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Abstract

An old yet appealing fact in conservation biology is the potential of sacred groves (SGs) and forest reserves (FRs) to harbor considerable biodiversity. Although fragmentation effects have been extensively investigated in several studies, the specific context pertaining to SG has rarely been discussed. Using data from two sites (Kétou and Pobè) in South Benin, we studied the similarities and connectivity between SG and FR, and the effects of fragmentation on forest ecosystems. Nonmetric multidimensional scaling and Moran index-based correlogram were used to analyze species-based similarities, distribution, and spatial autocorrelation. Fragmentation effects on characteristic species and forest structures were also tested. Results showed slightly greater similarity between SG and FR for Kétou SG–FR group compared with that of Pobè. Spatial association between SG and FR was also site specific and stronger in Pobè SG–FR group. The weak spatial dependence between SG and FR for the Kétou group reflects the state of degradation in the FR. Species richness and structural parameters were higher in SG than in FR for both sites. The results indicate that these forests emanated from fragmentation of primary forests and that the fragmentation effects were more pronounced in FR. The indicator species analysis further revealed some fragmentation effects on woody species composition, suggesting that forest isolation is potential threat for conservation of biological and structural diversity. In sum, this study shows that despite their limited spatial extent, SGs are key landscape features that play a vital role in local biodiversity conservation.

Keywords

sacred groves, fragmentation, landscape connectivity, forest reserves, Guineo-Congolese

Introduction

There is unequivocal evidence that human disturbances (tree logging, forest clearing for subsistence agriculture, and landscape fragmentation) are causally related to loss of natural habitat and biological diversity (Barima, Barbier, Ouattara, & Bogaert, 2010; Henle, Lindenmayer, Margules, Saunders, & Wissel, 2004; Rudel & Roper, 1997; Sánchez-Azofeifa, Daily, Pfaff, & Busch, 2003). Landscape fragmentation increases habitat isolation and leads to reduced size of forest patches (Barima et al., 2010; Bogaert, Ceulemans, & Salvador-Van Eysenrode, 2004; Fahrig, 2003). Forest fragmentation alters not only forest stand dynamics and biological cycles (Aguilar, Ashworth, Galetto, & Aizen, 2006;

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Lindenmayer, Fischer, & Cunningham, 2005) but also the microclimate within forest patches (Laurance, Ferreira, Rankin-de Merona, & Laurance, 1998) by promoting proliferation and growth of invasive and pioneer species (Barima et al., 2010). Therefore, fragmentation of natural habitats can induce changes in forest configuration and patterns (e.g., size reduction, fragment isolation), vegetation parameters, and structural variables (e.g., absolute stem density, basal area, dominant height; Freitas, Mello, & Cruz, 2005) and in floristic composition (Barima et al., 2010; Cabacinha & de Castro, 2009). Information on these vegetation parameters and structural variables is critical in assessing forest fragmentation and connectivity.

Tropical forests have been exposed to severe anthropogenic pressures, which have considerably altered the integrity of their habitat and their woody floristic composition. Human population growth, land use changes, and conversion of natural habitat are among the major drivers of deforestation and habitat degradation (Foley et al., 2005). There is increased awareness toward conservation of biological diversity, manifested by a number of political decisions insuring preservation of remaining natural habitats through demarcation of protected areas. Forest reserves (FRs) and protected areas have been shown as effective governmental policy tools in conservation of threatened species and old-growth forests (Bertzky et al., 2012; Brandt, Butsic, Schwab, Kuemmerle, & Radeloff, 2015), although conflict with local people and lax enforcement are recurrent constraints for their effectiveness.

Sacred groves (SGs; natural areas protected by local people for cultural or religious reasons) are known as biodiversity-rich communities, which provide refuge for a large number of endemic and rare plant taxa (Bhagwat & Rutte, 2006; Bongers, Alemayehu Wassie, Sterck, Bekele, & Teketay, 2006; Brandt et al., 2015; Brandt et al., 2013; Upadhyaya, Pandey, Law, & Tripathi, 2003). They mostly exist as isolated small patches of natural forests and play an important role in biodiversity conservation (Bhagwat & Rutte, 2006). SG forests were long ago reported in Africa, Asia, and Latin America and are protected by religious or cultural practices and beliefs, as being an endogenous form of biodiversity conservation. SGs were reported in Benin in the 1930s (Chevalier, 1933) but were first censused in studies by Agbo and Sokpon (1998). In total 2,940 SGs were enumerated, of which 70% are from 0.1 ha to 5 ha sized, and close to built-up areas. These SGs are generally reserved for cultural activities and regulated by traditional beliefs (Agbo & Sokpon, 1998; Oviedo & Jeanrenaud, 2007). The potential of SGs for maintenance of remnant forest vegetation species and biological diversity has also attracted many research studies (Agbo & Sokpon, 1998; Bhagwat, Kushalappa, Williams, & Brown, 2005;

Bhagwat & Rutte, 2006; Brandt et al., 2015; Brandt et al., 2013; Gao, Ouyang, Chen, & Koppen, 2013; Kokou & Caballé, 2000; Kokou & Kokutse, 2006; Kokou & Sokpon, 2006).

In the Benin Guinean zone (West Africa Dahomey gap), SGs and remnant dense semideciduous forests occur as small and large patches of secondary forests (Akoegninou, 1984; Akoegninou, 1998; Djègo & Oumorou, 2009; Paradis & Houngnon, 1977). They are theoretically considered as fragments of natural forests of the old and primary forest block of the Guinean zone (Adjakpa, Dassoundo, Yedomonhan, Weesie, & Akpo, 2011; Akoegninou, 1984; Djègo and Sinsin, 2007; Sokpon, 1995). Yet, very little is known about the vegetation succession and connectivity between FRs and SGs, despite the fact that their abundance and spatial configuration in southeastern Benin are indicative of probable fragmentation effects.

In the present study, we aim to assess the fragmentation effects on forest ecosystems and the connectivity between SGs and FRs. Using the Guineo-Congolese forest transition zone in southern Benin (White, 1983) as case study, we tested the hypotheses that (a) SGs are fragmented patches of FRs and (b) fragmentation has negative impacts on vegetation physiognomy, including indicator or characteristic species and stand structures. A focus was put on indicator species to reflect on the change in physiognomy of the vegetation as result of fragmentation.

Methods

Study Area

This study was carried out in the southeastern part of Benin, which lies from 1° 45' and 2° 45' E to 6° 30' and 7° 30' N. The study area is located in the Guineo-Congolese regional endemism center, mostly dominated by dense semideciduous forests, savannas, mangroves, swamp, and coastal forests (Assi-Kaudjhis, 2011; Sokpon, 1995; White, 1986). Three FRs, namely, Dogo-Kétou ("Kétou"), Itchède-Toffo ("Pobè"), and Sakété ("Sakété") and SGs surrounding each of these FRs were initially considered (Figure 1).

Dogo-Kétou FR (composed of Kétou forest bloc [11,000 ha] and Dogo forest bloc [31,850 ha]) are located in Kétou district and named hereafter as "Kétou." Due to constant human disturbances, the FR has received considerable attention in terms of protection from the "Office National du Bois," and further through "Plantations de Bois de feu" project.

Itchède-Toffo FR (191 ha) is surrounded by plantations of *Tectona grandis* L.f., Verbenaceae (7 ha), *Terminalia superba* Engl. & Diels., Combretaceae (2 ha) and *Cedrela odorata* L., Meliaceae (2 ha), and lies across

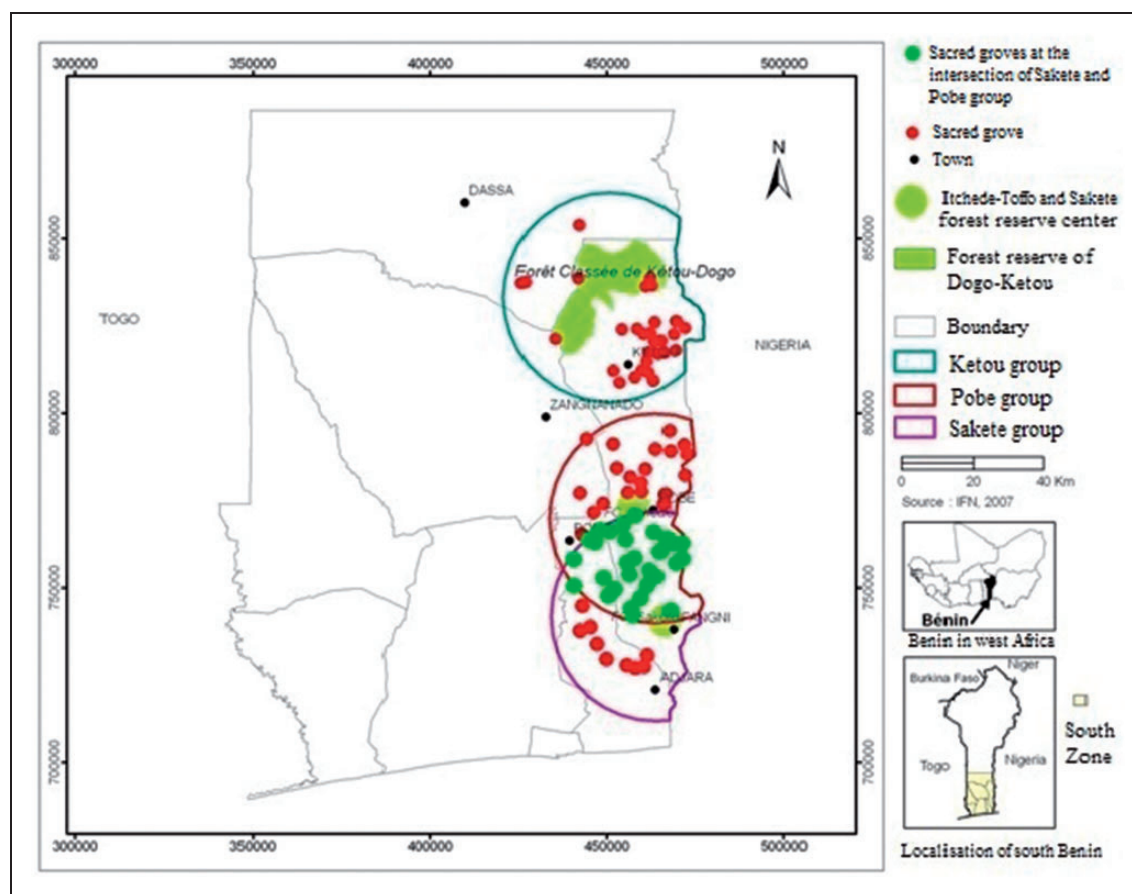


Figure 1. Location of the study area.

Adja-Ouèrè and Pobè district. For reason of simplicity, Itchède-Toffo FR is named hereafter as “Pobè.”

Sakété FR (60 ha) is located in Sakété district and is characterized by a vegetation of *Trilepisium madagascariensis* DC. (Moraceae) and *Dichapetalum crassifolium* Chod. var. *crassifolium* (Dichapetalaceae) semideciduous moist forest; *Anthonotha crassifolia* (Baill.) J. (Leguminosae-Cesalpinoideae) and *Symphonia globulifera* L.f. (Clusiaceae) flood forest; and *Anthostema aubryanum* Baill. (Euphorbiaceae) and *Alchornea cordifolia* (Shum. & Thonn.) Müll.Arg. (Euphorbiaceae) swamp forest. The climate is subequatorial with a bimodal rainfall regime: two rainy seasons (April–July and September–November) and two dry seasons (August–September and November–March). The mean temperature is 27°C, while the relative humidity varies from 78% in January/February to 95% in September (ASECNA, 2010).

Sampling and Data Collection

The data used in this study were collected from FRs and SGs. The SGs were randomly selected from those located within 30 km radius from each of the three FRs (Figure

2), and measuring at least 10,000 m² in size. Three groups of SGs plus FR were considered (Kétou, Pobè and Sakété; Figure 1), each group being composed of an FR and 30 surrounding SGs. Of the three groups of FRs–SGs, two (Pobè and Sakété) overlapped because of the proximity of Itchède-Toffo (Pobè) and Sakété FRs. As a result, one among the three groups (Sakété) was left out during data collection to avoid spatial autocorrelation. For each of the two remaining groups (“Kétou SG–FR group” and “Pobè SG–FR group”), 60 circular plots of 1,000 m² (30 inside the FR and at least 30 for the surrounding 30 SGs) were set up for data collection. SGs size varied from 1 ha to 500 ha for the Kétou group and from 1 ha to 1000 ha for the Pobè group. Thus, different sampling design was observed depending on the size of the SG. For SGs of less than 4 ha, only one circular plot was used, while two circular plots of 1000 m² were used for sacred forests with area larger than 4 ha. Minimal distance between plots in FRs was 100 m. The distance between SGs and the FR varied from 2 km to 30 km for Kétou group and from 5 km to 30 km for Pobè group. Inside each plot, species name was recorded, and individual trees were measured for their diameter at breast height (dbh) and total height (ht).

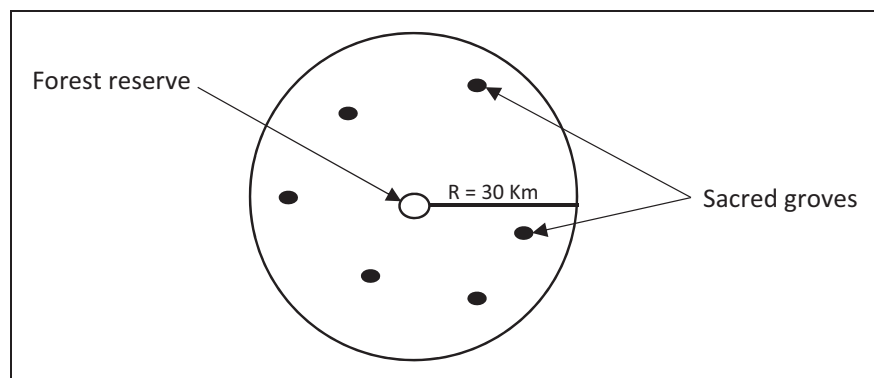


Figure 2. Sampling design showing forest reserve and surrounding sacred groves.

Data Analysis

To determine whether SGs are fragmented patches from the FRs, we tested for similarities in species diversity and distribution between SGs and FRs for “Kétou SG–FR group” and “Pobè SG–FR group,” separately. A non-metric multidimensional scaling (NMDS) was performed using species abundance data. We additionally tested for distance-based similarity between SGs and FRs for each group by calculating the Moran spatial autocorrelation index. Moran index was computed for each pair of sample plots within each group using the following formula:

$$I_{Moran} = \frac{n}{\sum_i \sum_j w_{ij}} \frac{\sum_i \sum_j w_{ij} (x_i - \bar{x})(x_j - \bar{x})}{\sum_i (x_i - \bar{x})^2} \quad (1)$$

where n is the number of spatial units (plots), x is the variable of interest (species richness), and w_{ij} is an element of a matrix of spatial weights. The Moran statistic varies from -1 to $+1$, with 0 indicating absence of autocorrelation and independence between the two plots. Values greater than 0 are indicative of positive spatial autocorrelation, while values less than 0 are indicative of negative spatial autocorrelation. Both positive and negative spatial autocorrelation suggest dependence between plots (Goodchild, 1986). The Moran index was calculated based on plot richness in the Geostatistics for the Environmental Science (GS +) software. The Moran index values were used to graphically represent the correlogram. We additionally tested whether the distance-based spatial autocorrelation varied between the two SG–FR groups using analysis of covariance.

To test whether fragmentation has negative impacts on indicator species and stand characteristics of these forest ecosystems, we first performed an indicator species analysis (Dufrêne & Legendre, 1997) to identify the characteristic species of SGs and FRs within each SG–FR group. We next assessed for both SGs and FRs, the diversity (species richness, S) and structural vegetation

parameters such as stem density (N , stem/plot), mean diameter (D_g , cm), and basal area (G , m^2). We tested for significant variations of the structural parameters between (a) SGs and FRs and (b) “Kétou SG–FR group,” and “Pobè SG–FR group,” by performing a two-way (groups and forest types as factors) analysis of variance (ANOVA). Normality and variance homogeneity were tested prior to the ANOVA, using the Shapiro–Wilk’s normality and Breusch–Pagan tests, respectively.

Results

Similarity Between SGs and FRs

Plant species richness was slightly higher for Pobè SG–FR group (118 species) than for Kétou SG–FR group (112 species). However, for both groups, species richness was higher in the SGs than in FR. Of the 118 identified species in the Pobè SG–FR group, 15 were shared by both SGs and FR, while 95 and 8 species were unique to SGs and FR, respectively. As for Kétou SG–FR group, 40 species were shared by both SGs and FR, 60 species were found in SGs only, while 12 species were unique to the FR.

The results from the NMDS revealed a weak discrimination of plots from SGs and FRs for the Pobè SG–FR group (Figure 3(a)) and for Kétou SG–FR group (Figure 3(b)). However, the discrimination was slightly stronger for Pobè SG–FR group, suggesting greater similarity in terms of species composition in SGs and FR for the Kétou SG–FR group.

Results of Moran spatial autocorrelation index based on species richness are plotted in Figure 4. Both positive and negative values of Moran index were obtained for Pobè SG–FR group and Kétou SG–FR group, indicating spatial dependence between SGs and FR in Pobè and Kétou (Figure 4). In addition, the spatial dependence seemed to be more pronounced for Pobè SG–FR group with increasing distance than for Kétou SG–FR group. We also found significant interaction effects of distance

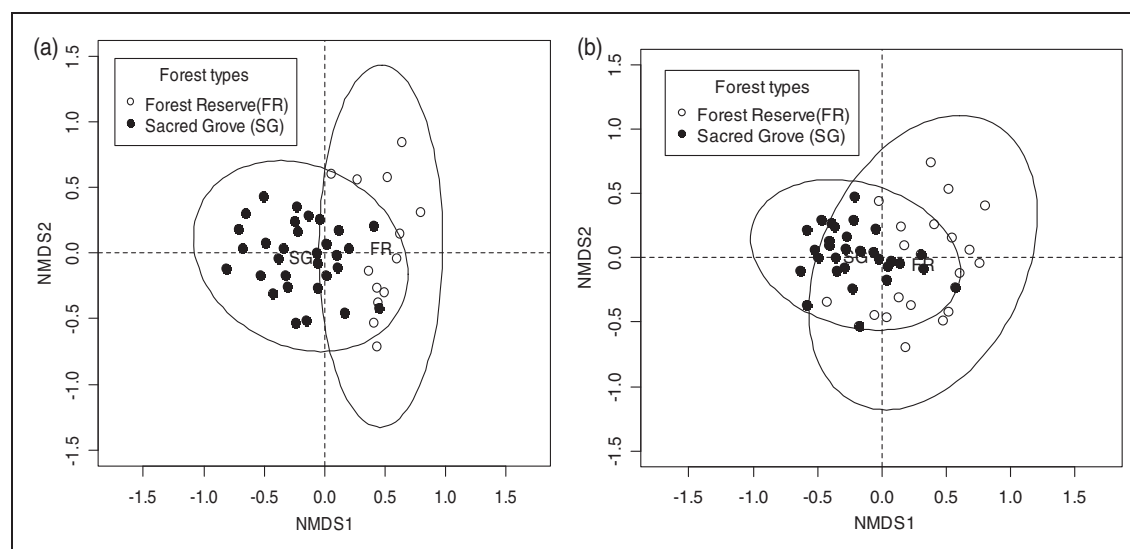


Figure 3. Nonmetric multidimensional scaling of plots from forest reserves and sacred groves in (a) Pobè and (b) Kétou groups.

and group on spatial autocorrelation patterns ($F=6.67$; $p=.011$; Table 1), indicating that the distance-based spatial dependency between plots varied with SG–FR groups. For Pobè SG–FR group, we observed negative spatial autocorrelation over increasing distance up to 10 km and positive spatial autocorrelation after 25 km (Figure 4). As for Kétou SG–FR group, Moran index was constantly positive up to 20 km and decreased sharply (Figure 4).

Fragmentation Effects on Indicator Species of SGs and FRs

The results showed that in Pobè SG–FR group, species such as *Albizia zygia* (DC.) J. F. Macbr. (Leguminosae-Mimosoideae), *Holarrhena floribunda* (G.Don) T. Durand & Schinz (Apocynaceae), *Spondias mombin* L. (Anacardiaceae), and *Treculia Africana* Decne. ex Trecul ssp. africana (Moraceae) were indicative (specificity=1, Table 2) of the SGs habitat, while *Triplochiton scleroxylon* K. Schum. (Sterculiaceae), *Trichilia megalantha* Harms (Meliaceae), *Cola gigantean* A. Chev. (Sterculiaceae), *Cola millenii* K. Schum. (Sterculiaceae), and *Ceiba pentandra* (L.) Gaertn. (Bombacaceae) were the indicator species of the FR (specificity=1). Specificity is the probability that the surveyed sites belong to the target group given the fact that the species has been found. Faithfulness is the probability of finding the species in sites belonging to the group (Table 2). As for Kétou SG–FR group, indicator species of the SGs habitat were *Antiaris toxicaria* Lesch. (Moraceae), *A. zygia* (Leguminosae-Mimosoideae), *Celtis zenkeri* Engl. (Celtidaceae), *T. scleroxylon* (Sterculiaceae), whereas *Cynometra megalophylla* Harms (Leguminosae-

Caesalpinioideae) and *Diospyros mespiliformis* Hochst. ex A.DC. (Ebenaceae) were the only two species indicative of the FR.

Vegetation Parameters in Both SGs and FRs

Among the three structural parameters, only stem density showed significant differences between SG–FR groups (Table 3). The results of ANOVA (Table 3) further showed that stem density, mean diameter, and basal area varied significantly with forest types within SG–FR group, higher values being observed in SGs (Table 4). These results suggest that woody species were more protected in SGs than in FRs.

Discussion

Fragmentation and Connectivity Between SGs and FRs

The results of this study revealed that SGs are habitat for native tree species of dense semideciduous forests. According to Avon, Bergès, Dumas, and Dupouey (2010), spatial or structural connectivity may reflect the existing linkages or associations between landscape components. We found strong spatial dependence between SGs and FR, especially for the Pobè SG–FR group, which confirms the existence of specific connectivity between the two forest types (Goodwin, 2003). The finding that tree species richness was higher in SGs than in FRs for both groups indicates that SGs were most likely less disturbed, as compared with FRs. These results corroborate the study by Sinasson (2010) in the dense semideciduous forests of Bonou and Itchède-Toffo

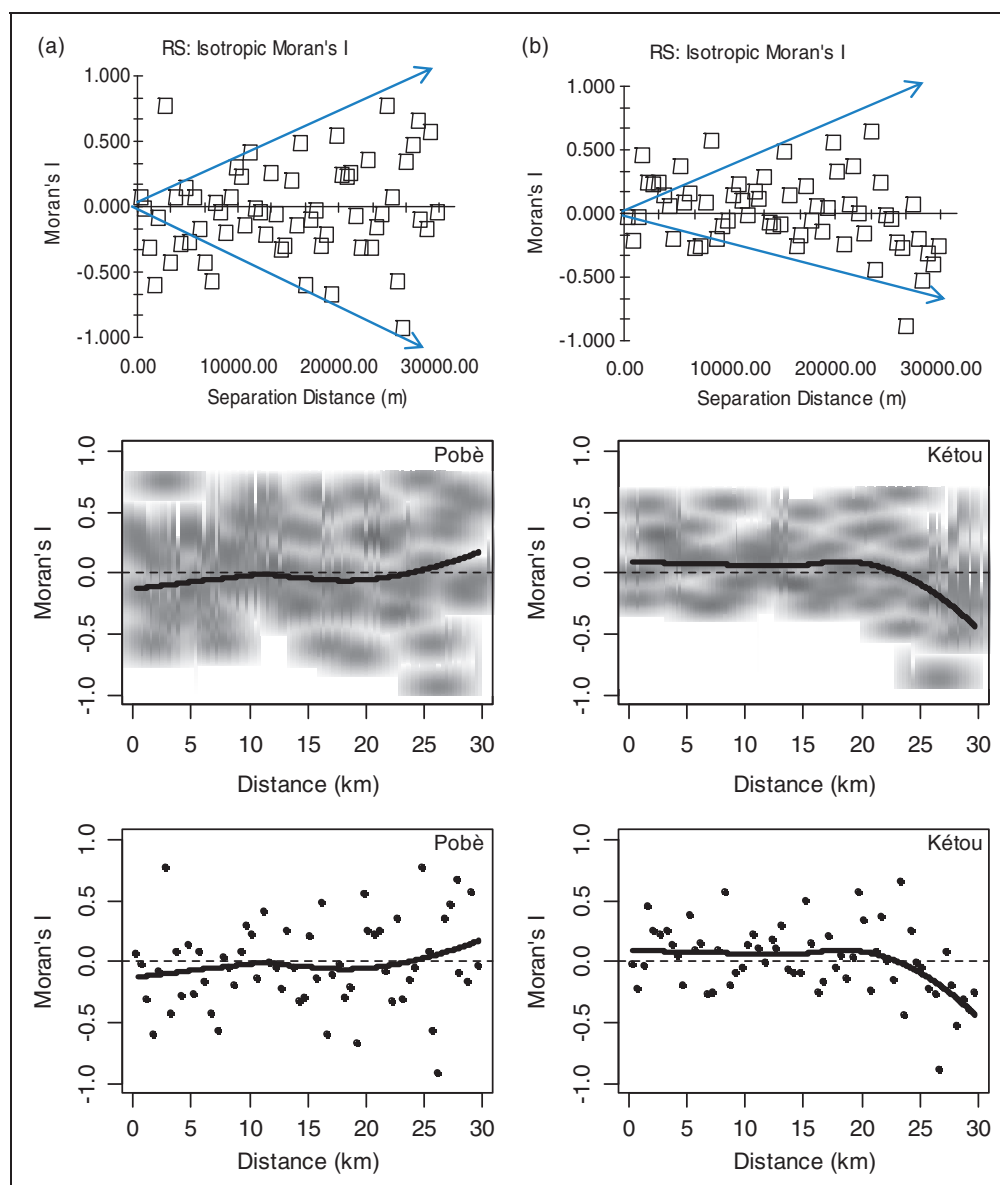


Figure 4. Spatial correlograms showing the patterns of spatial autocorrelation between plots from sacred groves and forest reserve in (a) Pobè and (b) Kétou groups, as function of distance (in km).

Table 1. Results of ANCOVA Showing the Variations of the Moran's Index According to the Distance, the Groups, and Their Interactions.

Source	df	SSq	RSS	AIC	F value	p (>F)
Distance	1	0.0403	11.66	-273.76	0.402	0.527
Group	1	0.6679	12.288	-267.47	6.667	0.011
Distance: Group	1	0.6685	12.288	-267.46	6.673	0.011

The results are based on the orthogonal (type III) sum of squares. *df*: degree of freedom; *SSq*: sum of squares; *RSS*: residual sum of squares; *AIC*: Akaike information criterion; *p*: probability; ANCOVA: analysis of covariance.

(southeastern Benin). The effectiveness of SGs in conservation of biological diversity and rare taxa was highlighted in many studies (Bhagwat et al., 2005; Bhagwat & Rutte, 2006; Brandt et al., 2013; Bossart & Antwi, 2016; Decher, 1997; Gao et al., 2013; Mgumia & Oba, 2003). While both SGs and FRs are frequently visited by local populations, the specific interest or reason to visit these forests makes the disturbance context different; for instance SGs are visited to hold initiation rituals and secret ceremonies or to light incense and pray for good luck, rain, or good harvest (Allendorf, Brandt, & Yang, 2014; Bossart & Antwi, 2016). On the contrary, as result

Table 2. Indicator Species of Sacred Groves and Forest Reserves Within Each Group.

Group	Species or combination of species	Specificity	Faithfulness	Index value	p
Pobè					
Sacred groves	<i>Albizia zygia</i> (Leguminosae-Mimosoideae)	1.00	0.70	0.83	.001
	<i>Holarrhena floribunda</i> (Apocynaceae)	1.00	0.56	0.75	.004
	<i>Spondias monbin</i> (Anacardiaceae)	1.00	0.50	0.70	.004
	<i>Treculia Africana</i> (Moraceae)	1.00	0.43	0.65	.008
	<i>A. zygia</i> (Leguminosae-Mimosoideae)+ <i>H. floribunda</i> (Apocynaceae)	1.00	0.43	0.65	.011
Forest reserve (191 ha)	<i>Triplachiton scleroxylon</i> (Sterculiaceae)+ <i>Trichilia megalantha</i> (Meliceae)	0.89	0.28	0.51	.030
	<i>Cola gigantean</i> (Sterculiaceae)	1.00	0.21	0.46	.030
	<i>Cola millenii</i> (Sterculiaceae)	1.00	0.21	0.46	.030
	<i>Ceiba pentandra</i> (Bombacaceae) + <i>C. gigantean</i> (Sterculiaceae)	1.00	0.21	0.46	.030
	<i>C. gigantean</i> (Sterculiaceae) + <i>T. scleroxylon</i> (Sterculiaceae)	1.00	0.21	0.46	.030
Kétou					
Sacred groves	<i>Antiaris toxicaria</i> (Moraceae)	0.95	0.80	0.87	.001
	<i>A. zygia</i> (Leguminosae-Mimosoideae) + <i>A. toxicaria</i> (Moraceae)	1.00	0.70	0.83	.001
	<i>A. zygia</i> (Leguminosae-Mimosoideae)	0.89	0.76	0.82	.001
	<i>Celtis zenkeri</i> (Celtidaceae)	1.00	0.46	0.68	.001
	<i>T. scleroxylon</i> (Sterculiaceae)	1.00	0.43	0.65	.004
Forest reserve (42,850 ha)	<i>Cynometra megalophylla</i> (Leguminosae-Caesalpinioideae)	0.94	0.26	0.49	.021
	<i>Diospyros mespiliformis</i> (Ebenaceae)	0.93	0.26	0.49	.014

Note. Specificity: probability that the surveyed sites belong to the target group given the fact that the species has been found; Faithfulness: probability of finding the species in sites belonging to the group; IndVal: Indicator Value Index; p value: probability value associated with the indicator value.

Table 3. Results of ANOVA Showing the Variation of Stem Density, Mean Diameter and Basal Area Between Groups (Kétou and Pobè) and Between Forest Types (Sacred Groves and Forest Reserve).

Source de variation	Stem density		Mean diameter		Basal area	
	F	p	F	p	F	p
SG–FR group	26.03	.000	2.53	.080	0.41	.660
Forest type	239.99	.000	51.26	.000	21.57	.000
Forest type: SG–FR group	18.79	.000	1.13	.320	0.09	.910

F = Fisher Statistic; SG: sacred groves; FR: forest reserves; ANOVA: analysis of variance.

of lax enforcement and conflict with local people, FRs are frequently exposed to human activities such as tree logging, harvesting of nontimber forest products, and agricultural practices. Although fuelwood and nontimber forest products can also be extracted from SGs (Allendorf et al., 2014), the disturbances are not likely to be as high as they are in FR because of the fear for rituals and dedication ceremonies for gods. Compared with high level of disturbance, intermediate levels of

Table 4. Mean Values and Standard Errors (SE) of Vegetation Parameters of Forest Types (Sacred Groves and Forest Reserve) in Kétou and Pobè Groups.

Forest type	Stem density		Mean diameter (cm)		Basal area (m ²)	
	Mean	SE	Mean	SE	Mean	SE
Kétou						
Forest reserve	12.80	8.60	26	0.12	0.98	7.92
Sacred groves	212.50	7.02	133	0.09	34.79	6.46
p	.000	–	.000	–	.000	–
Pobè						
Forest reserve	117.29	10.28	69	0.14	4.73	9.46
Sacred groves	224.36	6.91	140	0.09	44.57	6.36
p	.000	–	.002	–	.011	–

disturbance may allow plant community to recover and be maintained (Connell, 1978). Previous studies (Adou-Yao, Bakayoko, Akpatou, & N'Guessan, 2011; Martin, 2008; Molino & Sabatier, 2001) showed that disturbances, when not very important or frequent, contribute to maintain biological diversity in forest patches.

This seems to be the case for the studied SGs and also suggests that protection actions must be enforced in FRs. While the difference in species between SGs and FRs is attributable to the disturbance regimes and fragmentation effects, the variation observed in the number of woody species between Pobè and Kétou SG–FR groups can be explained by differential species distribution along latitudinal, soil, and local climate gradient (Adomou, 2005).

The results of the spatial correlograms based on species richness showed stronger spatial autocorrelation between SGs and FR in the Pobè SG–FR. These findings suggest that there is higher similarity in terms of species diversity between SGs and FR in Pobè group, unlike that of Kétou. This result suggests that SGs have species-based affiliation with the remnant FR of the primary forests within a distance of 30 km, corroborating our hypothesis that SGs are fragments of the old and primary forest block. Previous reports by Aubreville (1937) and Adjanohoun (1968) also highlighted the presence of these characteristic woody species of FRs. A recent socioempirical study conducted with aged people living in the surrounding environment of these forests revealed three categories of SGs that emanate from primary forest ecosystems (Alohou, Gbemavo, Ouinsavi, & Sokpon, 2016). While it is being pointed out that most current SGs came from primary forest block, as they served as repository for goddess carried away during past migrations or as places of protection against war, it must also be noted that population growth and human disturbances over time contributed to the loss of substantial areas of both FRs and SGs in southeastern Benin (Alohou et al., 2016).

Unlike the Pobè SG–FR group, the weak spatial dependence between both forest types for Kétou SG–FR group, as revealed by the values of Moran's index, can be attributed to the state of degradation of the FR. Human disturbances might have strongly affected the floristic composition, as well as the spatial distribution and abundance of characteristic species of the FR. These conclusions accord with several authors (Findlay & Houlihan, 1997; Goodwin & Fahrig, 2002) who reported that significant degradation and isolation of landscape features influence their specific connectivity. Increased spatial isolation between forests' fragments (SGs) impacts on both population stability and reduces genetic variability (Schmitt et al., 2009), which is also in line with the consequences of the theory of island biogeography (MacArthur & Wilson, 1967).

We found that certain species, although much fewer in number, were confined to the FRs. This can be attributed to many factors including the size of the forest groves, the local environment, and the weak dispersal potential of some tropical species. Forest groves are generally of smaller size as compared with FR. As we support the idea that these SGs emanate from the FRs, the finding that some

species are unique to the FR is probably due to the loss of their habitat in the SGs during fragmentation process. This seems to be in line with the species–area relationship ecology law, which describes an increase in species numbers with increasing area (Rybcicki & Hanski, 2013). The local environment may also act and favor the presence of these species in these forests; finally, species functional traits such as dispersal potential may limit the colonization potential of these species in the SGs (Whitmore, 1991).

Fragmentation Effects on Woody Species

In most SGs of the Pobè SG–FR group, *A. zygia* (Leguminosae-Mimosoideae), *H. floribunda* (Apocynaceae), *S. mombin* (Anacardiaceae), and *T. Africana* (Moraceae) were the indicator species. These species are typically found in secondary forest habitats and are indicative of anthropogenic disturbances. In fact, a low-intensity anthropogenic disturbance (selective timber harvesting and shifting cultivation) has the potential to change the floristic composition and structure of the forests (Turcati, 2011). Although temporary abandonment of disturbed areas can contribute to better succession in forest dynamic and recovery of forest vegetation in some degraded forest areas (Connell, 1978; Grime, 1998; Huston, 1979; Sheil & Burslem, 2003; Wilson, 1994), the occurrence of secondary forest species in dense forest fragments is probably the result of isolation and fragmentation caused by past anthropogenic factors (Laurance et al., 2012). More specifically, these species occur as results of favorable regeneration conditions in gaps created by windthrow in SGs and also by degradation and anthropogenic disturbances. The presence of these species generally suggests less diversity in their habitat as compared with primary or old growth forests; yet, they play an important role in local biodiversity conservation (birds, mammals, arthropods, etc.), thereby increasing the benefits of local conservation (Dent & Wright, 2009; Turner, Wong, Chew, & Ibrahim, 1997). In addition, species such as *T. scleroxylon* (Sterculiaceae), *T. megalantha* (Meliaceae), *C. gigantean* (Sterculiaceae), *C. millenii* (Sterculiaceae), and *C. pentandra* (Bombacaceae) were the indicator species in the FR of Pobè group. Relevant observations on these species were documented by Devineau (1976) and Sokpon (1995) who also pointed out that they are characteristic species of semideciduous dense forest. The presence of these indicator species in the FR is likely the results of the level of protection and conservation. Unlike SGs of Pobè SG–FR group, the indicator species of SGs of Kétou SG–FR group (*A. toxicaria*, Moraceae; *A. zygia*; *C. zenkeri*, Celtidaceae; *T. scleroxylon*) are indicative of dense semideciduous forests, while only two species *C. megalophylla* (Leguminosae-Caesalpinioideae) and

D. mespiliformis (Ebenaceae) were indicator species in the FR of Kétou group. *C. megalophylla* is known as gallery forest species, while *D. mespiliformis* is a species of drought-sensitive forests transition zone (Hounkpèvi et al., 2011). The presence of these two species in the FR of the Kétou group reflects the high level of deforestation. The FR has been invaded by field crops, causing habitat loss and fragmentation, and reducing forest vegetation to small forest patches, and to gallery forest fragments.

All being considered, it must be noted that the main factors favoring the biodiversity conservation in forest groves are policies and rules limiting access to these forests (Juhé-Beaulaton & Roussel, 2002). The species diversity and structures in these forests, compared with those in FRs are partly indicative of the better conservation implemented by SGs, despite constraints such as human population growth and increasing needs for resources. However, there are recent concerns regarding the long-term sustainability of the conservation role of these SGs, especially with occurrence of church and western religions and the weakness of traditional beliefs.

Implications for Conservation

Our study showed that both SGs and FRs were results of landscape fragmentation. The finding that tree species richness was highest in SGs suggests that fragmentation impacts were more pronounced in FRs. SGs constitute key landscape feature that can sustain higher levels of diversity; in southeastern Benin, they contribute to local conservation of native tree species of dense semideciduous forests. Small forest fragments can be very relevant in maintaining plant species diversity provided that their habitat is of high quality and the management appropriate. Our study suggests that protection actions must be enforced in FRs. Illegal tree logging must be fully prohibited, and activities in these forests controlled to enable restoration of natural forest vegetation in degraded areas. The limited physical access to the SGs due to their religious character seems to add greater value to conservation. Given the importance of these SGs, the government of Benin Republic initiated in 2011 a pilot project for integration of sacred forests into network system of protected areas and regularization of tree logging policies and laws. However, it must be taken into account that implementation of logging ban in FRs can drastically increase logging activities inside the sacred forests, as shown for old-growth forest protection in southwest China (Brandt et al., 2015). Therefore, incorporation of these SGs into conservation networks with participative support of key stakeholders (local communities, scientists, and forest officers) is suggested as alternatives to conservation of remnant forest fragments in southeastern Benin.

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References

- Adjanohoun, E. (1968). Le Dahomey. Conservation of vegetation in Africa South of the Sahara. Symposium of the "Association pour l'Etude Taxonomique de la Flore d'Afrique Tropicale". *Acta Phytogeographica Suecica*, 54, 86–91.
- Adjakpa, J. B., Dassoundo, H. A., Yedomonhan, H., Weesie, P. D., & Akpo, E. L. (2011). Diversité du peuplement ligneux d'une forêt dense en zone sub-humide: Cas de la forêt de Sakété dans le sud-Bénin en Afrique de l'Ouest [Woody species diversity in dense forest in a sub-humid zone: study case of Sakete forest in South Benin in West Africa]. *International Journal of Biological and Chemical Sciences*, 5(6): 2291–2305.
- Adomou, A. (2005). *Vegetation patterns and environmental gradients in Benin* (PhD thesis, p. 133). Wageningen University, the Netherlands.
- Adou-Yao, C. Y., Bakayoko, A., Akpatou, K. B., & N'Guessan, K. (2011). Impacts de pressions anthropiques sur la flore et la structure de la végétation dans la forêt classée de Monogaga, Côte d'Ivoire [Impacts of human disturbances on vegetation flora and structure in Monogaga forest reserve]. *Journal of Animal & Plant Sciences*, 12(2): 1560–1572.
- Agbo, V., & Sokpon, N. (1998). *Forêts sacrées et patrimoine vital au Bénin* (Projet CRDI n° 95-8170, p. 200). Université Nationale du Bénin, Faculté des Sciences Agronomiques, Benin.
- Aguilar, R., Ashworth, L., Galetto, L., & Aizen, M. A. (2006). Plant reproductive susceptibility to habitat fragmentation: Review and synthesis through a meta-analysis. *Ecology letters*, 9(8): 968–980.
- Akoegninou, A. (1984). *Contribution à l'étude botanique des îlots de forêts denses humides semi-décidues en République Populaire du Bénin* [Contribution to a botanical study in the semi-deciduous dense forest patches in Republic of Benin]. (Thèse de doctorat, p. 250). Université de Bordeaux III, France.
- Akoegninou, A. (1998). Les forêts denses humides semi-décidues du Sud-Bénin [Semi-deciduous dense forests in South Benin]. *Journal de la Recherche Scientifique de l'Université de Lomé*, 1(2): 125–131.
- Allendorf, T. D., Brandt, J. S., & Yang, J. M. (2014). Local perceptions of Tibetan village sacred forests in northwest Yunnan. *Biological Conservation*, 169, 303–310.
- Alohou, E. C., Gbemavo, D. S. J. C., Ouinsavi, C., & Sokpon, N. (2016). Local perceptions and importance of endogenous beliefs on sacred groves conservation in South Benin. *International Journal of Biodiversity and Conservation*, 8(5): 105–112.
- ASECNA. (2010). Les données météorologiques des stations de Kétou et Bonou et synoptiques de Bohicon et Cotonou

- [Meteorological data of the stations of Ketou and Bonou and synoptics of Bohicon and Cotonou]. (Rapport, p 210), Agence pour la sécurité de la navigation aérienne en Afrique et à Madagascar (ASECNA), Cotonou, Benin.
- Assi-Kaudjhis, C. (2011). *Dynamique des écosystèmes et biodiversité des montagnes du Cameroun au cours des derniers 20 000 ans: Analyse palynologique d'une série sédimentaire du lac Bambili* [Dynamics of ecosystems and biodiversity of mountains in Cameroon over the last 20000 years: Palynological analysis of sedimentary series of Bambili lake]. (These de doctorat). Versailles-St Quentin en Yvelines, France.
- Aubreville, A. (1937). Les forêts du Dahomey et du Togo [Forests in Dahomey and Togo]. *Bulletin du comité d'Etudes historiques*, 10, 1–113.
- Avon, C., Bergès, L., Dumas, Y., & Dupouey, J. L. (2010). Does the effect of forest roads extend a few meters or more into the adjacent forest? A study on understory plant diversity in managed oak stands. *Forest Ecology and Management*, 259(8): 1546–1555.
- Barima, Y. S. S., Barbier, N., Ouattara, B., & Bogaert, J. (2010). Relation entre la composition floristique et des indicateurs de la fragmentation du paysage dans une région de transition forêt-savane ivoirienne [Relationship between floristic composition and indicators of landscape fragmentation in a transition forest-savanna region in Ivory Coast]. *Biotechnologie, agronomie, société et environnement*, 14(4): 617.
- Bertzky, B., Corrigan, C., Kernsey, J., Kenney, S., Ravilious, C., Becançon, C., & Burgess, N. (2012). *Protected planet report 2012: Tracking progress towards global targets for protected areas*. Gland, Switzerland: IUCN/Cambridge, UK: IUCN/UNEP-WCMC.
- Bhagwat, S. A., & Rutte, C. (2006). Sacred groves: Potential for biodiversity management. *Frontiers in Ecology and Environment*, 4(10): 519–524.
- Bhagwat, S. A., Kushalappa, C. G., Williams, P. H., & Brown, N. D. (2005). A landscape approach to biodiversity conservation of sacred groves in the western ghats of India. *Conservation Biology*, 19, 1853–1862.
- Bogaert, J., Ceulemans, R., & Salvador-Van Eysenrode, D. (2004). Decision tree algorithm for detection of spatial processes in landscape transformation. *Environmental Management*, 33(1): 62–73.
- Bongers, F., Alemayehu Wassie, A., Sterck, F. J., Bekele, T., & Teketay, D. (2006). Ecological restoration and church forests in northern Ethiopia. *Journal of the Drylands*, 1(1): 35–44.
- Bossart, J. L., & Antwi, J. B. (2016). Limited erosion of genetic and species diversity from small forest patches: Sacred forest groves in an Afrotropical biodiversity hotspot have high conservation value for butterflies. *Biological Conservation*, 198, 122–134.
- Brandt, J. S., Butsic, V., Schwab, B., Kuemmerle, T., & Radeloff, V. C. (2015). The relative effectiveness of protected areas, a logging ban, and sacred areas for old-growth forest protection in southwest China. *Biological Conservation*, 181, 1–8.
- Brandt, J. S., Wood, E. M., Pidgeon, A. M., Han, L.-X., Fang, Z., & Radeloff, V. C. (2013). Sacred forests are keystone structures for forest bird conservation in southwest China's Himalayan Mountains. *Biological Conservation*, 166, 34–42.
- Cabacinha, C. D., & de Castro, S. S. (2009). Relationships between floristic diversity and vegetation indices, forest structure and landscape metrics of fragments in Brazilian Cerrado. *Forest Ecology and Management*, 257(10): 2157–2165.
- Chevalier, A. (1933). Les bois sacrés des Noirs, sanctuaires de la nature [Sacred groves in Africa, sanctuaries of nature]. *Compte Rendu de la Société de Biogéographie*, 1–37, Des patrimoines en permanente évolution.
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, 199(4335): 1302–1310.
- Decher, J. (1997). Conservation, small mammals, and the future of sacred groves in West Africa. *Biodiversity & Conservation*, 6, 1007–1026.
- Dent, D. H., & Wright, J. S. (2009). The future of tropical species in secondary forests: A quantitative review. *Biological Conservation*, 142(12): 2833–2843.
- Devineau, J. L. (1976). Principales caractéristiques physiologiques et floristiques des formations forestières de Lamto (moyenne Côte d'Ivoire) [Principal physiognomy and flora characteristics in Lamto forest stands]. *Annales de l'Université d'Abidjan, série E*, 9, 274–303.
- Djègo, J., & Oumou, M. (2009). Phytosociologie de sous-bois et impact des plantations forestières sur la diversité floristique dans la forêt classée de la Lama [Phytosociology of understory and impact of forest plantations on floristic diversity in Lama forest reserve]. *Annales des Sciences Agronomiques*, 12(1): 35–54.
- Djègo, J., & Sinsin, B. (2007). Structure et composition floristique de la forêt classée de la Lama. In: Fournier, A., Sinsin, B., Mensah, G. A. (Eds.) *Quelles aires protégées pour l'Afrique de l'Ouest? Conservation de la biodiversité et développement*. Marseille: IRD Éditions.
- Dufrène, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological monographs*, 67(3): 345–366.
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34(1): 487–515.
- Findlay, C.S., & Houlihan, J. (1997). Anthropogenic correlates of species richness in south eastern Ontario wetlands. *Conservation Biology*, 1, 1000–1009.
- Foley, J. A., Defries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., ... Snyder, P. K. (2005). Global consequences of land use. *Science*, 309, 570–574.
- Freitas, S. R., Mello, M. C., & Cruz, C. B. (2005). Relationships between forest structure and vegetation indices in Atlantic Rainforest. *Forest Ecology and Management*, 218(1): 353–362.
- Gao, H., Ouyang, Z., Chen, S., & Koppen, C. S. A. (2013). Role of culturally protected forests in biodiversity conservation in Southeast China. *Biodiversity & Conservation*, 22, 531–544.
- Goodchild, M. F. (1986). *Spatial autocorrelation* (Vol. 47). Norwich, England: Geo Books.
- Goodwin, B. J. (2003). Is landscape connectivity a dependent or independent variable? *Landscape Ecology*, 18(7): 687–699.
- Goodwin, B. J., & Fahrig, L. (2002). How does landscape structure influence landscape connectivity? *Oikos*, 99(3): 552–570.
- Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, 86(6): 902–910.
- Henle, K., Lindenmayer, D. B., Margules, C. R., Saunders, D. A., & Wissel, C. (2004). Species survival in fragmented landscapes: Where are we now? *Biodiversity & Conservation*, 13(3): 1–8.

- Houngkpèvi, A., Yévidé, A. S. I., Ganglo, J. C., Devineau, J. L., Azontonde, A. H., Adjakidje, V., ... De Foucault, B. (2011). Structure et écologie de la forêt à *Diospyros mespiliformis* Hochst. ex A. DC. et à *Dialium guineense* Willd. de la réserve de Massi (La Lama), Bénin [Structure and Ecology of *Diospyros mespiliformis* Hochst. ex A. DC. and *Dialium guineense* Willd. stands forest in the Lama Forest Reserve]. *Bois et forêts des tropiques*, 308(2): 34–46.
- Huston, M. (1979). A general hypothesis of species diversity. *The American Naturalist*, 113(1): 81–101.
- Juhé-Beaulaton, D., & Roussel, B. (2002). Les sites religieux vodun. In: Marie-Christine, C. S., Juhé-Beaulaton, D., Jean, B., Roussel, B. (Eds.) *Patrimonialiser la nature tropicale: dynamiques locales, enjeux internationaux* (pp. 415–438). Paris (FRA), Paris: IRD, MNHN.
- Kokou, K., & Caballé, G. (2000). Les îlots forestiers de la plaine côtière togolaise (isolated forest blocks of the coastal lowland in Togo). *Bois et forêts des tropiques*, (263): 39–50.
- Kokou, K., & Kokutse, A. D. (2006). Rôle de la régénération naturelle dans la dynamique actuelle des forêts sacrées littorales du Togo [the role of natural regeneration in the current dynamics of coastal sacred groves in Togo]. *Phytocoenologia*, 36(3): 403–419.
- Kokou, K., & Sokpon, N. (2006). Les forêts sacrées du couloir du Dahomey [Sacred groves in the Dahomey gap]. *Bois et forêts des tropiques*, 288(2): 15–23.
- Laurance, W. F., Ferreira, L. V., Rankin-de Merona, J. M., & Laurance, S. G. (1998). Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology*, 79(6): 2032–2040.
- Laurance, W. F., Useche, D. C., Rendeiro, J., Kalka, M., Bradshaw, C. J., Sloan, S. P., ... Arroyo-Rodriguez, V. (2012). Averting biodiversity collapse in tropical forest protected areas. *Nature*, 489(7415): 290–294.
- Lindenmayer, D. B., Fischer, J., & Cunningham, R. B. (2005). Native vegetation cover thresholds associated with species responses. *Biological Conservation*, 124(3): 311–316.
- MacArthur, R. H., & Wilson, E. O. (1967). *Theory of island biogeography*. (MPB-1) (Vol. 1, p. 203). Princeton, NJ: Princeton University Press.
- Martin, P. (2008). *Influence de la fragmentation forestière sur la régénération des espèces arborées dans le Sud-Ouest de la Côte d'Ivoire* [Influence of forest fragmentation on woody species regeneration in South-Western part of Ivory Coast] (PhD thesis, p. 320). University of Geneva, Switzerland.
- Mgumia, F. H., & Oba, G. (2003). Potential role of sacred groves in biodiversity conservation in Tanzania. *Environmental Conservation*, 30, 259–265.
- Molino, J. F., & Sabatier, D. (2001). Tree diversity in tropical rain forests: A validation of the intermediate disturbance hypothesis. *Science*, 294(5547): 1702–1704.
- Oviedo, G., & Jeanrenaud, S. (2007). Protecting sacred natural sites of indigenous and traditional peoples. In: J.-M. Mallarach, & T. Papayannis (Eds.). *Protected areas and spirituality proceedings of the first workshop of the Delos initiative* (pp. 77–99). Gland, Switzerland: International Union for Conservation of Nature.
- Paradis, G., & Hounnon, P. (1977). *La végétation de l'aire classée de la Lama dans la mosaïque forêt-savane du Sud-Bénin (ex Sud-Dahomey)* [The vegetation of the protected area of the Lama in the mosaic forest-savanna of South-Benin (formerly South-Dahomey)]. *Bulletin du Muséum National d'Histoire Naturelle* (Paris) 3e ser, 503, 1–197.
- Rudel, T., & Roper, J. (1997). Forest fragmentation in the humid tropics: A cross-national analysis. *Singapore Journal of Tropical Geography*, 18(1): 99–109.
- Rybicki, J., & Hanski, I. (2013). Species-area relationships and extinctions caused by habitat loss and fragmentation. *Ecology Letters*, 16(1): 27–38.
- Sánchez-Azofeifa, G. A., Daily, G. C., Pfaff, A. S., & Busch, C. (2003). Integrity and isolation of Costa Rica's national parks and biological reserves: Examining the dynamics of land-cover change. *Biological Conservation*, 109(1): 123–135.
- Schmitt, C. B., Burgess, N. D., Coad, L., Belokurov, A., Besançon, C., Boissier, L., ... Kapos, V. (2009). Global analysis of the protection status of the world's forests. *Biological Conservation*, 142(10): 2122–2130.
- Sheil, D., & Burslem, D. F. (2003). Disturbing hypotheses in tropical forests. *Trends in Ecology & Evolution*, 18(1): 18–26.
- Sinasson, S. K. G. (2010). *Dynamiques des forêts naturelles de Bonou et d'Ichède-Toffo au Sud-Bénin* [Dynamics of natural forests of Bonou and Itchede-Toffo in South Benin] (Master dissertation, p. 134). Mémoire de DEA, Faculté des sciences agronomiques, Université d'Abomey-Calavi, Bénin.
- Sokpon, N. (1995). *Recherches écologiques sur la forêt dense semi-décidue de Pobè au Sud-Est du Bénin: Groupements végétaux, structure, régénération naturelle et chute de litière* [Ecological research on the semi-deciduous dense forest of Pobè in south-east Benin: plant communities, structures, natural regeneration and litterfall] (Thèse de doctorat, p. 365). Université Libre de Bruxelles, Belgium.
- Turcati, L. (2011). *Mesurer la biodiversité pour comprendre l'effet des perturbations sur les communautés végétales: Apport des caractéristiques écologiques et évolutives des espèces* [Measuring biodiversity to understand disturbance effects on plant communities: contribution of ecological and evolutionary characteristics of species] (These de doctorat, p. 263). Université Pierre et Marie Curie.
- Turner, I. M., Wong, Y. K., Chew, P. T., & bin Ibrahim, A. (1997). Tree species richness in primary and old secondary tropical forest in Singapore. *Biodiversity & Conservation*, 6(4): 537–543.
- Upadhyaya, K., Pandey, H. N., Law, P. S., & Tripathi, R. S. (2003). Tree diversity in sacred groves of the Jaintia hills in Meghalaya, northeast India. *Biodiversity & Conservation*, 12, 583–597.
- White, F. (1983). The Guineo-Congolian Regional Centre of Endemism. *The vegetation of Africa: A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa*. Retrieved from <http://unesdoc.unesco.org/images/0005/000580/058054eo.pdf>.
- White, F. (1986). *La végétation de l'Afrique. Recherche sur les ressources naturelles* [The vegetation of Africa. Research on natural resources] (p. 384). Paris: Orstom-Unesco.
- Whitmore, T. C. (1991). Invasive woody plants in perhumid tropical climates. In: P. S. Ramakrishnan (Ed.) *Ecology of biological invasion in the tropics* (pp. 35–40). New Delhi, India: International Scientific Publications.
- Wilson, J. B. (1994). The “intermediate disturbance hypothesis” of species coexistence is based on patch dynamics. *New Zealand Journal of Ecology*, 18, 176–181.