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Increased isolation of two Biosphere Reserves and surrounding protected areas (WAP ecological complex, West Africa)

Nicola Clerici[a,b], Antonio Bodini[b], Hugh Eva[a], Jean-Marie Grégoire[a,*], Dominique Dulieu[c], Carlo Paolini[c]

[a]*Institute for Environment and Sustainability, Joint Research Centre, European Commission, TP. 440, I-21020 Ispra (VA), Italy*
[b]*Department of Environmental Sciences, University of Parma, V.le delle Scienze, 43100 Parma, Italy*
[c]*Programme Régional Parc W/ECOPAS, 01 BP:1607, Ouagadougou 01, Burkina Faso*

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Summary

Protected areas such as nature reserves have been found to be effective in preventing habitat destruction and protecting ecosystems within their borders. Recent studies however found extensive loss of tropical forest habitat around protected areas, vastly contributing to increase the levels of ecological isolation. Using high-resolution satellite data we investigated the isolation trend occurring in the W-Arly-Pendjari (WAP) ecological complex in West Africa. A land-cover change analysis was performed for the period 1984–2002: savanna vegetation extension and loss were derived within the complex and in a 30 km peripheral buffer. Sample regions in the buffer were also analysed using selected spatial indicators to quantify temporal trends in habitat fragmentation. Implications for change in relative capacity to conserve biodiversity were discussed through the calculation of the species richness capacity (SRC). More than 14.5% of savanna habitat was lost in the WAP peripheral areas, while 0.3% was converted inside the complex. The degree of fragmentation of remnant savanna habitat has also drastically increased. Despite the effectiveness of the park conservation programme, we found through the SRC approach that the WAP complex is decreasing its potential capacity to conserve species richness. This process is mainly due to the rapid and extended agricultural expansion taking place around the complex. A better understanding of the ecological

*Corresponding author. Tel.: +39 0332 789215; fax: +39 0332 789073.
E-mail addresses: nclerici@nemo.unipr.it, nicola.clerici@jrc.it (N. Clerici), jean-marie.gregoire@jrc.it (J.-M. Grégoire).

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dynamics occurring in the peripheral regions of reserves and the consideration of development needs are key variables to achieve conservation goals in protected areas.

Introduction

Protected areas are the cornerstones of conservation strategies worldwide. They preserve key ecosystems against biodiversity loss (Myers, Mittermeier, Mittermeier, da Fonseca, & Kents, 2000), promote sustainable management and offer unique 'laboratories' to investigate ecosystem functioning and complexity. In tropical areas especially, nature reserves have been found to be effective in preventing habitat destruction and protecting ecosystems within their borders (Bruner, Gullison, Price, & da Fonseca, 2001). Although their extension represents 11.5% of the Earth's land surface (Rodrigues et al., 2004), some studies suggested that at least 50% of total land would be needed to protect the actual global biodiversity (Soulé & Sanjayan, 1998).

Protected areas are important targets of research on *insularity*, i.e. the isolation and fragmentation by anthropogenic conversion of natural habitats (Ramade, 2003). Recent research highlighted extensive loss of tropical forest habitat around protected areas with consequent increasing ecological isolation (DeFries, Hansen, Newton, & Hansen, 2005; Struhsaker, Struhsaker, & Siex, 2005). Reserves where surrounding original biotopes have been degraded or converted to non-natural cover can be subject to a series of changes in microclimate, soil, and vegetation composition that affect population structure and dynamics of species living inside the core protected areas (Gascon, Williamson, & Da Fonseca, 2000; Margules & Pressey, 2000). Such a process of isolation can reduce the likelihood of persistence of certain species, decrease population sizes and increase their extinction risk (Brooks, Pimm, & Oyugi, 1999; Davies, Margules, & Lawrence, 2000; Pimm, Jones, & Diamond, 1988). Species extinction in protected areas is in fact often linked with reserve isolation and limited size (Wilcove & May, 1986; Woodroffe & Ginsberg, 1998). The overall *functional* size of protected areas can comprise their surrounding regions of preserved habitats or a mosaic of natural biotopes and human-managed land; as a consequence, peripheral lands are strongly linked to the ecological processes occurring in the core reserve. Outside the reserve, animals can find nutrients, water and accomplish processes such as feeding, reproduction and migration. Population dynamics may take advantage of higher reproduction rates occurring outside the reserve, contributing to maintain inner *sink* populations or, the contrary, be subjected to human-induced mortality (Hansen & Rotella, 2002). In many protected areas, population sinks are located beyond the reserve's peripheral areas, where conflicts with humans are more evident and higher number of individuals are killed. Hence, for some species such as large carnivores, conservation priority should be given to counteract human persecution within peripheral areas, and to maximise the reserves' size (Woodroffe & Ginsberg, 1998). Reserves' edge areas, due to changes in land-use and to the action of exogenous factors acting from the surrounding lands (e.g. cattle grazing, fires, hunting, etc.), are more prone to impoverishment of vegetation and changes in biotic composition (Laurance et al., 2002). As they act as exchange interfaces, their structure plays a key role for the future of the internal protected habitats (Gascon et al., 2000). To counteract the effects of isolation and external disturbances, buffer zones around the protected core areas are often adopted in the architectural strategy of natural reserves planning (Laurance & Gascon, 1997): here restrictions are applied on resources use, and development policies and actions are taken to enhance conservation of valuable habitats (Sayer, 1991).

Habitat conversion into human exploited lands produces harmful effects on biodiversity conservation not only by decreasing portions of valuable natural habitats but also by fragmenting the *continuum* of eco-mosaics constituting the landscape (*sensu* Forman, 1997). Habitat fragmentation is in fact recognised as one of the major threats to species survival in human-disturbed environments by contributing to the isolation of inhabiting populations and by decreasing their size (Lienert, 2004; Saunders, Hobbs, & Margules, 1991). Biotopes isolation depending on species characteristics and the intensity of the phenomenon, can lead to local population extirpation (Vos & Stumpel, 1995; Young, Boyle, & Brown, 1996), can decrease available resources and modify the abiotic conditions of the landscape, e.g. by altering the amount of radiation and nutrients exchange with the surrounding land (Lienert & Fischer, 2003).

Detecting extent of native vegetation loss and habitat fragmentation around protected areas is of fundamental importance to identify the social and physical driving forces running the modification processes at the landscape level and to permit eventual responses towards conservation actions. This is the case especially for developing countries, where the conversion of natural habitat represents also a loss of one of their more valuable source of income (Costanza et al., 1997; Velázquez et al., 2003). In Africa, biodiversity conservation targets contrast dramatically with demographic expansion and development needs, which constantly require productive lands to exploit (Musters, de Graaf, & ter Keurs, 2000). Africa's 1999 population (767 million people) was projected to nearly double by 2035 and Sub-Saharan Africa's population had growth rates higher than any other world region over the past 40 years (UNPF, 2005). Trends of conversion of natural habitats in the continent are likely to continue increasing, and thus the need of constant monitoring activities. Assessing landscape modifications by quantifying *both* changes in native vegetation extent and its spatial structure is critical to the management of protected areas (Margules & Pressey, 2000).

This study investigates the trend in isolation of two biosphere reserves and surrounding protected areas (W-Arly-Pendjari ecological complex, West Africa) by analysing the conversion of inner and peripheral savanna habitats and their degree of fragmentation. The W-Arly-Pendjari site (hereafter WAP) has been selected for its exceptional importance for the conservation of West African biotopes and because of the presence of two UNESCO-MAB Biosphere reserves. The 'W du Niger Transnational Park' is also part of the sites monitored by the European Commission Joint Research Centre (JRC) through the Global Environment Monitoring Unit's research activities (http://www-gem.jrc.it). Specific objectives of this study include:

- Identify through a quantitative assessment the loss of natural savanna vegetation in the core and peripheral areas of the WAP complex for the period 1984–2002 (*isolation* trends).
- Analyse landscape fragmentation of peripheral remnant savanna habitats using selected spatial metrics.
- Discuss ecological implications and conservation issues.

Study area

The WAP transfrontier ecological complex of protected areas is located between 0.4°E and 3.15°E and 12.6°N to 10.7°N, at the triple point between southern Niger, eastern Burkina Faso and northern Benin (West Africa). The complex (Fig. 1, 2002 boundaries) extends for more than 26,500 km^2 and it is composed by the W du Niger Transfrontier Park, the national parks of Arly and Pendjari, and a complex of contiguous protected areas and hunting reserves regulated by different statutory regulations, restrictions and type of rights. The reserves can be broadly divided into four classes: national parks, total or partial faunal reserves and hunting concessions. In partial faunal reserves some exploitation activities are allowed, such as hunting, fishing and fruit collection. These activities are not allowed in total faunal reserves and national parks, with some regional exceptions (ritual hunting in some regions of Pendjari National Park or commercial fishing in total reserves in Burkina Faso). Hunting zones are given in concession by governments to local entities and were created to block the more threatening practice of conversion into farmlands.

Management of protected areas in the WAP depends also on country ownership. In Benin the administration of natural parks and reserves is guided by the Strategic Plan for the Conservation and Management of Protected Areas (1994); this led to the creation of the National Centre for Wildlife Reserves Management (CENAGREF), which outlined and implemented the Action Plan for the management and conservation of protected areas (together with buffer zones and transition areas). Locally, CENAGREF co-finances the Village Associations for Wildlife Reserve Management (AVIGREF), who participate in management decisions and have the right to organise hunting in specific areas. In Burkina Faso a legislative reform in 1995 increased the role of private involvement and community participation in the administration and management of protected areas. Twelve Wildlife Conservation Units (WCU) control protected areas in the country through the supervision of a government officer, while local management and commercial exploitation are assigned to private entities that pay fees. In Niger protected areas are under the control of the Directorate of Fauna and Fisheries (DFPP). The country adopted a National Strategy and Action Plan for Biodiversity (NBSAP) and a National Environmental Action Plan for Sustainable Development (NEAP), however a specific national programme for protected areas management is still absent.

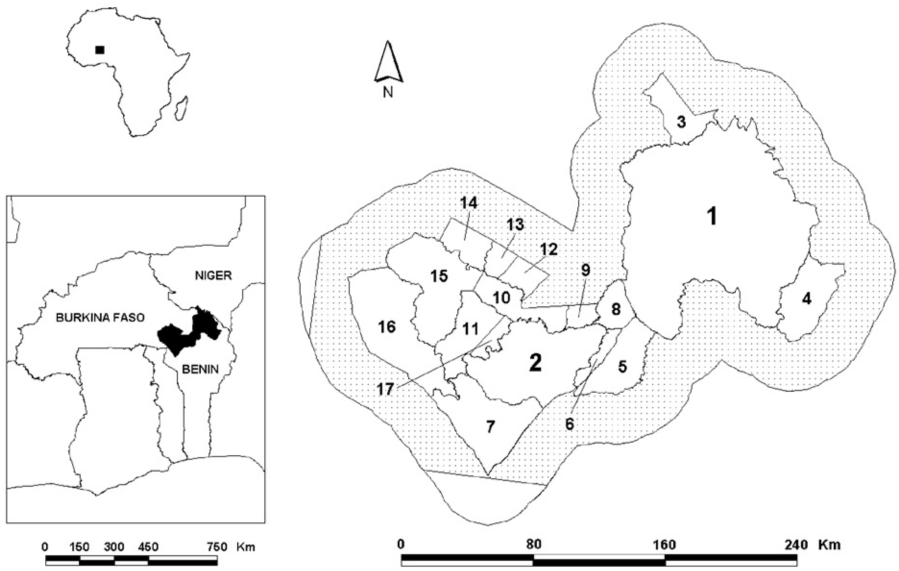


Figure 1. Location of the W-Arly-Pendjari (WAP) ecological complex in Africa (left). The WAP administrative boundaries of protected areas (in 2002, ECOPAS data) and the 30 km buffer around the complex are shown on the right. Reserves and their correspondent IUCN category (in parenthesis) are: (1) Transfrontalier National Park of 'W du Niger (II); (2) Pendjari National Park (II); (3) total faunal Reserve of Tamou (I); (4) Cynegetic zone of Djona (VI); (5) Cynegetic zone of Mekrou (VI); (6) Cynegetic zone of Atakora (VI); (7) Cynegetic zone of Pendjari (VI); (8) partial faunal reserve of Kourtiagou (IV); (9) hunting concession of Koakrana (VI); (10) total faunal reserve of Arly (IV); (11) partial faunal reserve of Arly (IV); (12) hunting concession of Pagou (VI); (13) hunting concession of Tandougou (VI); (14) hunting concession of Ouamou (VI); (15) total faunal reserve of Singou (I); (16) partial faunal reserve of Pama(IV) and (17) total faunal reserve of Madjori (I). No data was present for the white areas in the buffer zone.

The WAP has heterogeneous climate conditions and vegetation distribution. The complex is characterised by the presence of a rainy season (approximately from May to October) and a dry season (November–April); climate characteristics belong to the *Soudanian* White/UNESCO bioclimatic classification (White, 1983), although the WAP has drier conditions in the northern part (average rainfall of 500 mm) and more humid in the south (average rainfall of 1200 mm). Vegetation cover in the northern part of the complex is characterised by grasslands and open shrublands (*brousses*) degrading towards open savanna woodlands with sparse trees. From the central to the southern part of the complex, shrub savanna gradually becomes savanna woodlands, while the climate tends to the *Guinean* domain. The northern parts are often dominated by bush species and representatives of the *Combretum–Terminalia* association, such as *Acacia ataxacantha*, *Combretum glutinosum*, *Bombax costatum* and *Anogeissus leiocapus*. The herbaceous layer is frequently represented by *Loudetia* spp. and *Andropogon* spp. In the southern regions the tree component often becomes dominant and the vegetation is characterised by representative species like *Anogeissus leiocarpus*, *Terminalia avicennioides* and *Isoberlinia* spp. (Dulieu, 2004). Other characteristic habitats are gallery forests, riparian vegetation and marshlands, of high interest for conservation issues.

The WAP complex represents the biggest continuum of terrestrial and aquatic ecosystems in the West African savanna belt, and one of the most important areas for the conservation of western African ecosystems and fauna (Lamarque, 2004). The complex hosts the bigger population of elephant *Loxodonta africana* in West Africa (more than 3800 individuals), which represent 50% of total abundance in the region (UNDP, 2004). The WAP system is one of the last refuges in West Africa for a number of threatened species and it is of critical importance for the conservation of Sahelian and Sudanese mammal populations, such as dwarf buffalo (*Syncerus caffer brachyceros*), kobs (*Kobus kob kob*), roan antelopes (*Hippotragus equinus koba*), giraffes (*Giraffa camelopardalis peralta*), hippopotami (*Hippopotamus amphibious*), lions (*Panthera leo*), and several monkey species. The presence of rare species such as the manatee (*Trichecus senegalensis*) or the leopard (*Panthera pardus*) was demonstrated, and new butterfly species were also recently discovered (Lamarque, 2004). Overall, at least 670 plant species were identified in the complex, some of them endangered or vulnerable species. The fact that between the three countries sharing the WAP the relevant conservation legislation is often not consistent is a factor that threatens conservation efforts. Many species have a different status depending on the national regulation, producing incongruent situations where, for example, hippopotami can be hunted in Benin while they are protected in Burkina Faso.

For the complex's outstanding biodiversity significance, the 'W du Niger' Transfrontier Park (hereafter W Park) was accepted in 2002 as the first Transboundary Biosphere Reserve in Africa by the Man and the Biosphere Programme of UNESCO (MAB). Part of the complex is also an UNESCO World Natural Heritage Site (W National Park of Niger, in 1996), while extended areas are protected by the Ramsar Convention (total reserve of Arly). At its south-western portion the WAP complex hosts the Pendjari National Park, which has been a Biosphere Reserve since 1986.

Benin, Burkina Faso and Niger are involved in coordinated trans-boundary conservation efforts through specific programmes regarding the WAP, for instance:

- Regional programme 'Park W-ECOPAS' (*Ecosystèmes Protégés en Afrique Soudano-Sahélienne*), which is funded by the European Union development funds and it is designed to control the degradation of natural resources, ensure sustainability and safeguard biodiversity;
- Regional project "Building Scientific and Technical Capacity for Effective Management and Sustainable Use of Dryland Biodiversity in West African Biosphere Reserves" financed by GEF-UNESCO-MAB and whose objective is to strengthen scientific and technical competence for effective management of the reserves;
- Renewable Energy Programme, funded by Electricité de France, designed to provide solar energy to tourist structures and riparian population to reduce wood and charcoal collection within the WAP.

Furthermore, the three countries have also signed an anti-poaching agreement.

Research activities in the WAP are the result of a number of agreements with international organisations, regional research institutes and local or foreign universities (especially from Germany, Italy and France). In the case of the W ecological complex, a Scientific Council of the reserve within the ECOPAS programme coordinates the research activities to support the biosphere management plan, covering themes like: dynamics of animal populations (Lamarque, 2004); agriculture (Doussa, 2004); social dynamics, ecological characterisation (Dulieu, 2004; Fournier et al., 2003); fires (Eva, Grégoire, & Mayaux, 2004) and transhumance.

Within the peripheral areas of the WAP, agriculture (sorghum and cotton especially) and hunting activities are widespread. The *élevage* (cattle raising) is also a common practice for some populations. Poaching is still a diffused phenomenon and a major threat to the reserves.

Evidence shows human presence has existed around the WAP area for thousands of years (Lamarque, 2004). Equilibrium, or an adaptation, was found between human disturbances and ecological conditions, particularly relating to vegetation cover. However, some drastic changes occurred during the 1970s and 1980s with the development of new villages around the W Park (Boluvi, 2005). There is therefore an increasing anthropic pressure around the reserves which, as a probable consequence, are creating a breaking of the equilibrium between the ecological conditions and level of human disturbance. Currently, around the W Park a peripheral region limits productive activities only to agriculture, acting as buffer against the pressure of grazing, hunting and expansion of urban centres. In some other areas of the WAP complex no buffers are present and reserves and hunting concessions are directly connected to villages and agricultural areas.

From outside the complex and from the WAP hunting reserves, fire is commonly propagating into the protected areas through the continuum of savanna vegetation layer, often due to poaching and illegal grazing activities (ECOPAS data). Additionally, park managers set prescribed fires every year to open vegetation and increase visibility of fauna for tourists. The ecological effects of these fires are still not well understood (Dulieu, 2004; Sawadogo & Fournier, 2004; Sawadogo et al., 2005). Fires are considered fundamental regulation elements of savanna's vegetation structure and a permanent driving force that initiated the formation of savanna ecosystems (Goldammer, 1993). In African savannas, fires and vegetation coexisted at least since the Quaternary period (Kershaw et al., 1997), however the human-driven control of biomass burning is currently producing more frequent fires, and unnaturally lit at the beginning of the dry season (Saarnak, 2001). These practices decrease the intensity of combustion, which in turn potentially affects the savanna tree-grass ratio and produces effects such as the 'bush encroachment' phenomenon (Roques et al., 2001; Scholes & Archer, 1997), as observed in southern W Park. Outside the WAP, fires are lighted annually, beginning at the end of September at the north and ending in late April at the south (Eva et al., 2004). Fires are widespread and are used to generate resprouting for grazing activities, to hunt and in agricultural or other land management practices (Grégoire, 1996). Fire can be considered as one of the main indicators of land-cover change (Eva & Lambin, 2000; Turner et al., 1995): in the peripheral areas of the WAP decrease in burned surface and modification in spatial properties of burned areas are processes that accompany savanna habitat loss and landscape fragmentation (Clerici, Hugh, & Grégoire, 2005).

Materials and methods

Data sources

From the United States Geological Survey (USGS) we acquired images by Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper+ (ETM+), respectively from 14th to 23rd November 1984 and 17th to 24th November 2002 (early dry season) covering the WAP complex; the images have a nominal pixel resolution of 30 m. To help the interpretation process 12 scenes of the ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer, onboard the NASA *Terra* platform) were acquired for the periods of November 2001 and 2002, as the 15 m resolution of the visible/near infrared bands can provide significant additional information. Thematic layers (administrative boundaries, vegetation maps, etc.), were provided by the ECOPAS project. Landsat TM and ETM+ data were acquired in the same season in order to minimise variations in vegetation phenology and weather conditions; however, differences in soil moisture level and intensity of vegetation signal were still present in some areas of the images. The TM and ETM+ images were co-registered using 172 ground control points and a second-order polynomial function to achieve a sub-pixel precision (26.4 m RMSE).

Analysis of isolation: savanna vegetation loss

The isolation analysis was performed considering a 30 km wide peripheral zone delineated outside the WAP administrative border, and all the area inside the complex. The periphery is shared by Benin, Burkina Faso, Niger and Togo; limited portions of the buffer were not covered by the satellite images. As some techniques of image differencing and rationing are less effective if phenological and radiometric variations are evident (Coppin, Jonckheere, Nackaerts, Muys, & Lambin, 2004), we adopted a *post-classification* change detection approach (Jensen, 1996) to analyse changes in savanna vegetation extension and critical land-cover changes, e.g. agriculture distribution. In this method independent classifications of the datasets are performed using a supervised or unsupervised classification algorithm; one of the main advantages of such approach is that it minimises radiometric calibration between dates. We performed an unsupervised classification based on an ISODATA classifier, excluding TM/ETM+ band 1 (0.45–0.53 μm) because of its sensitivity to haze and fire smoke.

Main land-cover classes were identified based on previous validated vegetation maps (DeWispelaere, 2003), high-resolution imagery (Terra ASTER data), waypoints collected during field missions and visual interpretation. A detailed analysis of the land-cover change trajectories is not reported here as it is not within the scope of the paper. The initially over-segmented classified images were interpreted by cross-referencing all information sources, and classes assigned to seven broad categories (gallery forests and riparian vegetation, wooded savanna, shrub savanna, open savanna dominated by herbaceous vegetation, agriculture, water, other). Overall extension of vegetation was derived by merging the four vegetation types (hereafter savanna vegetation class). Change statistics were derived for the countries sharing the WAP complex and peripheral areas. Formal overall accuracy assessment was not performed because of the extension of the study area (ca. 57,000 km^2) and the costs associated with a prolonged field mission. However, field validation points were collected in the Pama, Diapaga and Tapoa Djerma regions.

To illustrate the potential implications of ecological isolation of the WAP, we calculated the change in relative capacity of conserving species richness of the reserve complex, *species richness capacity* (SRC). Following DeFries et al. (2005) and Brooks et al. (1999), SRC can be calculated through the equation:

$$\mathrm{SRC} = \left[(I_t + S_t)/(I_\mathrm{I} + S_\mathrm{I})\right]^z,$$

where I_t and S_t represent, respectively, the area of habitat inside the complex and the surrounding region at time t, while I_I and S_I correspond to the areas inside and surrounding the WAP in the case of completely intact habitat. Coefficient z depends on habitat conditions and species; we adopted the values $z = 0.25$ as a previously used value estimated for fragmented tropical and subtropical landscapes, with values interval of ± 0.10 (Brooks et al., 2002; DeFries et al., 2005). The SRC is an index based on the direct proportionality between species richness and habitat extension (species–area relationship, e.g. Brooks et al., 1999), and represents a loss of potential capacity of maintaining biodiversity richness for the reserve, postulating that all areas surrounding the reserve would be suitable habitat if intact.

Fragmentation analysis of remnant savanna habitats

The land-cover change map identified the regions where there is evidence of conversion of savanna habitat. These areas are subject to higher anthropic pressure and where it is more urgent to assess the conditions of habitat spatial alteration due to land-cover conversion. We assessed the degree of landscape fragmentation of remnant savanna vegetation habitats by selecting five subset regions. The choice of using sampling regions (subsets) instead of the whole study area was made as otherwise the fragmentation trends of the entire study region would be an average of surfaces characterised by a high degree of fragmentation with ones with low degree or absence, hence giving an overall less meaningful result (*trend*). Using subsets we can focus on hot-spots, understanding local fragmentation dynamics and landscape modification processes.

One method to analyse landscape fragmentation is through the use of quantitative indicators based on the spatial arrangement of habitat patches within the eco-mosaic (Herzog & Lausch, 2001; Narumalani, Mishra, & Rothwell, 2004). Numerous studies adopted these indices to measure the degree of fragmentation of habitats as a basis to understand potential harmful effects on ecosystems and biota (see Cumming & Vernier, 2002; Nagendra, Munroe, & Southworth, 2004). Moreover, modifications in spatial pattern over time also provide help in identifying and understanding social and ecological processes driving landscape change (Brown, Duh, & Drzyzga, 2000).

Through the use of dedicated software (FRAGSTATS, McGarigal, Cushman, Neel, & Ene, 2002) we calculated a series of habitat patch-based indices selected from the ecological literature to assess the degree of fragmentation of savanna vegetation (Forman, 1997; O'Neill et al., 1988; Southworth, Munroe, & Nagendra, 2004). The analysis was performed for 1984 and 2002 on a vegetation/non-vegetation layer (savanna habitat) to investigate trends in increase/decrease in habitat fragmentation. These metrics (Table 1) take into account habitat patch dimension, number, shape's complexity and their spatial arrangement within the landscape (see McGarigal & Marks, 1995). Number of patches in a landscape (NP) or patch density (PD, number of patches over total landscape area) is a simple measure of the extent of subdivision or fragmentation of a patch class. They are the simplest metrics of fragmentation but the results of their interpretation are more meaningful in conjunction with other indicators. Habitat patch size (PA_MN) measures the surface extension of patches and it is related with population extirpation risk and with the number of species that a patch generally holds (Farina, 1998). Largest Patch Index (LPI) measures the area of the largest patch of the class of interest. Edge density (ED) provides information on density of habitat patch perimeters. Shape metrics as SHAPE_MN and PAFRAC_MN detect the complexity of patch geometry and have been previously used to assess the level of anthropic pressure on landscapes (McGarigal & Marks, 1995). LSI and Contiguity Index (CONTIG_MN) measure, respectively, the aggregation

Table 1. Spatial indices adopted in the landscape fragmentation analysis

Index category	Fragmentation indices
Patch density and size metrics	Number of patches (NP) Mean patch size (PA_MN) Patch density (PD) Largest Patch Index (LPI)
Edge metrics	Edge density (ED)
Shape metrics	Mean Shape Index (SHAPE_MN) Contiguity Index (CONTIG_MN) Mean patch fractal dimension (PAFRAC_MN) Landscape Shape Index (LSI)
Isolation/proximity metrics	Mean Proximity Index (PROX_MN) Mean nearest neighbour distance (ENN_MN)

and "spatial connectedness" of a habitat class (Major, Christie, Gowing, & Ivison, 1999). Isolation and proximity metrics (PROX_MN, ENN_MN) are measures of patch context and assess the degree of patch isolation (Gustafson & Parker, 1992). This has important consequences for the disruption of movement patterns to other neighbouring habitat patches and the isolation of local populations (Vos & Stumpel, 1995).

Additionally, a field mission was conducted in November 2004 around Diapaga (west of W Park, Burkina Faso) and Ougarou (north-west of WAP). The field mission had multiple objectives that sought to assess the degree of discontinuity in the landscape at a field scale in a mosaic of cultivated/uncultivated areas and within the WAP, combined with the understanding of the mechanisms that are at the basis of land-cover change. We collected data from three transects (each 1 km in length) located inside and outside the protected areas; for each transect we recorded a GPS waypoint every time there was clear presence of a discontinuity in land-cover/land-use (e.g. from bare soil to set aside). This provided a first indication of the degree of discontinuities present inside and outside the WAP and on what processes create landscape fragmentation.

Results

Isolation analysis

Our analysis documents an extended conversion of natural savanna vegetation in the peripheral areas of the WAP complex. Within the 30 km-wide buffer surrounding the outer perimeter of the reserves, more than 14.5% of savanna vegetation was lost from 1984 to 2002 revealing a rapid process of land conversion (3514.4 km^2). The higher rate of native vegetation loss is found within the Benin portion of the WAP peripheral areas, i.e. 17.3% of its 1984 extension, corresponding to an approximated 1764 km^2 loss (Fig. 2). Lower rates of habitat loss are found in the territories of Burkina Faso (13.1%), Niger (11.2%) and Togo (5.2%). Overall, change trajectories revealed that conversion of native savanna habitats in the complex's periphery resulted primarily from the strong expansion of agricultural activities, in total this class represented 15.8% of land-cover in 1984 and 26.9% in 2002. The greatest agricultural expansion is found in the Benin region, where 15.1% of its peripheral territory was converted into productive lands during this temporal interval,

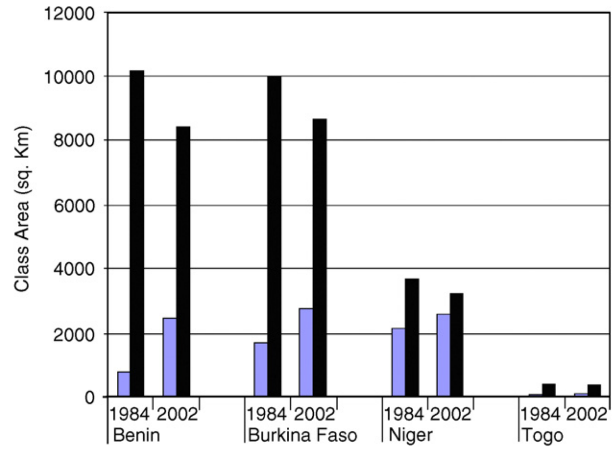


Figure 2. Total area of savanna vegetation (in black) and agriculture (blue) classes for the countries within the 30 km peripheral areas of the WAP (1984 and 2002).

followed by Burkina Faso (9.1%) and by Niger (7.5%), where the presence of tabular hills (*mesas*) often characterised by unproductive ferralithic cuirasses represent strong physical constraints to agriculture expansion. A major change is located at the south of Pama partial reserve, where a large portion of woodland savanna was converted into flooded lands following the construction of the Kompienga dam, current surface of approximately 106 km^2.

As expected, within the WAP complex the rate of habitat loss is much lower. Overall inside the whole complex we detected the loss of 82.5 km^2 of native savanna habitat (1984–2002), corresponding to 0.3% of the overall complex extension. The hot-spots of habitat conversion are located in the enclaves within the partial reserves of Pama (*Tintangou*) and Arly (*Madjoari*), and to a lower extent in Tamou total reserve and in the southern part of the Cynegetic zone of Pendjari. Arly and Pendjari National Parks revealed no significant loss of habitat, but in the Benin portion of the W Park a limited number of cultivated fields have appeared within the southern border revealing explicitly the high pressure of agriculture expansion towards the park's edge.

Changes in potential capacity of the complex to preserve biodiversity were assessed through the calculation of the SRC, derived from the empirical area–species relationship (DeFries et al., 2005; Pimm & Raven, 2000). Based on this relationship, in 1984 the WAP complex capacity to conserve species richness is 97.7 ± 0.9% of the ideal intact case (Fig. 3). In 2002, mainly due to the loss of natural savanna habitat in the peripheral areas, the complex decreased its SRC to 95.9 ± 1.6%. In the case of a complete isolation case (total loss of

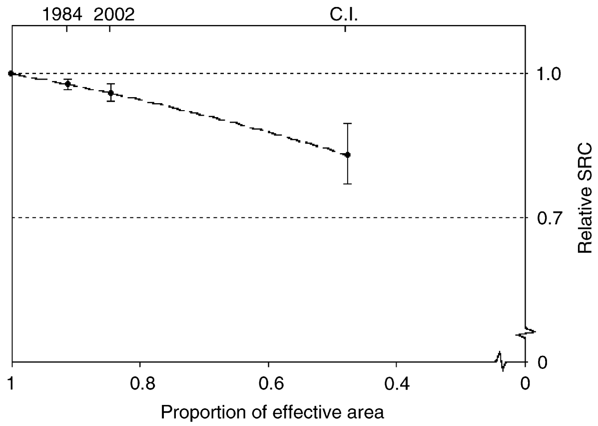


Figure 3. Relative species richness capacity (SRC) for the year 1984, 2002 and for the complete isolation case (C.I.), calculated with $z = 0.25 \pm 0.10$.

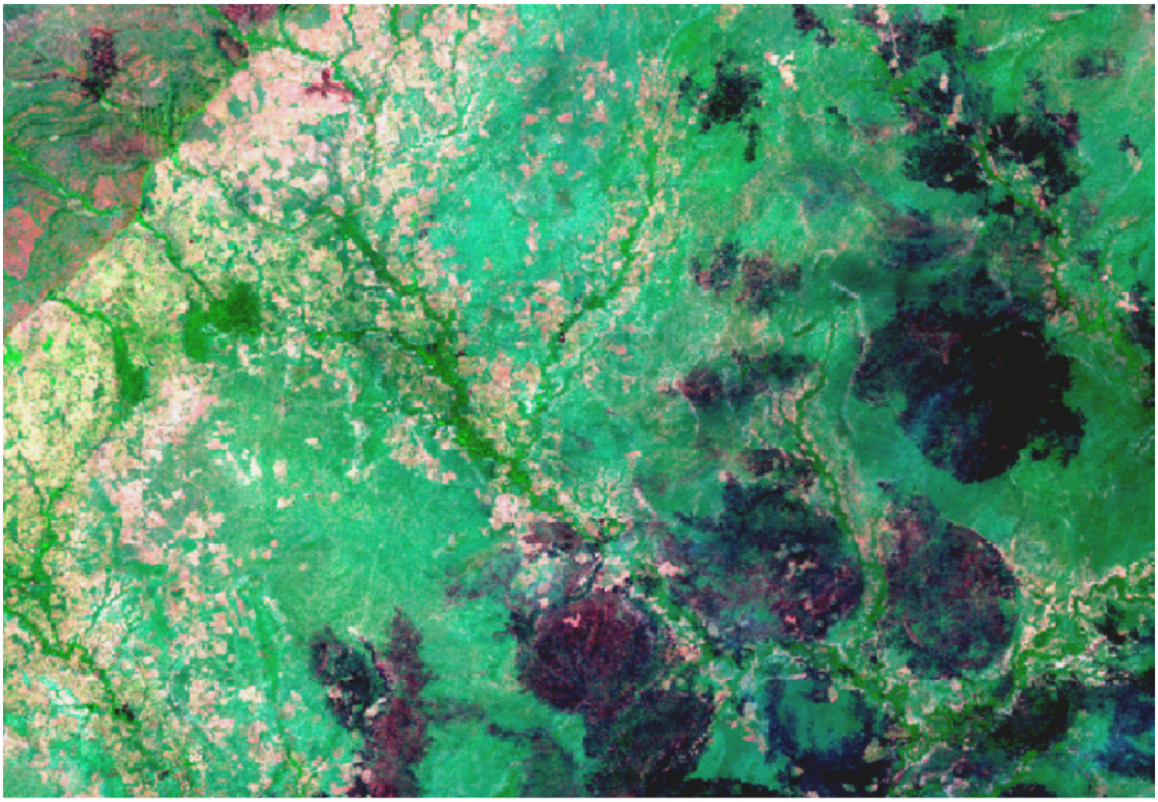
surrounding areas) the WAP complex would reach a SRC equal to $83.0 \pm 6.2\%$.

Fragmentation analysis

In all the five regions analysed we detected an extended loss in savanna vegetation; this is mainly derived from agricultural expansion that consistently increased from 1984 to 2002 for all sampled regions (Table 2). Analysis of spatial indices (1984–2002) revealed that eight out of 11 indicators showed an increase in fragmentation of remnant savanna habitat for *every* subset region (first eight indices columns in Table 2). Number of savanna patches (NP) tends to increase, sometimes drastically (Region 1), while at the same time their mean dimension decreases (PA_MN). As a consequence savanna patches' density is increased (PD). This is especially clear when large homogeneous patches of native vegetation (especially dense wooded savanna) are involved in the conversion into little dense crop fields (Fig. 4) thus the intensity of fragmentation appears more intense at the south of the WAP where this type of vegetation dominates the landscape. At the north of the WAP (e.g. Region 4), vegetation patches are smaller and characterised by open sparse savanna and *brousse*, with bare soil fields often interposed in the vegetation matrix. In this situation where a high degree of heterogeneity is already present in the landscape, changes in fragmentation are less evident, however always present. Degree of dominance of the savanna class in the landscape is always reduced (lower values for LPI). The process of fragmentation has increased the ED of altered habitat patches: ED reveals an increase in overall length of savanna patches' boundaries, following

Table 2. Fragmentation indices value of savanna habitat, calculated for 1984 and 2002 in five selected sample regions within the 30 km peripheral areas of WAP

Sample region (km²)	Year	Savanna habitat (%/tot. region)	Agriculture (%/tot. region)	Fragmentation indices										
				PA_MN (km²)	NP	SHAPE_MN	PD (n/km²)	LPI	ED	LSI	PROX_MN	CONTIG_MN	ENN_MN	PAFRAC
1. Yaoberegou-Kandi, Benin (1675.3)	2002	73.6	25.3	0.396	3108	1.46	1682.31	52.271	56.056	89.018	71447.283	0.353	90.434	1.508
	1984	89.8	9.6	2.367	660	1.35	356.20	69.625	26.110	36.809	177071.390	0.384	86.187	1.444
2. Kourtiagou, Burkina Faso (2559.4)	2002	74.2	25.1	0.431	4373	1.43	1874.42	65.406	98.296	158.678	163334.585	0.360	86.091	1.532
	1984	85.1	14.6	0.926	2304	1.38	987.89	75.574	89.960	136.486	257213.242	0.285	81.100	1.522
3. Mekrou–Banikoara, Benin (2432.3)	2002	67.8	30.9	0.326	4876	1.45	1589.55	38.480	53.981	125.281	76897.351	0.350	92.841	1.495
	1984	89.7	9.8	2.200	990	1.37	323.87	58.956	36.268	71.747	263509.069	0.320	80.461	1.519
4. Zoukwara, Niger (1951.8)	2002	58.3	27.6	0.207	5126	1.53	1844.10	24.649	90.621	193.468	24715.344	0.338	89.564	1.533
	1984	64.1	20.3	0.356	3516	1.48	1264.90	30.535	58.908	115.687	38561.391	0.409	106.534	1.501
5. Pama-Mandouri, Burkina Faso (3281.2)	2002	43.7	34.9	0.090	12,820	1.65	1761.30	4.520	36.900	293.650	12289.600	0.370	90.067	1.592
	1984	57.1	25.1	0.156	9917	1.47	1365.48	14.290	25.610	168.190	49763.840	0.381	100.842	1.509



A

B

Figure 4. The expansion of the "cotton front" is vastly converting and fragmenting savanna habitats around the WAP (vegetation in green, fields in pink, burned areas in black). North of Kourtiagou-Kondio (Burkina Faso) in 1984 (A) and in 2002 (B). Landsat TM/ETM+ data.

human interventions. Also, these change processes produced an increase in complexity of habitat patch shape, as observed by the augmentation of the mean Shape Index (SHAPE_MN), and an increase in disaggregation of patches as observed by an increased LSI. Other fragmentation indices, mean perimeter/area ratio, mean nearest neighbour distance and mean patch fractal dimension showed trends that vary depending on the test region. In some cases the limited number of savanna patches and size due to their gradual disappearing, also influences the simplicity of patches shape and their spatial/distribution properties. This is also reflected in the CONTIG_MN, ENN_MN and PAFRAC indices, which at a first analysis can provide counter-intuitive results.

Discussion

The outcomes of the isolation analysis carried out for the period 1984–2002 require careful interpretation. A certain amount of savanna habitat (14.5% of 1984 extension) has been lost in the peripheral areas of the WAP complex. Land-cover change trajectories showed that this was mainly the consequence of agricultural expansion taking place in the area, with the greatest expansion in the part under the jurisdiction of Benin and Burkina Faso, where the remunerative business of cotton is driving an already fast growing agriculture (Doussa, 2004; Palm, 2005). At the same time no significant proportion of habitat conversion was detected within the national parks of W, Arly and Pendjari, which witnesses the level of effectiveness reached by the conservation and management programmes implemented in the parks (e.g. ECOPAS). African protected areas are not, contrary to what is sometimes said, purely administrative entities but they can really play a key role in supporting habitat conservation policies. Concerning the overall extension of the WAP complex, a limited proportion of native savanna habitat was lost due to the expansion of enclaves within some partial reserves (e.g. Tintangou and Pama). In particular the expansion of the Madjoari area can play an important role in the potential spatial division of the complex.

Apart from the fact that the overall savanna habitat loss corresponds to a large area in absolute terms, concern is generated by the way such loss is distributed in the peripheral area. Certainly the risk to the integrity of the WAP would be lower if erosion of natural habitats, in favour of cultivated fields, occurred uniformly starting from the external border of the buffer zone. However, fragmentation analysis in all areas of investigation reveal that habitat loss has followed a patchy trend and this may have consequences well beyond the effective damage associated to the simple extension of the habitat loss. From 1984 to 2002 the number of habitat patches has increased noticeably in all the five areas that have been monitored; in some cases (Regions 1 and 3) this number more than doubled. Given that any habitat patch could represent, at least in principle, a new front of expansion for further colonisation, patchy erosion has brought converted areas closer to the park border than a colonisation front that uniformly moved from the external border.

Furthermore, the ecological integrity of the protected area strongly depends on the ecological function that its surrounding environment can perform. This can be also detected by using indices of fragmentation. Landscape patterns metrics operate as quantitative links between landscape structure and the ecological or environmental processes taking place. Particular attention should be given to their theoretical understanding and selection. We chose a set of fragmentation indices based on landscape ecology literature and our experience. This set of metrics can hold a certain amount of information redundancy. As univocal consensus does not exist on the choice of individual metrics we preferred to analyse a larger set of indices instead of a parsimonious set in search of more robust conclusions on habitat fragmentation trends.

Given these premises, the results we obtained from fragmentation indices all point to a reduced ecological functionality of the peripheral border. Average size of savanna patches (PA_MN, see Table 2) has decreased all around the peripheral area. Smaller size reduces the potential of patches to host animal species (Farina, 1998), which consequently need to move in search of more suitable habitats. Average distances between patches have increased in three out of five regions (ENN_MN, see Table 2). Also, the index of proximity (PROX_MN, Table 2) has diminished in all five regions. Although not the case in all regions, results demonstrated patches were less connected functionally with one another because mean distances decreased, with the consequence that animal movement is made more difficult by the presence of cultivated fields that may act as barriers. More and more isolated patches, as is the case presented here, may give rise to higher sensitivity to environmental and demographic stochasticity, decrease access to resources, genetic drift of populations and alteration of landscape-level processes necessary for population survival and persistence (Leach & Givnish, 1996; Suarez, Bolger, & Case, 1998).

The ED index increased in all cases, revealing a general increase in the overall length of savanna's patch boundary following human intervention. Increase in edge relative to core areas can have profound effects on ecological processes and biota ('edge effects'), like increased vulnerability to invasion by exotic species or augmented abiotic influences as radiation and wind (Debinski & Holt, 2000; Saunders et al., 1991).

Moreover, these change processes produced an increase in complexity of habitat patch shape, highlighted by augmentation of the mean Shape Index (SHAPE_MN). The degree of complexity of patch shape can have strong influences on ecological processes, e.g. animal space-use behaviour, dispersion dynamics and population structure (Cumming, 2002; Harper, Bollinger, & Barrett, 1994; Major et al., 1999). Increase in LSI shows a disaggregation of savanna patches due to the augmentation of distance between them, provoked by the increased amount of interposed converted land. All these effects potentially produce higher susceptibility to disturbance by environmental and anthropic agents (Lienert & Fischer, 2003).

We believe the combination of isolation analysis and fragmentation analysis presents an overall scenario of concern. Despite the presence of administrative borders inside the WAP a limited extension of native habitat was lost, the type and extension of savanna loss produced in the peripheral areas has reduced significantly the complex's potential capacity to conserve biodiversity. In a fully eroded case of the buffer areas (complete isolation of the complex), the WAP can loose more than a quarter of this capacity. Isolation and fragmentation analysis, read in conjunction, suggest that the relative capacity to preserve biodiversity may be underestimated by the SRC. The chart in Fig. 3 shows that complete isolation, which would lower SRC to some 85% of the present capacity, would occur in more or less 100 years; this type of analysis makes use of an index that is based upon the extension of the reference areas, and does not take into account other important factors such as the way in which the reduction in surface takes place. It follows that the loss of conservation capacity estimated between the reference periods (1984 and 2000) has been potentially underestimated. Also, the calculation of SRC is affected by the uncertainty implicitly present in the species–area approach. However, it does provide a preliminary quantitative indication of the effects of isolation trends on potential capacity of the reserves to conserve biodiversity. The SRC can be a very valuable tool if combined with results obtained from other types of investigation, such as fragmentation analysis.

The present approach more than provides precise quantitative results showing the harmful trend the complex is experiencing and highlights the potential consequences of its isolation. The analyses performed on five different test regions revealed an increasing trend of fragmentation within remnant savanna habitat in the peripheral areas of the WAP. This potentially produces harmful effects, as it isolates inhabiting populations (Stratford & Stouffer, 1999), increases their demographic stochasticity, and alters crucial ecological processes (e.g. dispersal, feeding, reproduction) taking place in the ecological *continuum* between core protected areas of the WAP and the surrounding habitat (Lienert, 2004; Wu, Thurw, & Whisenant, 2000).

The methods involved in this study have some limitations: first of all the extension of savanna vegetation in the peripheral areas can be potentially overestimated by the satellite classification, due to its spectral similarity with fallow fields (*jachères*). This type of ephemeral habitat is not ecologically suitable for many species living within the WAP: the overall loss of savanna extension thus can be potentially underestimated. Moreover, the SRC approach does not consider other factors that are currently contributing to threaten the conservation capacity of the WAP, like poaching, illegal foraging and the unclear ecological effects of fires on parks ecosystems (Fournier, Sawadogo, & Gregoire, 2003).

Extension of valuable habitat and its degree of fragmentation are fundamental indicators of biodiversity conservation (Balmford et al., 2005). The isolation and fragmentation trends documented in this study for the WAP complex illustrate the need for a better understanding of the relationships between protected areas and the surrounding habitat, finalised to increase the performance of conservation programmes. Hence, we stress the fundamental importance to understand sink–source dynamics taking place in protected areas within more extended regional settings, and the need to conciliate the inevitable conversion of peripheral native habitat with the preservation of landscape ecologically important elements (e.g. spatial connectivity or ED). From a management point of view, our results show that interventions should be currently concentrated on the peripheral areas of the WAP, and more particularly in the Benin portion. The presented approach appears to be an effective tool for prioritisation of activities in the geographical context.

Protected areas are not entities confined in their administrative limits; they depend upon, and interact with the surrounding habitat, influencing their fundamental ecological flows and capacity to conserve biodiversity (Chape, Harrison, Spalding, & Lysenko, 2005). As economic development is considered an essential condition for conservation projects in Africa (Kramer, van Schaik, & Johnson, 1997), it is of crucial importance to integrate protection with compensating mechanisms that promote the value of the ecosystems surrounding the parks, such as benefit sharing from tourism activities, local community-based wildlife management and sustainable agriculture. Developing systems of sustainable use and appropriate compensation could in fact achieve conservation goals while respecting the aspirations of the associated population. Local human welfare is in fact one of the most important elements to be taken into account when directing protected areas into effective conservation strategies (Wells & Brandon, 1992).

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