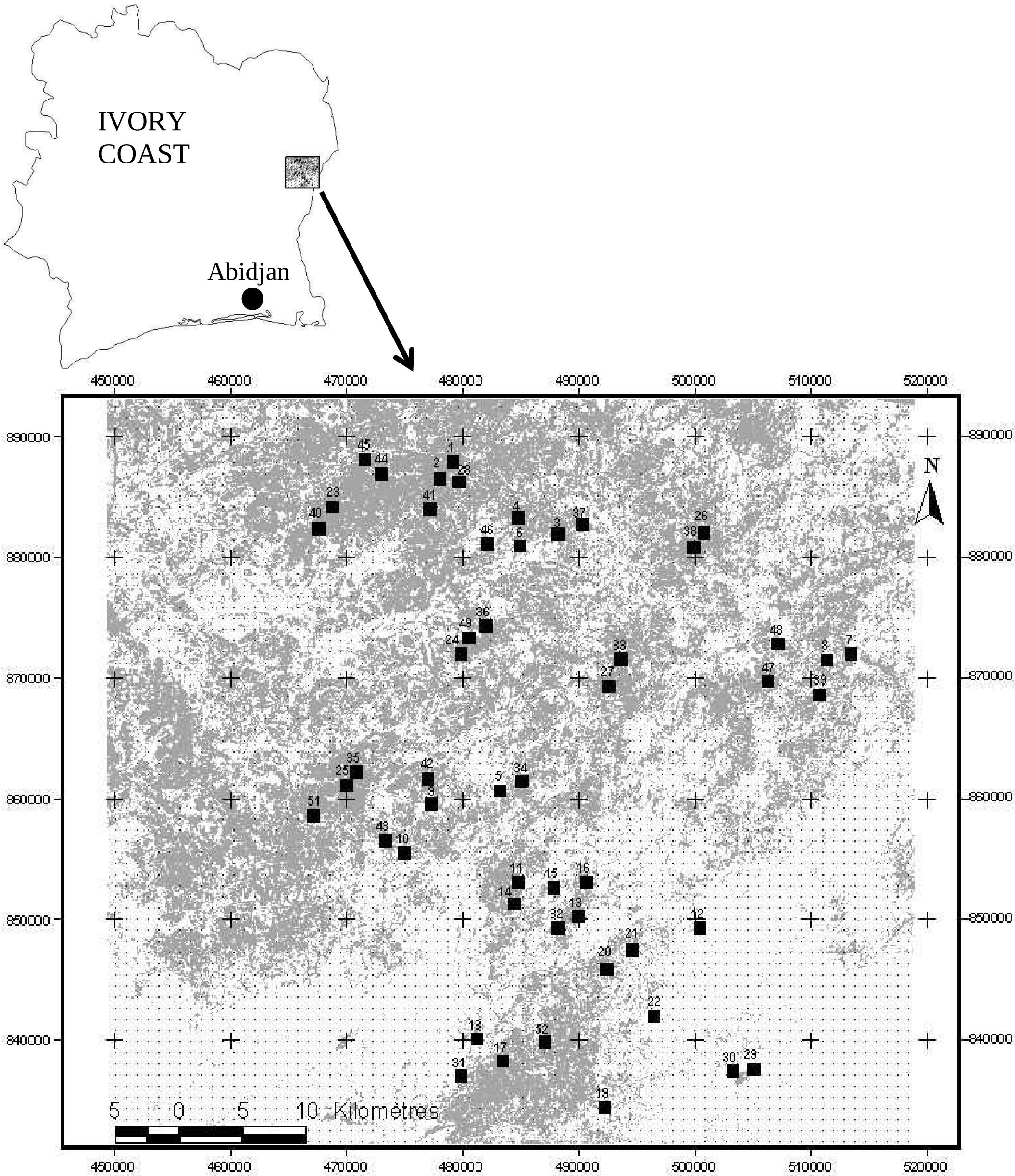

Figure 1: Location of study area in Ivory Coast and distribution of sites sampling. Study area is delimited by the quadrilateral of UTM coordinates *x* (449388; 518985) and *y* (831288; 893133). Black squares were the sampling areas. Grey colour areas were forest patches.

Forest extent

Forest Area forests were identified and mapped based on a radiometric classification of two Landsat images (30-m resolution), dating from January 18, 1986, (Landsat TM) and December 26, 2002, (Landsat ETM+) performed by Barima et al. (2009). We briefly review their classification.

These 30-m resolution images were first orthorectified based on geographical coordinates of landmarks located on the ground with GPS (intersections of major roads, large buildings, etc.). The geometric precision of calibration between these points and Landsat ETM+ image was less than one pixel (30 m), the minimum required for a change analysis (Lillesand et al., 2008). Radiometric correction was done by linear regression based on radiometric invariants. Radiometric reference points (200 points), characterized by an invariant reflectance, were identified on Landsat images, and transformation coefficients were determined by using statistics of these points. A mixed classification (unsupervised then supervised classification) was made on these images. An unsupervised classification was performed by maximum likelihood (Lillesand et al., 2008) on the basis of green (0.52-0.60 µm), red (R: 0.62 – 0.70 µm), and near infrared (NIR: 0.70-1.30 µm) bands. This enabled to identify 12 land cover classes that were grouped visually into eight land cover categories on the basis of *in situ* knowledge acquired during field visits. Next, radiometric statistics of classes were extracted from R and NIR spectral bands and projected onto orthonormalized axes in order to group similar radiometric classes. Finally, a land cover map containing two forest classes, among others, was obtained and validated on field references data. A *kappa* coefficient of 80% was obtained (Barima et al., 2009).

Forest landscape structure

Fifty-two survey points were set up in forests by means of stratified random sampling on basis of images processed. A surface of 1000 m x 1000 m (approximately 1231 pixels) was defined around each point, thus making up one site. For each site, degradation state of forest structure in 2002 compared to 1986 was determined by comparison of total number of forest patches (*np*) and forest area (*A*) (Bogaert et al., 2004). Structural degradation of forest landscape is marked by processes of dissection (np_{2002} / np_{1986} > 1 and 0.5 < A_{2002} / A_{1986} < 1), fragmentation (np_{2002} / np_{1986} > 1 and A_{2002} / $A_{1986} \leq 0.5$) or attrition (np_{2002} / np_{1986} < 1 and A_{2002} / A_{1986} < 1). These processes characterize structurally degraded forest. Forests are considered to be non-degraded when spatial transformation process between 1986 and 2002 is enlargement (np_{2002} / np_{1986} = 1 and A_{2002} / A_{1986} > 1) and/or creation (np_{2002} / np_{1986} > 1 and A_{2002} / A_{1986} > 1).

Fragmentation degree of each site was determined by a robust and simple fragmentation index, denoted *F*, which shows a relationship between the total number of forest patches and the total number of forest pixels (*m*) (Monmonnier, 1974 cited by Bogaert and Barima, 2008) i.e.:

$$F = \frac{np-1}{m-1} \qquad (1)$$

Landscape is fragmented if *F* is close to 1; when the entire landscape is occupied by forest, *F = 0*. *np*, *A* and *m* were determined by means of ArcGis 3.3 and Fragstats 3.3 software.

Tree diversity

In the study of forest typology and habitat diversity compared, it is important to consider a constant and quantified sampling effort. Moreover, although most inventories are still fixed in terms of area, it has now been clearly demonstrated that diversity comparisons could not be done by taking into account sampling effort expressed in terms of individuals number observed and not in terms of area (Condit et al., 1996). Most records related to phytosociology principles do not usually extend far beyond 1ha (Senterre, 2005). Moreover a homogeneous area of 1 ha is not easy to found even in forest called primary, let alone in a moderately degraded forest, it is concluded that an inventory of trees is constrained to be limited to approximately 100 individuals in order to ensure compliance with the constraint of homogeneity and representativeness (Condit et al., 1996; Senterre, 2005). More number of individuals (corresponding to a larger area) greatly increases the difficulty to define a homogeneous area while a smaller area can lead serious problems of representativeness and reliability of abundance estimates.

In our study, plant inventories were conducted on 52 sites, where 100 individual trees of diameter at breast height > 10 cm were randomly selected. Nomenclature was followed (Lebrun and Stock, 1991-2010). Taxa (or species) were grouped according to their ecological strategies with regard to light into light-demanding species and shade tolerant species (Molino and Sabatier, 2001). A high proportion of light-demanding species in a forest stand is considered to be an indicator of its degradation (Hubbell et al., 1999).

For each vegetation type (degraded and non-degraded), species richness was estimated using rarefaction curves that show expected specie number evolution as a function of individuals number. It enables a comparison of (expected) species richness, even if sample sizes (species inventories) are different in the two forest types. The number of species that can be expected in a sample of n individuals, noted $E(S_n)$, drawn from a population of N total individuals distributed among S species is (Hurlbert, 1971):

$$E(S_n) = \sum_{i=1}^{S}\left[1 - \frac{\binom{N-n_i}{n}}{\binom{N}{n}}\right] \quad (2)$$

where n_i represents the number of individuals of the species i,

Tree diversity was determined by Shannon index (H') and Pielou's evenness index (E'). For a survey, H' is defined as follows (Ludwig and Reynolds, 1988):

$$H' = -\sum_{i=1}^{S}\left[\left(\frac{n_i}{n}\right)\ln\left(\frac{n_i}{n}\right)\right] \quad (3)$$

H' = 0 where population is made up of only a single species; $H_{max} = lnS$ when all species present have an equal abundance. Pielou's evenness index is the ratio between observed species diversity (H') and maximum diversity (H_{max}):

$$E' = \frac{H'}{\ln S} \quad (4)$$

E' varies from 0 to 1; it is maximal when species have identical abundances in the population and it is minimal when a single species dominates entire population. Evenness index is not sensitive to species richness and is very useful for comparing potential dominances between sites.

Degraded and non-degraded stands were compared according to the ecological parameters (np, A, F) by Student's t test (α = 0.05). Informations provided by Shannon diversity index and Pielou's evenness index are also compared in the two forests stands. A linear regression was made between diversity indices and fragmentation index in order to determine landscape pattern impact on light-tolerant species presence and plant diversity. Quality of linear regression is assessed by a coefficient of determination (R^2) which measures the fit between the model and the observed data.

Species abundance distributions

Forest species abundance distributions were compared to the best-known theoretical distributions, i.e., log-normal, broken-stick and log-series distributions. According to log-normal distribution, plant community will contain individuals of several different species (Hubbell, 2001; Ricklefs and Miller, 2005). Number of species expected was obtained by the following equation:

$$S_{LN(R)} = S_0 e^{-a^2R^2} \quad (5)$$

$S_{LN(R)}$ represents number of species expected in R^{th} octave. Octaves are abundance classes (number of individuals); each octave represents a doubling of abundance (Ludwig and Reynolds, 1988). S_0 is species number in modal octave and a is an inverse measurement of distribution width (Ludwig and Reynolds, 1988).

In broken-stick distribution, species abundance within a community is determined by a random division process of resources along a continuous resource gradient

(Fattorini, 2005). Expected species number according to this distribution (S_{BS}) was as follows:

$$S_{BS} = \frac{S(S-1)}{N} \times \left(\frac{1-n}{N}\right)^{S-2} \quad (6)$$

According to log-serie distribution, species represented by few individuals should be found more frequently in surveys. Number of species expected (S_{LS}) according to this model was determined from the mathematical expression below:

$$S_{LS} = \delta \ln\left(1 + \frac{N}{\gamma}\right) \quad (7)$$

γ represents less common species number when S_{LS} = 1. δ, obtained by iteration, is a constant proportional to species number (Buzas and Culver, 1999).

Abundance distributions expected with these models were compared to observed distributions by a χ^2 test (α = 0.05) in order to determine which of these models fits best with species abundances observed (Fattorini, 2005).

RESULTS

Forest types

Observations of patches number and their areas on both dates allow us to distinguish two types of forests based on their spatial pattern (Figure 2). Structurally non-degraded forests (18 surveys) are characterized by patches numbers and areas equal or larger in 2002 than in 1986. Processes of spatial transformation observed for these forests are enlargement (Figure 2a: np_{2002} / np_{1986} = 1 and A_{2002} / A_{1986} > 1) and creation (Figure 2b: np_{2002} / np_{1986} > 1 and A_{2002} / A_{1986} > 1). Thirty-four other surveys are taken from forests that were structurally degraded by dissection (Figure 2c: np_{2002} / np_{1986} > 1 and A_{2002} / A_{1986} > 0.5), by fragmentation (Figure 2d: np_{2002} / np_{1986} > 1 and A_{2002} / A_{1986} ≤ 0.5) or by attrition (Figure 2e: np_{2002} / np_{1986} < 1 and A_{2002} / A_{1986} < 1).

Tree diversity

A quantitative analysis of inventories showed that 5200 trees from 186 species, 124 genera and 37 families have been recorded. The most frequent family was the Fabaceae, with 14 genera in non-degraded forest and 23 genera in degraded forest. In terms of individuals, Meliaceae (22.08% of individuals) and Moraceae (17.13% of individuals) were more abundant in non-degraded and degraded forest, respectively.

Rarefaction curves (Figure 3) revealed that in degraded stand, species richness grows faster in function of sample core than in non-degraded forest. Thereby, species richness can be considered higher in degraded forest than in non-degraded forest.

Diversity parameters of forest types (Table 1) indicate that average values are significantly different between forest types, which justify forests division into two types according to their degradation state. Degraded forests contain more light-demanding species (44.48%) and are more fragmented (F = 0.21) than non-degraded forests (light-demanding species = 28.55%; F = 0.08). These results suggest that forests fragmentation leads to a spread of light-tolerant species. Diversity indexes were higher in non-degraded forests than in degraded forest, suggesting that individuals were more evenly distributed among species in the non-degraded stand. These results indicate that despite their greater species richness, species present in degraded forest are less evenly distributed throughout the community than those in non-degraded forest.

Landscape fragmentation and tree diversity

Coefficient of regression between Pielou's evenness index and forest fragmentation intensity (Figure 4) was negative (r = -0.78) and regression was significant (R^2 = 0.61; p< 0.05). Likewise, a positive significant relationship (r = 0.58; R^2 = 0.34; $p < 0.05$) exists between forest fragmentation and number of light-demanding species. Landscape fragmentation thus leads to an increase of light-tolerant species.

Species abundance distributions

Species abundance distribution of non-degraded forest deviates from log-series and broken-stick distributions (Table 2), but fits log-normal distribution. For degraded forest, observed species abundance distribution is not statistically different from log-series distribution, but it diverges from log-normal and broken-stick distributions. Species abundance distribution seems to be more regular in non-degraded forest than in degraded forest, confirming aforementioned evenness index tendencies.

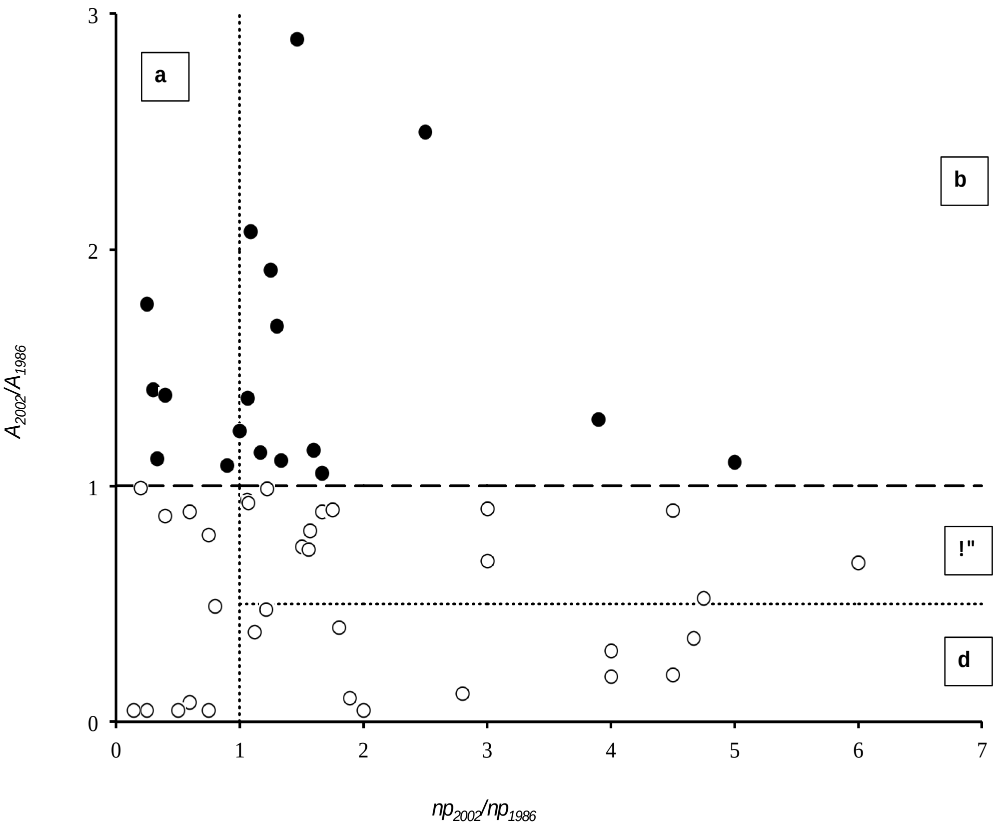

Figure 2: Plots classification according to forest patches structure and composition of a forest-savannah transition in Eastern Ivory Coast. Group of plots located above the indent are non-degraded forests and contain plots of which transformation process between 1986 and 2002 is (a) enlargement (np_{2002} / np_{1986} = 1 and A_{2002} / A_{1986} > 1) and (b) creation (np_{2002} / np_{1986} > 1 and A_{2002} / A_{1986} > 1). Plots located below the indent (round vacuum) represent degraded forests. They include plots of which landscape transformation process between 1986 and 2002 is (c) dissection (np_{2002} / np_{1986} > 1 and A_{2002} / A_{1986} > 0.5), (d) fragmentation (np_{2002} / np_{1986} > 1 and A_{2002} / $A_{1986} \leq 0.5$) and (e) attrition (np_{2002} / np_{1986} < 1 and A_{2002} / A_{1986} < 1).

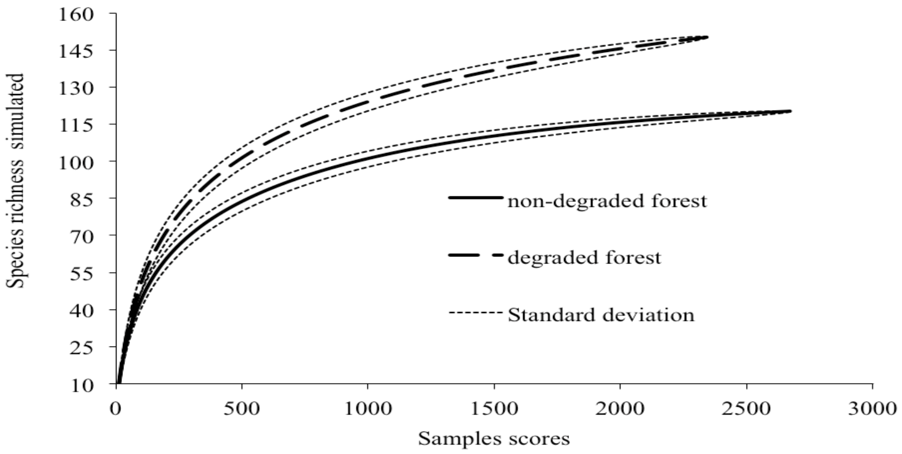

Figure 3: Trees rarefaction curves of degraded and non-degraded forest of a forest-savannah transition zone in Eastern Ivory Coast. Zone indicated in dotted line represents standard deviation of rarefaction curve average.

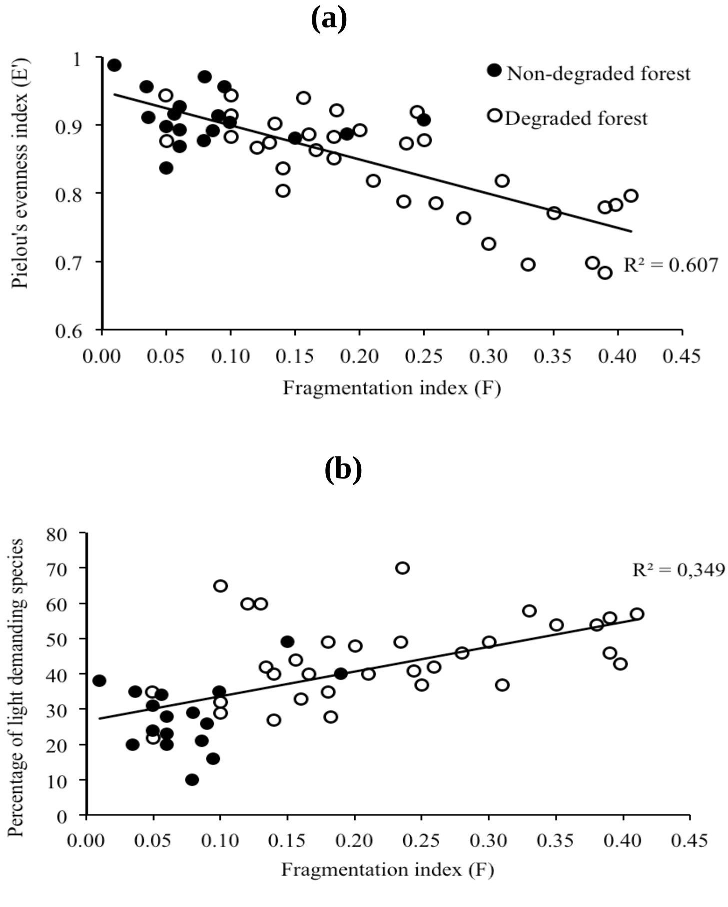

Figure 4: Evenness (a) and light-demanding species rate (b) of plots according to fragmentation index of forest-savannah transition in Eastern Ivory Coast.

Table 1: Characteristics of landscape structure and composition of forest-savannah transition in Eastern Ivory Coast.

		Non-degraded forest	**Degraded forest**
Average number of forest patches per km² (*np*)	1986	9.10	8.10
	2002	10.20	9.90
Average area of forest per km² (*A*)	1986	0.71	0.68
	2002	0.77	0.41
Shannon diversity index (H')		3.00	2.79
Pielou evenness index (E')		0.91	0.83
Fragmentaton index (*F*)		0.08	0.21
Percentage of light-demanding species		28.55	44.48

These values represent average characteristics according to 18 sites of non-degraded forest and 34 sites of degraded forest. These averages are significantly different (test *t*; $p < 0.05$) in the two types of forests.

Table 2: Test of species abundances distributions. ns = not significant. Significance rate: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

	Non-degraded forest		**Degraded forest**	
	ddl	χ^2	**ddl**	χ^2
Log-normal distribution	8	8.30 ns	8	70.06*
Broken-stick distribution	7	865.02***	7	29625***
Log-series distribution	7	14.57**	8	7.65 ns

DISCUSSION

Methods

There are several definitions of forest and landscape degradation relative to canopy density, ecological function and other forest attributes. Among these definitions, degradation defined by structural changes in canopy density is one that is directly observable by remote sensing (DeFries et al., 2007). However, reflectance differences between degraded and non-degraded forest are not sharp (Kinyanjui, 2011; Ropars and Boudreau, 2012) as those, for example, between forest zone and deforestation. For this reason, two different methods were used to confirm forests typology that was determined by satellite images. Number of forest patches and their respective areas were considered as essential parameters of landscape configuration (Bogaert and Barima, 2008), and allowed landscapes structural changes determination. Furthermore, fragmentation index *F* applied is a robust and simple measure that can be directly interpreted in terms of landscape structure (Bogaert and Barima, 2008).

Species richness remains commonly used index for synthesizing available data. Species richness standardization by rarefaction curve enables however a better comparison of vegetation in which samples number and observations are different (Ludwig and Reynolds, 1988). Derivation of Pielou's index from Shannon index is done to determine species evenness, i.e. the second component of diversity (Hamilton, 2005), although in certain cases, these two variables are found to be correlated.

The natural existence conditions of a plant community are complex and involve many other factors beside those on which species abundance models we have used (Brokaw and Busing, 2000). However, these models remain useful for understanding the structure and functioning of species community by a mathematical law (Ulrich and Ollik, 2004).

Forest type and species richness

We have shown that forest fragmentation leads to an increase in species richness (Figure 3). This observation seems to be contradictory to numerous other studies (Benitez-Malvido and Martinez-Ramos, 2003; Lindborg et al., 2012) and could be due to the difference in sampling methods. However, forest degradation, which is essentially due to anthropogenic effects (selective exploitation for timber, slash-and-burn agriculture, wildfire) creates openings in the canopy (DeFries et al., 2007) which favours growth of new species that are more tolerant to light (Figure 4a) (Arim et al., 2006; Barima et al., 2010a). Light-demanding species dominance in more fragmented forests provides data on the past of these forests and suggests that fragmentation of studied sites has occurred relatively recently, in the 1980s as demonstrated by Barima et al. (2010b). This period corresponds to the second and third stage of succession, in which light-tolerant species already established in previous stages profit from conditions of increased growth and become progressively dominant (Swanson et al., 2011). This increase of light-tolerant species could be an indication of a regressive succession towards earlier stages due to anthropogenic disturbances that are too intense, a prelude to their disappearance (Do et al., 2011).

Comparing natural stands likes those we study with Shannon diversity index is not easy. This index is suitable for each natural stand and represents an information index that is sensible to many intrinsic factors of the stand. Therefore, comparing stands using Shannon index only could lead to a confuse interpretation. But this index will give at least an indication on the structures of the two communities studied.

Forest type and species evenness

Despite their higher species richness, taxa present in degraded forest are unevenly distributed throughout the community when compared to those of non-degraded forest (Figure 4a). Consequently, species richness cannot be used as the single criterion for plant diversity, contrary to definitions given to diversity concept that reduce it to species number (Dunstan et al., 2012). Richness and evenness may be effectively independent (Jost, 2010) since plant diversity may vary with ecological processes such as competition, predation and succession. Each of these processes can influence diversity by changes in evenness without changing the species richness itself (Jost, 2010).

Species abundance distributions

Results of our study have also shown that landscape fragmentation is accompanied by a reduction in species evenness (Figure 4b). Thus, only a few species dominate the ecology in such fragmented plant community, as abundance distributions confirm (Table 2). Species abundance distribution of conserved forest belongs to log-normal distribution model, thus indicating that species are evenly distributed in community (Magurran and Henderson, 2003; Masharabu et al., 2010). From Ricklefs and Miller (2005), we can conclude in this case that forest is relatively large, because samples resulted from non-fragmented forests, consequently large compared to those that have been fragmented and perturbed. This conclusion confirms observations on satellite images showing that conserved forests belong to large forest that exist in the study region (Barima et al., 2009; Barima et al., 2010b). Abundance distribution of degraded forest (log-series) reflects presence of large number of rare species (Yin et al., 2005). In fact, log-series distribution should result from a process in which species arrive in an non-saturated habitat at random time intervals, and that each specie should consequently occupy a constant share of remaining resources (Gotelli and Graves, 1996). This distribution model, observed in degraded forest, results situations in which one or few factors (here disturbance leading to fragmentation) control community ecology (Buzas and Culver, 1999). This distribution thus characterize relatively small communities subject to various pressures (Gotelli and Graves, 1996). Consequently, numerous occasional species are encountered (Magurran and Henderson, 2003; Ulrich and Ollik, 2004) in degraded forest.

Conclusion

Although species richness is larger in degraded forests, biodiversity as a whole (i.e. including both the number of species and their relative abundance) increases in non-degraded forest. Consequently, it is useful, or even necessary, to treat species richness and evenness separately and to use these concepts to explain more correctly the concept of diversity.

ACKNOWLEDGMENTS

The International Foundation for Science (Sweden) supported this research by a Research Fellowship awarded to the first author.

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