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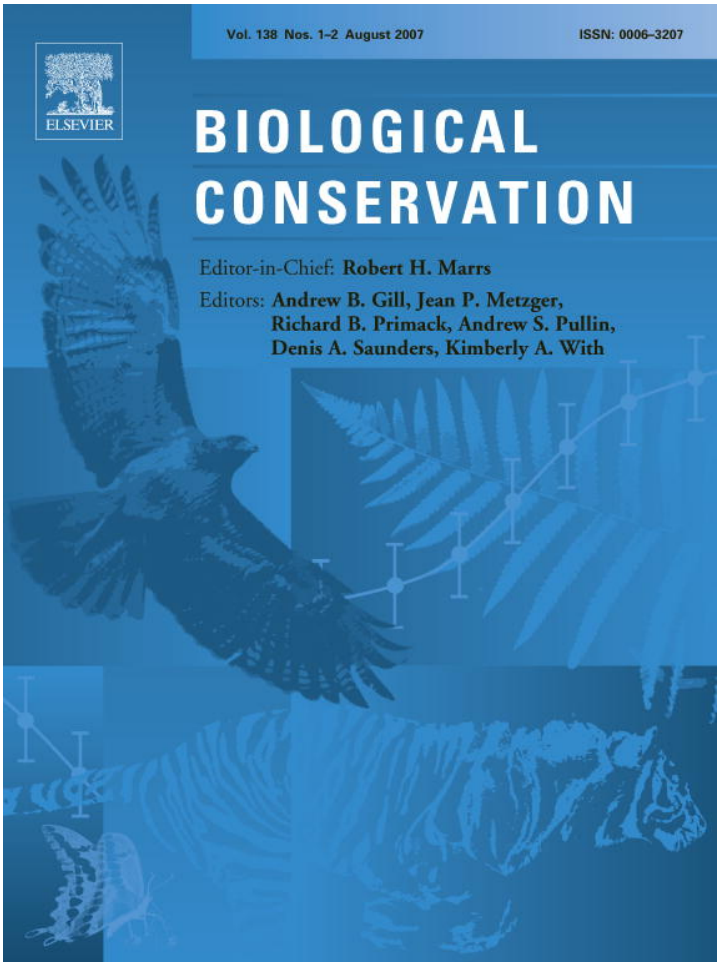

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Identification of ecological indicators for monitoring ecosystem health in the trans-boundary W Regional park: A pilot study

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ABSTRACT

The sustainable management of the W Regional park and its peripheral areas is based on a trade-off between conservation and the generation of economic income for local populations. This work is a pilot study for the identification of ecological indicators to monitor ecosystem health in Sudanian Savannah ecosystems. Ecological indicators are needed to warrant the efficiency of the protection measures, particularly in the mosaic landscapes of the peripheral areas. Two insect families (Coleoptera: Scarabaeidae (Cetoniinae) and Lepidoptera: Nymphalidae) were trapped along transects crossing landuse units submitted to various human pressures (none, hunting, traditional and intensive crops, grazing) in two countries (Burkina Faso and Bénin). Plant species richness was found to be correlated with the abundance of four fruit-feeding insect species and with the fruit-feeding butterflies species richness, but not with the Cetoniinae species richness. The abundance of Nymphalidae species generally dropped with human activities, but that of Cetoniinae species followed the intermediate disturbance theory. The likely impact of the various management practises on the general ecosystem health is discussed, as is the potential value of fruit-feeding insects as bioindicators and the points that still need to be clarified.

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1. Introduction

The W Regional park (Bénin, Burkina Faso and Niger) was recently classified as the first trans-boundary biosphere reserve in Africa by the UNESCO-MAB (November 2002). Thanks to the involvement of the neighbouring populations in the management and the exploitation of the peripheral areas surrounding the protected one, it is becoming a model of sustainable conservation for West-African Savannah ecosystems. To be sustainable, the conservation policies must

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reconcile the conservation of the diversity with the generation of income for local populations of the peripheral areas (buffer areas, transition areas). Monitoring of the health of ecosystems appeared to be of critical importance while evaluating the various technical strategies involved in the project. To achieve this aim, the identification of ecological indicators, sensitive to slight ecosystem changes in a predictive manner, thus allowing the detection and measurement of the effect of various human pressures and activities, was of high priority. These indicators should fulfil two main attributes:

- be a tool to select the best management strategies to maintain the maximal biodiversity given the space available,
- be demonstrative for the local populations and environmental services, so that they can use it themselves and be encouraged to apply the conservation measures.

Our selection scheme (presented in Section 2) led to the choice of two fruit-feeding insect groups and to test the relation between their apparent densities at a species level, and the various landuse units encountered in the park periphery. Insects represent half of the global diversity and are influenced by many ecologic factors, like micro-climate, geology or vegetation structure (Ramos, 2000). Their relation to the ecosystem attributes are not still fully understood. Both bait-attracted insect families are taxonomically well-known and ecologically highly diversified (Allard, 1991; Sakay and Nagai, 1998; Larsen, 2006). Bait-attracted butterflies are well studied, as attested by the many references available and their recent classification in well-defined categories of habitat and distribution by Larsen (2006). Bait-attracted Cetoniinae are not as well studied, but we are preparing a similar classification than Larsen for this group (only the species of West-African Savannah areas), thanks to other trials in various localities in Burkina Faso, Niger and Bénin (Legrand et al., 2006).

The relations between ecosystem disturbance and insects in general (Holloway et al., 1992; Eggleton et al., 1995; Brown, 1997; Hamer et al., 1997), fruit-feeding butterflies in particular, have been investigated in tropical forests (Kremen, 1992; Beck and Schulze, 2000; Fermon et al., 2000; Ramos, 2000; Bobo et al., 2006). Fruit-feeding butterflies revealed themselves sensitive to disturbance and allowed an evaluation of the ecological impact of various conservation strategies (thinning, agroforestry, crops). However, the impact of disturbance on species richness is ambiguous, a slight disturbance or a border effect being able to increase local biodiversity (Lovejoy et al., 1986; Brown, 1997; Wood and Gillman, 1998), thus jeopardising the use of this parameter as a bioindicator. Authors generally agree that the use of species level parameters in well known environments is much more precise, provided that the sampling method can be standardised. This is particularly easy in the case of fruit-feeding insects that can be attracted to banana traps. All these studies were achieved in forest ecosystems and no data concerning the relation between disturbance and fruit-feeding butterflies or beetles densities is available in Savannah ecosystems. We chose to study both families together because their ecological roles and trophic levels of their larval stages (phytopageous and saprophytic) are completely different, thus ensuring a better indication of the global ecosystem health.

2. Materials and methods

2.1. *Selection of indicator taxa*

The selection of our indicator taxa is based on three reviews presenting the general properties of bio-indicator taxa and step-wise decision-making frameworks for the selection of indicator taxa (Noss, 1999; Hilty and Merenlender, 2000; Dale and Beyeler, 2001).

Authors generally agree that the first step is "to decide what ecosystem attribute indicator taxa should reflect" (Hilty and Merenlender, 2000). The activities considered as creating an income for local populations in the peripheral areas of the W Regional park are hunting, gathering, cropping and cattle grazing. Various crops have been developed, ranging from traditional crops (millet, sorghum, corn) to commercial crops using a lot of pesticides (especially cotton). The aim of this study was to compare the impact of various human activities on ecosystem health. The property of the environment to be monitored is thus its general health under various human pressures.

The second step was to "list all species in the area that best satisfy the baseline information criteria" (Hilty and Merenlender, 2000). Good information was already available about vertebrate taxa represented in the W Regional park (Lamarque, 2004), as opposed to most invertebrate taxa. During 3 years, 20 higher level insect taxa have been listed including Cerambycidae, Cetoniinae, Cicindelidae, Scarabaeidae, Reduviidae, Ascalaphidae, Myrmeleontidae, Papilionoidea, Hesperiidae, Saturniidae, Sphingidae, Lasiocampidae, Glossinidae, Tabanidae and Stomoxinae. These inventories are still being continued for some families and are about to be published for others. A new species of Sphingidae, a new species of Saturniidae, two species of Cerambycidae and four new species of Scarabeideae Ontophagini have already been described (Adlbauer and Sudre, 2003; Haxaire and Bompar, 2003; Adlbauer, 2004; Rougerie and Bouyer, 2005; Josso and Prévost, 2006). New species of Reduviidae and at least two other Cerambycidae species are to be described (J.M. Berenger and J. Sudre, com. pers.).

The third step was to "retain species that best meet the suggested niche and life history criteria" (Hilty and Merenlender, 2000). Because of their high mobility, most vertebrate species present in the W Regional park are not appropriate, nor are many invertebrate families (Sphingidae, Lasiocampidae, etc.). Despite the capacity to fly, less mobile invertebrates like butterflies were not removed at this stage since other studies revealed significant variations in their abundance according to degree of disturbance, even over short distances (Fermon et al., 2000; Ramos, 2000). The criterion "to be easily measured" further limited the list, leaving no taxa but the Glossinidae, Tabanidae, Stomoxinae, Cetoniinae and some Nymphalidae, especially the genus *Charaxes*. Actually, the authors understood the word "easy" as comprising a trapping technique that can easily be replicated. All active measures of density are too dependent of the operator to be standardized,

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although butterfly transect walks might be used for relatively unbiased sampling. On the contrary, species that can be trapped are very attractive.

The fourth step was to "remove species that may respond to changes occurring outside the system of interest" (Hilty and Merenlender, 2000). It was difficult to judge what family should be eliminated at this stage: is there a single species not affected by global warming on earth? However, the regional distribution of most of the species listed in the families referred to above indicated that some of them should not be more susceptible to general changes than the ecosystem they should represent, i.e. the Savannah woodland of the Sudanian zone.

The fifth criterion was to "use only those species that can be easily detected and monitored with available funds" (Hilty and Merenlender, 2000). Only two families, the Cetoniinae and the Nymphalidae, whose trapping cost were low, met this criterion.

The last criterion was to "select a set of complementary indicator taxa from different taxonomic groups so that all selection criteria are met by more than one taxon" (Hilty and Merenlender, 2000). This last criterion supposes a full understanding of the relations between the sampled taxa and the ecosystem attributes, which is beyond our data set: the present paper is only a pilot study trying to evaluate the potential of two fruit-feeding families to be used as indicators. However, the evaluation of the selected set of indicators was achieved using Brown's criteria (1991) thanks to our results and the data available in the literature.

2.2. *Research site*

The W Regional park is located in a woodland Savannah area with annual rainfall between 600 and 900 mm. The eco-climatic area ranges from Sahelian in the North to Sudanian in the South. Two transects of about 30 km were implemented between peripheral and protected areas, the first in Burkina-Faso next to the village of Tapoa-Djerma, henceforth called the northern transect, and the second in Bénin, next to the village of Sampeto, called the southern transect (Fig. 1).

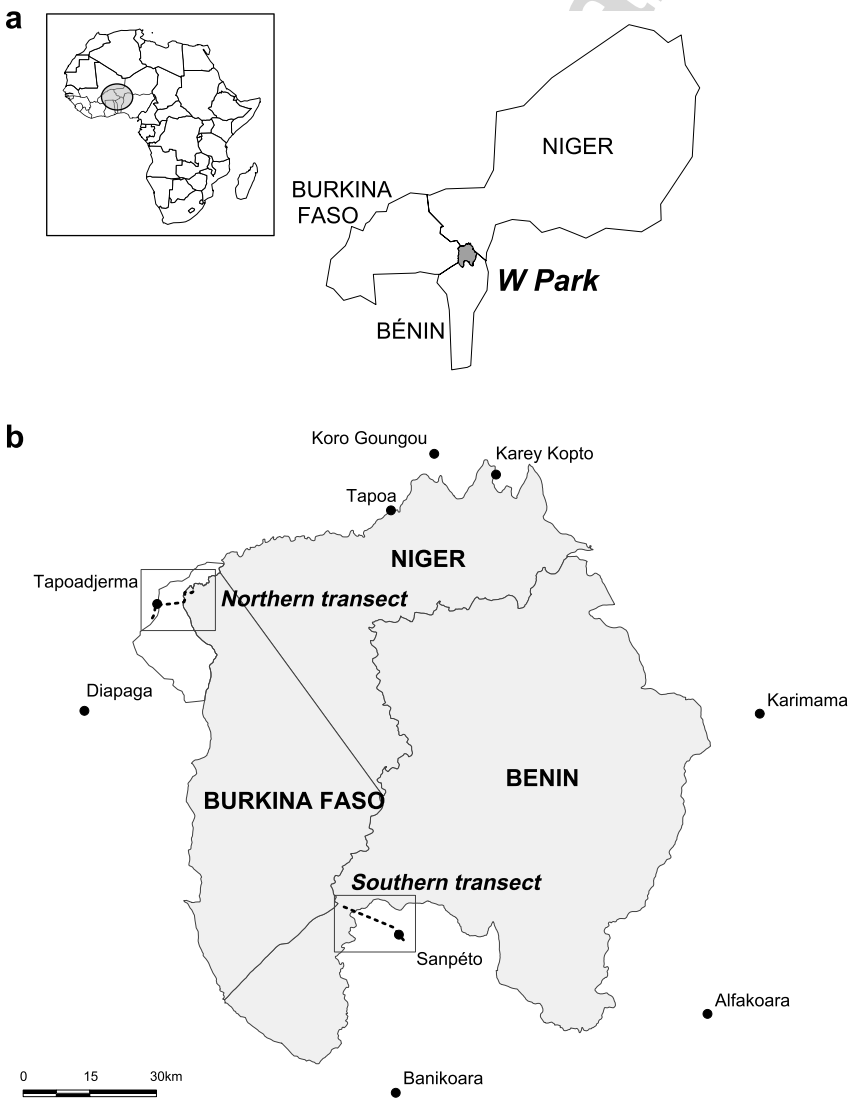

Fig. 1 – (a) Location of the transboundary W Regional Park between Bénin, Burkina Faso and Niger and (b) location of the northern and southern transects (in boxes) in Burkina Faso and Bénin, respectively. Protected areas are indicated in grey and the hunting area of Tapoa Djerma in white. The boundaries within the greyish area are the country borders.

Trapping sites were located along tracks and traps were separated by about 500 m. We chose these transects to represent the two extreme parts of the park but their definitive locations were determined by the presence of suitable tracks. Actually, it is impossible to walk through the park without a track during the rainy season, the best sampling period for insects in Savannah ecosystems. The natural vegetation can be related to woodland and Savannah woodland of the Sudanian climatic zone in the southern transect, to Savannah woodland in the northern one (Aubreville, 1950, 1957).

The southern transect, located in Bénin (Fig. 1), crossed seven land-use classes from West to East:

- the W Regional park (traps 1–6),
- a buffer area with no authorized activity (traps 7–10),
- an area where moderate cattle grazing is authorized, with a fixed-price contract of 1 Euro per animal per year,
- a traditional cropping area (traps 13–19), opened recently (<10 years) to biological crops with few insecticides (corn, sorghum, millet) covering less than 25% of the surface; grazing also occurs in this area,
- an area where cotton crops were recently authorized (<10 years), covering less than 50% of the surface (traps 20–25),
- recent fallow areas (traps 26, 27 and 32),
- an area where cotton has been intensively grown for a long time: more than 75% of the surface is cultivated (traps 28–31 and 33–34).

The northern transect, located in Burkina Faso (Fig. 1) crossed four land-use classes from West to East:

- old fallow areas (traps 1–5 and 10),
- a traditional cropping area around the village of Tapoa-Djerma (traps 6–9 and 11–13), cultivated since a very long time but where only biological crops with few insecticides (corn, sorghum, soja) are authorized; more than 75% of the surface is cultivated,
- a hunting area (traps 14–22),
- the W Regional park (traps 23–30).

2.3. *Sampling*

At each trapping site, a phyto-sociological census was carried out, including both ligneous and herbaceous species and using a standard cover grid (cover classes were <5%, 5–25%, >25%).

Two standardized traps (one for *Charaxes* and one for Cetoniinae) were set in all trapping sites. The location of each trapping site was recorded using a Global Positioning System (GPS). Thirty and thirty-four locations were trapped along the northern and southern transects, respectively. They were monitored between the 11 and 22 October 2004 and the 14 and 23 October 2004, respectively. Traps were emptied between 12.00 h and 14.00 h, alternatively in one direction and then the other (from 1 to 30 and then 30 to 1) every second day. Insects were recorded by species and by trap (apparent density per trap and per day or ADT) and released after diagnosis. Only few doubtful insects were stored for subsequent identification by taxonomists. Daily densities in a trap were thus considered as successive measurements of the apparent density of the trapping site.

The trap used for Cetoniinae was a plastic water bottle of 1.5 l, into which two windows of about 8×5 cm were made in the upper part. It was free of charge. The trap used for Nymphalidae was constituted by a cylindrical net (60 cm high and 30 cm of diameter) placed 3 cm over a square plank (35 cm sides). It is a classical trap often used in fruit-feeding butterflies surveys (Fermon et al., 2000). The cost is about 7.5 Euros per trap. In both trapping methods, the bait was decomposed bananas mixed with sugar and exposed to the sun in a closed container for 4 days before being used. Insects, attracted by decomposed fruits, could enter the trap but rarely exit. To trap 30 locations, about 25 kg of bananas were needed, corresponding to a cost of 12–19 Euros. Every 3 days, about 12 kg of bananas were added to the traps in each transect.

2.4. *Statistical analyses*

The statistical units to be compared were the land-use classes described above. The spatial patterns of species were analyzed only when their ADT was higher than 1 in at least one trap location. For each insect species and land-use class, the normality of the distribution of apparent densities was tested using Kolmogorov–Smirnov test (Conover, 1971). Since the distributions of apparent densities were not normal, they were compared in all landuse units with the Kruskal–Wallis rank sum test (Hollander and Wolfe, 1973), then by pairs using using the Steeltype non-parametric multiple comparisons test (npmc package) (Munzel and Hothorn, 2001) (results presented in Appendix). The correlation between variables was investigated at the trapping site level using Kendall's rank correlation tau (Hollander and Wolfe, 1973). The autocorrelation of insect densities between traps was investigated using Morand I test, applied on neighboring matrix, generated with 1 km distance, from 0 to 6 km. Six matrices of neighbours (traps) were thus analyzed for each species in each site, as previously described in detail in the analysis of tsetse fly distribution (Bouyer et al., 2006). All the statistical analyses were computed with R statistical software (Ihaka and Gentleman, 1996).

3. Results

3.1. *Vegetational transition*

In the southern transect, the vegetation has been regularly burned for a very long time. The characteristic and dominant tree is *Isoberlinia doka* Craib & Stapf, which gives the aspect of natural woodland to this vegetation, corresponding to a fire-climax, especially from trapping sites 1–6 (Table 1). The herbaceous stratum is dominated by grasses, principally *Schizachyrium sanguineum* (Retz.) Alston and *Diheteropogon amplectens* (Nees.) Clayton. Under anthropogenic pressure, the vegetational formation is disturbed and becomes Savannah woodland and tree Savannah. *I. doka* disappear and the dominant tree is *Daniellia oliveri* (Rolfe) Hutch. & Dalz. (Table 1, sites 7–13). The herbaceous layer is occupied by *Andropogon chinensis* (Nees) Merr. and *Andropogon gayanus* Kunth, the last species being found until fallows and disturbed Savannahs.

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Table 1 – Distribution of vegetational indicator species and mean apparent densities by trap and by day (standard deviation in brackets) of the selected insect indicator taxa in the landscapes of the southern transect, W Regional Park, Bénin

Trap number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	32	29	30	31	33	34
Vegetal species	Park						Buffer				Gathering		Traditional crops							Recent Cotton crops						Fallow			Old cotton crops				
Vitellaria paradoxa	1	1	1	1	1	1	1		1	1	1		1	1					1		1						1	1			1	1	1
*Terminalia laxiflora***	2						1																1			1			1				
Andropogon gayanus	3	3	3	3	3	3	2	3	3	3	3	3	2	2	1	1	1	1			2	1		2									
Daniellia oliveri	2		1	1	1	1		1	1	1	1				1					1			1		1								
*Combretum glutinosum***		2	2	2										2		1										1							
Diospyros mespiliformis	2	1	1	1	1					1																							
Schizachyrium sanguineum	2	2	2	2	2	2																											
*Isoberlinia doka**	2	2	1	1	2	2		2																									
Diheteropogon amplectens	2	2	2	2	2	2	2	2	2																								
Andropogon chinensis	2	3	2	2	2	2	2	2	2	3		2	3								1												
*Combretum collinum***					2			2	2	2				2	1	1	2	2								1		1		1	1		
*Piliostigma thonningii**								2	2									2		2	2	2	2	2			2	1		1			
*Afzelia africana**					1												1		1	1	1	1											
Andropogon pseudapricus														2	3	1	3	3			1	1	1	2								
Loudetia togoensis														2		2	3	2	2							2	2						
*Combretum micranthum***																		2															
Flueggea virosa																		1		1	1		1	1				1		1			
Pennisetum pedicellatum																2			2	3	2	1	2	2	2	1	2	1	1	2	1	1	1
Setaria pumila																												1	1	1	1	1	1
Insect species	Park						Buffer				Gathering		Traditional crops							Recent Cotton crops						Fallow			Old cotton crops				
***P. marginata* complex**	0.55 (1.03)						2.80 (2.85)				1.85 (1.69)		3.14 (4.21)							0.17 (0.62)						0.63 (1.07)			0.20 (0.48)				
***P. cordata* complex**	0.98 (1.55)						2.33 (2.91)				2.75 (2.20)		1.96 (2.44)							0.08 (0.33)						0.40 (0.72)			0.20 (0.58)				
C. epijasius	3.18 (3.92)						3.77 (3.35)				2.65 (2.96)		2.49 (2.65)							0.58 (1.08)						1.37 (2.04)			0.38 (0.72)				
H. daedalus	12.08 (12.37)						8.5 (7.38)				5.35 (3.51)		3.64 (4.50)							0.85 (0.99)						2.47 (2.47)			0.55 (0.93)				

The food plants of *C. epijasius* are marked with * and those of *H. daedalus* with **. The cells are merged to highlight homogeneous phytosociological associations.

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When the trees are destroyed by cropping activities, a shrub Savannah occurs (Table 1, trapping sites 14–32), where the density of bushes increases through the effect of cattle grazing – for example *Flueggea virosa* (Roxb. ex Willd.) Voigt. or *Piliostigma thonningii* (Schum.) Milne-Redh. The herbaceous layer is composed of fallows-species (*Andropogon pseudapricus* Stapf, *Pennisetum pedicellatum* Trin.) and weeds (*Setaria pumila* (Poir.) Roem. & Schult) in sites 28–34 (Table 1).

In the northern zone, *I. doka* woodland is missing and characteristic species of disturbed Savannahs are abundant even in the most protected parts (*A. pseudapricus* Stapf., *Loudetia togoensis* (Pilger) C.E. Hubbard), corresponding to a drier climate and sandy soils. The most natural part is composed of Savannah woodland characterized by *Afzelia africana* Sm. ex Pers. and *A. chinensis* (Nees) Merr. (Table 2, sites 14–29). These Savannahs are included in the *Combretum glutinosum* Perr. ex DC. Savannah woodland. Two sites dominated by *Mitragyna inermis* (Willd.) O.Ktze (Table 2, sites 23 and 30) indicate swampy vegetation of river-side forest. Protected and hunting areas hardly differ. Two species appear in the last zone: the shrub of disturbed areas, *Guiera senegalensis* J.F.Gmel and the grass of young fallows, *P. pedicellatum* Trin. *A. chinensis* (Nees) Merr. becomes rare in fallows, while *A. gayanus* Kunth and the well grazed tree *Pterocarpus erinaceus* Poir. disappears from the village and cropping areas.

3.2. Entomological results

3.2.1. Nymphalidae

Seven species of Charaxes were captured in the southern transect (*C. epijasius* Reiche, *C. varanes vologeses* Mabille, *C. achaemenes atlantica* van Someren, *C. viola viola* Butler, *C. boueti boueti* Feisthamel, *C. brutus* Cramer, *C. candiope candiope* Godart), whereas only the first four species were captured in the northern one. Of these species *C. epijasius* was the most abundant, but another Nymphalidae, *Hamanumida daedalus* Fabricius, was even more abundant in both sites and was thus considered for further analysis. In the southern transect, *C. brutus* and *C. candiope* were found only in the protected habitats (Park and Buffer) but only two and one specimen respectively were caught. In the northern transect, the four species were found in every habitat.

In the southern transect, the densities of *C. epijasius* did not differ significantly between traditionally cropped and/or gathering areas and the protected areas (Fig. 2). They significantly dropped in the cotton areas with no difference between old or recent activity. The fallow allowed some recovery (almost significant). The density of *H. daedalus* was significantly higher in the protected than in all cultivated areas but the differences with slightly disturbed areas (gathering and buffer units) were not significant. It dropped significantly between recent traditional crops and recent cotton crops but was similar in old and recent cotton crops. *C. viola* had a very similar distribution pattern, with less significant results.

In the northern transect, *C. epijasius* was found in high and similar densities in the protected and the hunting areas (Fig. 2). These densities were significantly lower in the fallow area and also significantly lower in the cultivated area than in the latter. The transitions between areas were sharp. *H. daedalus* behaved similarly to *C. epijasius* except that there was no significant recovery in the fallow areas, as in *C. viola*.

In the southern transect, three larval host species were recorded for *C. epijasius* (*I. doka*, *P. thonningii*, *A. africana*). The last two species were also recorded in the northern one. There was no good match between presence of host species and abundance of *C. epijasius* in the southern transect (data not shown) but the correlation was good in the northern one. Four larval host species of *H. daedalus* (*Terminalia laxiflora* Engl., *Combretum collinum* Fres., *C. glutinosum* and *C. micranthum* G. Don) were found in the southern transect. The two latter and *C. molle* R. Br. Ex G. Don were found in the northern one. In both places, *Combretum* spp. were found almost all along the transects, without apparent correlation with the butterfly abundance.

The comparison between the protected areas of the two transects revealed similar densities for *C. epijasius* but significantly higher densities for *H. daedalus* in the natural southern part of the W Regional park (Tables 1 and 2).

The autocorrelation tests revealed that mean densities of *C. epijasius* and *H. daedalus* were spatially correlated (Morand I test, $p < 0.05$) up to 4 km in the northern transect, up to 5 km in the southern one.

3.3. Scarabaeidae, Cetoniinae

Sixteen species of Cetoniinae were caught in the southern transect: *Pachnoda marginata fernandezi* Rigout, *Pachnoda vuilleti* Bourgoin, *Pachnoda concolor* Schürhoff, *Pachnoda cordata tigris* (Herbst), *Pachnoda tridentata* (Olivier), *Pachnoda berliozi* Rigout, *Chondrorrhina abbreviata* (Fabricius), *Diplognatha gagates* (Bainbrige), *Charadronota quadrisignata* (Gory et Percheron), *Tephrea pulverulenta* (Gory et Percheron), *Gametöides sanguinolenta* (Olivier), *Phonotaenia aequinoctalis* (Olivier), *Oxythyrea (Stichothyrea) guttifera* (Afzelius), *Rhabdotis sobrina* (Gory et Percheron), *Uloptera* sp., *Polystalactica stellata* (Harold), of which six were also captured in the northern one (*P. marginata*, *P. vuilleti*, *P. concolor*, *P. cordata*, *D. gagates*, *G. sanguinolenta*).

P. marginata, *P. vuilleti* and *P. concolor* form a complex of almost identical species (non-toxic), very difficult to discriminate for non-specialists, as do *P. cordata*, *P. tridentata* and *P. berliozi*. Due to identification difficulties in the field, the two complexes, called *P. marginata*- and *P. cordata*-complexes respectively, were analyzed as two distinct species-groups in both sites. This was possible thanks to very similar distribution patterns of the *P. marginata* complex species (paired Fisher test, $p > 0.05$), and to the very low abundance of *P. tridentata* and *P. berliozi* in the southern transect (they were absent from the northern one).

In the southern transect, the highest biodiversity was observed in the traditional cropping area (13 species), followed by the grazed and buffer areas (10 species). The protected, fallow and old cotton cropping areas harbored the same number of species (9) whereas the recent cotton cropping area harbored only seven species. *P. tridentata*, *P. berliozi*, and *T. pulverulenta* were found only in the traditional cropping area. *Polystalactica* sp. was found only in the grazed area. *C. quadrisignata* was found only in the old cotton cropping area. However, these species were all captured in small numbers (<5). *P. marginata*, *P. vuilleti*, *P. concolor*, *P. cordata*, *D. gagates*, *P. sangu-*

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Table 2 – Distribution of vegetational indicator species and mean apparent densities by trap and by day (s.d. in brackets) of the selected insect indicator taxa in the landscapes of the northern transect, W Regional park, Burkina Faso

Trap number	1	2	3	4	5	10	7	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Vegetal species	Fallow						Traditional crops						Hunting area									Park							
Andropogon pseudapricus	2	1	2	3	3	3	3	3			3	3	2		3	3	3	1			3	1	2		1	3	3	3	1
*Combretum micranthum***	1			3	3	3	3				3		2	1					3	3	3		3	3	2	3	3	3	3
Loudetia togoensis			2	2	3		3	3		3	3	3		2	3	3			1		1		3	1	1	3	3	3	
*Combretum molle***	2			1						2		3	1	1	2	2	1	1	3	1	1		1		1	1	1	1	
*Piliostigma thonningii**	1						2	3					2	3	3	3		3	3	1	1	2	3	3	3	3	3		
*Combretum glutinosum***													1	1	3	2	3	3			1				1	1	1	1	1
*Afzelia africana**													3	3			3	3	3	3	3	2	3	2	3	3	2	3	3
Andropogon chinensis	1				1								3	3			3	3	2	3		3	3		3	3	1	1	1
Daniellia oliveri						1					1								1			1	1				1		1
Andropogon gayanus	1			1	1	1							3	3	2		2	3	3	3	3	3	2		3	1	1	1	3
Pterocarpus erinaceus	2	1	3		1								2	2	2	2	2	2	3	2		2	3	1	2	2	2	3	2
Balanites aegyptiaca	1	2												1	1	1			1	1	1			1		1	1	1	1
Spermacoce stachydea			1			2																							
Guiera senegalensis	2	2	2	2	2	2	2			2	2	2		2		1	1		1	1								1	
Pennisetum pedicellatum			3	3		2	3	3		2	3	3		1			1									2	2	
Insect species	Fallow						Traditional crops						Hunting area									Park							
***P. marginata* complex**	0.12 (0.33)						0.04 (0.19)						1.11 (1.20)									1.11 (0.99)							
***P. cordata* complex**	0.05 (0.37)						0.02 (0.22)						0.82 (1.25)									1.25 (2.18)							
C. epijasius	0.87 (0.99)						0.28 (0.55)						3.18 (2.20)									3.37 (2.39)							
H. daedalus	1.44 (1.47)						1.01 (1.24)						4.22 (2.83)									5.47 (3.88)							

The food plants of *C. epijasius* are marked with * and those of *H. daedalus* with **. The cells are merged to highlight homogeneous phytosociological associations.

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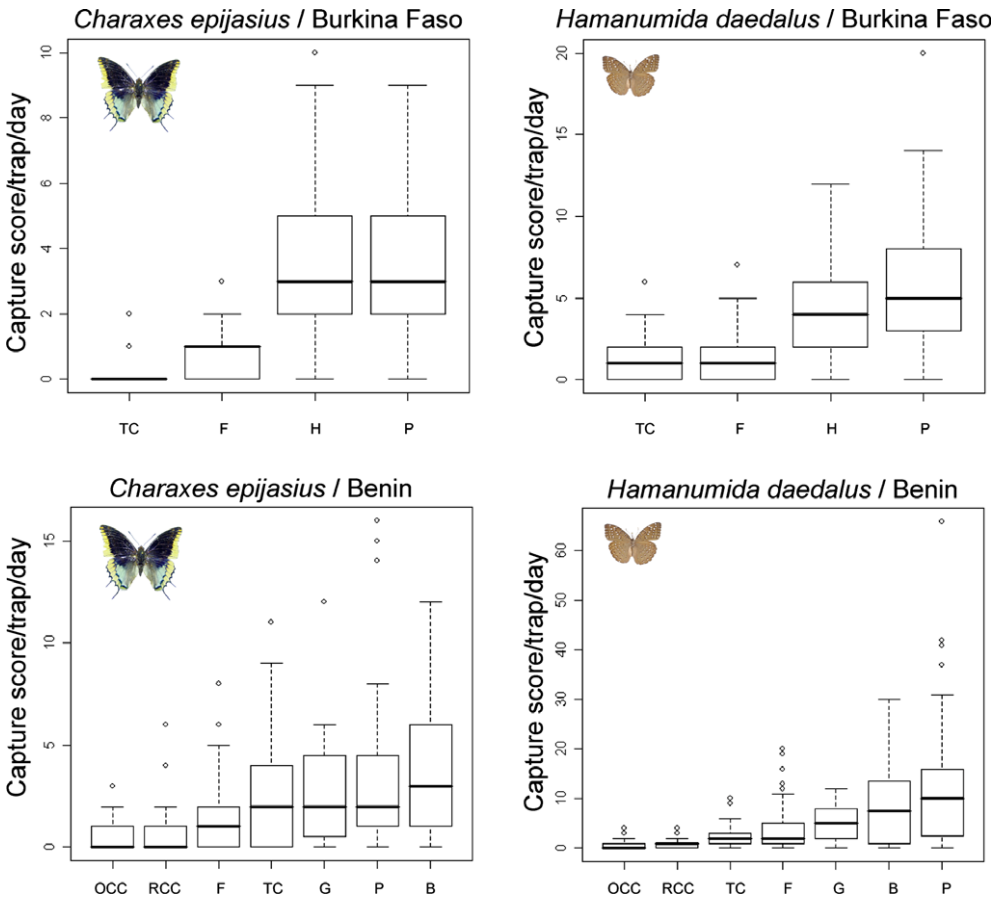

Fig. 2 – Mean apparent densities by trap and by day of *Charaxes epijasius* and *Hamanumida daedalus* in the landuse units of the northern (Burkina Faso) and southern (Bénin) transects, W Regional park. (TC, traditional crops, OCC, old cotton crops, RCC, recent cotton crops, F, fallow, G, gathering, B, Buffer, H, hunting area and P, Park).

inolenta and *C. abbreviata* were found in all habitats. The maximal ADT of the *P. marginata*- and *P. cordata*-complexes was observed in lightly exploited areas, particularly traditional cropping and gathered areas respectively, with significantly higher densities than in the protected areas (Table 1 and Fig. 3) and than in the cotton cropping areas. Some resilience was observed in the fallows, significant only in the *P. cordata*-complex. No significant difference was observed between old and recent cotton crops. *C. abbreviata* and *P. sanguinolenta* had very similar distribution patterns but with less significant differences, because of lower densities.

In the northern transect, all six species were captured in all habitats except *P. sanguinolenta*, which was absent from the cropping areas. The mean ADT of the *P. marginata*- and *P. cordata*-complexes was not significantly different between the protected and hunting areas (Table 2, Fig. 3). They were significantly higher in these areas than in the fallow and traditional cropping areas. The densities of both complexes were slightly higher in the fallow area than in the cultivated one, but the difference was not significant. *C. abbreviata* and *P. sanguinolenta* had very similar distribution patterns.

The comparison of the protected areas in the two transects revealed that both *P. marginata*- ($p < 0{,}001$) and *P. cordata*-complexes (not significant) were more abundant in the northern one. However, their densities became significantly higher in slightly exploited areas of the southern transect than in the northern part of the W Regional park ($p < 0.05$).

The autocorrelation tests revealed that mean densities of *P. marginata*- and *P. cordata*-complexes were correlated (Morand test, $p < 0.05$) up to 3 km in the northern transect, up to 3 and 4 km, respectively in the southern one.

3.4. *Correlation between plants and insects*

Species richness of ligneous plants was significantly correlated with that of the *Charaxes* genus ($\tau = 0.48$, $z = 5.0116$, $P = 5.399\,e{-}07$) but not to that of the Cetoniinae sub-family. The two latter were not correlated. Species richness of the *Charaxes* genus was correlated with both *C. epijasius* ($\tau = 0.33$, $z = 3.5526$, $P = 0.0003814$) and *H. daedalus* ($\tau = 0.31$, $z = 3.2722$, $P = 0.001067$) apparent densities, which were in turn good indicators of plant species richness (*C. epijasius*: $\tau = 0.42$, $z = 4.7102$, $P = 2.475e{-}06$; *H. daedalus*: $\tau = 0.42$, $z = 4.9011$, $P = 9.53e{-}07$). Species richness of the Cetoniinae was strongly correlated with the apparent densities of both the *P. marginata*- ($\tau = 0.39$, $z = 4.1908$, $P = 2.779e{-}05$) and *P. cordata*- ($\tau = 0.45$, $z = 4.8553$, $P = 1.202e{-}06$) complexes. Interestingly, the apparent densities of theses complexes were also associated with plant species richness (*P. marginata*: $\tau = 0.25$, $z = 2.8003$, $P = 0.005106$; *P. cordata*: $\tau = 0.25$, $z = 2.7271$, $P = 0.006389$).

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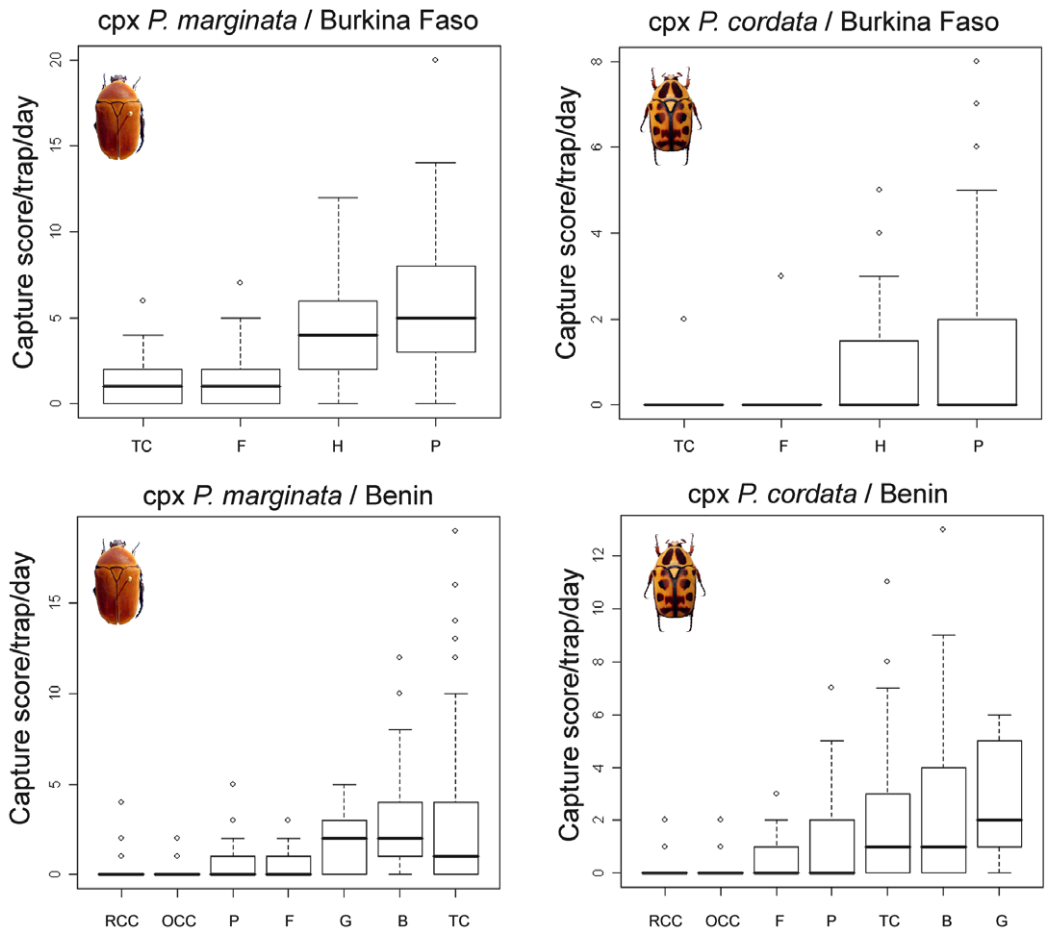

Fig. 3 – Mean apparent densities by trap and by day of *Pachnoda marginata*- and *P. cordata*-complexes in the landuse units of the northern (Burkina Faso) and southern (Bénin) transects, W Regional park. (TC, traditional crops, OCC, old cotton crops, RCC, recent cotton crops, F, fallow, G, gathering, B, Buffer, H, hunting area and P, Park).

3.5. *Evaluation of the indicator groups*

The two bait-attracted groups were evaluated thanks to Brown's evaluation criteria (1991) (Table 3). They both reached a score of 19 (maximum score = 24), which is among the best scores among insect groups, and even a score of 23 if the two groups were evaluated together, like in the present study (we then considered the best score between the

Table 3 – Evaluation of the two groups of insects according to Brown's criteria (Brown, 1991)

Desirable quality for an indicator group in ecology and biogeography	Bait-attracted Nyumphalinae (Lepidoptera: Nymphalidae)	Bait-attracted Cetoniinae (Coleoptera: Scarabeidae)
Taxonomically and ecologically highly diversified	++	++
Species have high ecological fidelity	+	+
Relatively sedentary	+	++
Species narrowly endemic, or if widespread, well differentiated	+	++
Taxonomically well known, easy to identify	++	++
Well studied	++	++
• Abundant, non-furtive, easy to find in the field	++	++
• Damped fluctuations (always present)	++	++
• Easy to obtain large random samples of species and variation	++	++
Functionally important in ecosystem	+	+
Response to disturbance Predictable, rapid, sensitive, analysable and linear	+	+
• Associates closely with and indicates other species and specific resources	++	+
Total value as indicator (maximum score = 24)	19	19

The criteria where a change of score from their original evaluation is proposed for the bait-attracted Nymphalinae, thanks to recent studies of the group, are preceded by a •.

two groups for each criterium). The scores are discussed below.

4. Discussion

4.1. *Evaluation of the indicators*

The four species selected as indicators are widely distributed and do not display high ecological fidelity. *H. daedalus* and *C. epijasius* are butterflies of open formations, centered on the Guinean Savannahs, but even found up to the disturbed places of the rainforest area (Joly, 2003; Larsen, 2006). The *P. marginata*- and *P. cordata*-complexes are ubiquitous and found in most African countries (Sakay and Nagai, 1998). However, in England, it was demonstrated that widespread species may have declined as much as rare species (Leon-Cortes et al., 2000), and the former are easier to follow. Both families displayed a significant sensitivity to disturbance in the Savannah area, as previously demonstrated for the bait-attracted Nymphalinae in other studies (Kremen, 1992, 1994; Ramos, 2000), even in the same sub-region (Fermon et al., 2000; Bobo et al., 2006), but always in forest areas.

The mobility of both insect groups did not affect their indicator value in our systems: despite a significant spatial autocorrelation between trapping scores, linked to active dispersal and demonstrating a distant impact of disturbance, their densities dropped or increased very quickly depending on human activity. Mark-recapture trials have nevertheless been planned to better quantify this parameter.

The four species were found in high densities in the two extreme climatic parts of the W Regional park, i.e. in all its protected ecosystems. Like in other studies (Fermon et al., 2000; Ramos, 2000), the capture scores allowed strong statistical analyses, which lead us to switch three of Brown's criteria (1991) to the maximum level for bait-attracted Nymphalinae (abundant, non-furtive, easy to find in the field, damped fluctuations, easy to obtain large random samples of species and variation). In forest ecosystems, it has been demonstrated that seasonal, annual and vertical variations can lead to important evolution of the distribution of fruit-feeding butterflies (Devries and Walla, 2001). Seasonal variations should be taken into consideration in Savannah areas, where the wet season is related to strong increase of most insect densities. Further studies are needed on this point. The vertical variations are not likely in Savannah ecosystems, where the canopy is not continuous and the trees generally small (<10 m).

The importance of both groups to the ecosystem is likely to be modest, although the Cetoniinae larvae are saprophytic and play a role in the recycling of organic matter (Deprince, 2004). It would be worth adding another insect group to the follow-up, with greater ecosystem importance, like bees, which are also attracted to banana traps. Actually, it has recently been demonstrated that protecting natural ecosystem can increase the pollination efficiency of honey bees through behavioural interactions with wild bees (Greenleaf and Kremen, 2006).

From our dataset, it can only be concluded that the response to ecosystem disturbance of both groups seemed sensitive and analysable. More data are needed to understand all the ecosystem properties involved (other trapping sites, longitudinal follow-up), and the rapidity and predictability of the observed patterns. However, we can already conclude that the response to disturbance was not linear in the Cetoniinae subfamily, actually favored by a slight disturbance, as it was observed in forest butterflies in other studies (Lovejoy et al., 1986; Brown, 1997; Wood and Gillman, 1998). Concerning the butterflies, our results do not necessarily contradict the former, since the study was located in a Savannah ecosystem: in the forest area, an opening of the environment is associated to a reduction in moisture leading to the colonization by more xerophile opportunistic species (generally species centered on the Guinean Savannah type), which compensate the disappearance of true forest species (Fermon et al., 2000), whereas in the Sudanian Savannah area, this opening cannot be compensated by a hypothetical Sahelian complex, which is mainly composed by the more ecologically flexible Sudanean species. It is known that drought can reduce the reproductive success of some butterfly species (Pollard et al., 1997), and the reduction of butterfly species richness from south to north is well documented in our area (Larsen, 2006). This tendency is clear, even within the W regional park, where the vegetation of the northern zone of the protected area seemed more disturbed than the southern one. This might be explained by less favourable climate and soils, emphasising the effect of old human practices and delaying ecosystem recovery. This was related to a drop in species richness of both families, which might thus constitute good climatic indicators. However, the realisation of a north–south transect within the park would be necessary to design efficient climatic indicators.

Finally, a linear relationship was found between plant species richness and the apparent densities of four insect species, which were also correlated together, although belonging to very different families. The larval stages of the Nymphalidae species are phytophageous, each species exploiting a restricted number of plant species (Williams, 1969; Larsen, 1991). The larval stages of Cetoniinae eat dead wood and humus (Deprince, 2004), sometime mixed with cow feces (P. Juhel and J.P. Vesco, com. pers.) and are thus less resource-specific. In some studies, a good relation has been found between insect abundance and species richness and vegetation abundance and structure on the one hand (Hamer et al., 1997; Ramos, 2000; Bouyer et al., 2005; Foote and Hornung, 2005), and plant species richness on the other hand (Panzer and Schwartz, 1998; Schulze et al., 2002). In others, it was pointed out that insects were poor indicator of plant diversity (Kremen, 1992, 1994), but good for environmental (topographic/moisture) gradients. In Australian tropical Savannahs, it has been demonstrated that the response of grasshopper assemblages to disturbances associated with human land use do not simply reflect those of plants (Andersen et al., 2001). In our study, no clear relation was found between larval host plant availability and butterflies density, as observed elsewhere (Van Nouhuys et al., 2003). The relation between plants and insects could thus be related to adult feeding resources, as it was demonstrated before for other butterfly species (Schneider et al., 2003; Dennis, 2004) and beetles (Hegland and Boeke, 2006). Concerning the other animals, Schulze et al. (2002) found that the biodiversity of plants, birds and insects were significantly correlated. However, other studies demonstrated no relation between the

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diversity of insects and insectivorous birds (Sekercioglu et al., 2002), butterflies and moths (Ricketts et al., 2002), and even fruit-feeding butterflies and other butterflies (Wood and Gillman, 2004)! Thus, further efforts associating experts of various groups should be planned by the ECOPAS project to elucidate the overall association between these fruit-feeding insects and other animal groups.

4.2. *Ecosystem properties to be monitored*

The ECOPAS program needs a survey protocol to monitor the global ecosystem health under various management strategies. The simplification of this protocol is very important to ensure its use by development projects (Andersen et al., 2002). For this reason we propose to follow up only a few characteristic species easily captured. During the study, the drop in butterfly densities between the protected and disturbed areas was very demonstrative for the resident populations and forest services. The metamorphosis allows testing various trophic levels within the same species: whereas the adults of both families eat fruits and can be attracted by similar traps baited with bananas, the larval stages have quite different ecologies.

We propose to review below the disturbance factors that could be related to the apparent densities of our groups in the W park.

4.3. *Grazing*

The Cetoniinae's species richness is higher in these slightly disturbed areas of the southern transect, following the intermediate disturbance theory (Connell, 1978). Some Cetoniinae species might be favoured by cattle, since they are likely to consume cowpats. A similar behaviour has been noticed in *Pachnoda ephippiata* Gerstaecker in Kenya where it can be found even in Nairobi (Legrand, 1986). In Bobo Dioulasso, *P. marginata*'s larval stages are also often found in dunghills. Moreover, cattle grazing might even increase dead wood availability by favouring the development of ligneous species (César and Zoumana, 1999) and compensate for the reduction of wild fauna abundance associated to human disturbance. In Glossinidae, it was demonstrated that the abundance of adult feeding resources in the border ecosystems (domestic prey animals or men) favour the pullulating of the flies (Buxton, 1955; Bouyer et al., 2006). Cattle grazing did not significantly reduce the abundance of fruit-feeding butterflies. In very different ecosystems, a decrease of odonate abundance was associated with cattle grazing (Canada) (Foote and Hornung, 2005), while in the montane grasslands of Argentina, the effects of grazing disturbance on insect communities were significant only for intensive use (Cagnolo et al., 2002).

4.4. *Hunting*

Among all human activities, hunting was the one with the lowest measurable impacts on biodiversity and on the densities of monitored species. For this particular human pressure, the authors however doubt that Cetoniinae and butterflies can be considered as good indicators of the ecosystem health because of their relative freedom from hunting pressure. Recent inventories of a forest relict (Foret du Kou) near Bobo Dioulasso demonstrated similar biodiversity and densities of the four targeted species whereas big mammals have almost completely disappeared (Bouyer et al., in preparation).

4.5. *Crops*

The impact of crops on butterfly diversity is generally recognised to be negative (Bobo et al., 2006). In the Cetoniinae, food crops were associated with a small reduction in biodiversity in the northern area, but with an increase of biodiversity in the southern part where crop densities are still low. In the *Charaxes* genus, they were associated with a small reduction in the southern transect. The impact of this management strategy should be followed up, all the more if the climate became drier (in relation to the global warming).

On the contrary, cotton crops had a strong negative impact on the densities of all the monitored species and their families' biodiversity, even in the areas cultivated for less than 10 years. This negative impact was significant up to 1.5 km and 3 km from the border of the cultivated areas in the Nymphalidae and Cetoniinae species respectively. This practice should thus be limited in the peripheral areas, or at least localised in the most distant buffer belts. The use of transgenic cotton crops might reduce their impact on invertebrate biodiversity.

4.6. *Landscape fragmentation*

At the species level, frugivorous butterflies have been shown to be good indicators of landscape fragmentation (Rogo and Odulaja, 2001; Uehara-Prado et al., 2007). However, Sekercioglu et al. (2002) demonstrated that birds were more sensitive to fragmentation than insects, depending on their dispersal abilities in the deforested countryside. The comparison of our own inventories of both groups between the W regional park (23 600 ha excluding the WAPO complex, that is connected) and a forest relict near Bobo Dioulasso (Forêt du Kou, 120 ha) indicate that both groups seem very resilient to landscape fragmentation since we found a similar species richness with similar trapping efforts: 35 and 37 Cetoniinae species respectively (Legrand et al., in preparation), and 98 and 96 butterfly species respectively (Bouyer at al., in preparation). These insect groups might be more resilient to fragmentation than other groups thanks to higher population densities.

4.7. *Importance of ecological indicators in the management of the W park*

The economical income that can be generated in the peripheral areas from the traditional activities (hunting, fishing, cattle raising, gathering, beekeeping, food crops) is far less important than that of modern activities, essentially cotton crops, that reach 160–200 US$ per ha. Even if desirable and more sustainable than cotton monoculture, the diversification of peripheral activities to generate landscape mosaics including areas of village hunting with a strong increased valuation, following the *Campfire* model (Murombezi, 1994), extensive cattle raising, gathering (baobab fruits,...) or beekeeping, that can maintain biodiversity and ecosystem health, is subject to a serious obstacle: the average family

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income pass from 80 US$/month to more than 150 US$. The "zero cotton" option is thus not worthy of attention for producers.

Yet, negative environmental impacts of this profitable crop have been well documented in the study area: the race for land and clearance, the reduction of the fallow durations, and the presence of insecticide residuals in the surface water and wild animals' flesh. The seek for options that allow to benefit from cotton incomes without its environmental counterparties has been a priority for the ECOPAS program which has been promoting alternative systems called "biological cotton" or "green cotton" (Vodouhé, 1997; Valenghi et al., 2003) thanks to low input but high intensification levels: biological insecticides extracted from the *neem* (*Azadirachta indica*), manure, animal traction,...

The objective of the managers is to constitute, in the immediate neighbouring of the park (the MAB UNESCO buffer area) and in the transition area, a "bocage" landscape harbouring traditional and modern activities, and favourable to both local resident populations and biodiversity. Being able to appreciate the ecosystem health and act on its determinants are clearly key factors for the long-term survival of the W Savannahs and its fauna. The ECOPAS program considers looking directly at different land uses to appreciate ecosystem health, by calculating remote sensing indicators like species richness capacity (Clerici et al., 2007). However, in such mosaic landscapes, only ecological indicators like those proposed here can warrant the efficiency of the protection measures.

The presence of *Pachnoda ardoini* Ruter and *P. orphanula* Herbst in the W Regional park, although not recognised in the present study, has to be pointed out. Belonging to the *P. marginata*-complex, they could also have contributed to the capture scores of the latter.

5. Conclusion

The present study is a step toward the use of fruit-feeding insects in the management of Savannah ecosystems, but a better understanding of communities that will be obtained only through long-term studies is still needed to design an appropriate management of the W regional park. The question whether these insect taxa are good predictors for other groups also need further study.

In the South-western part of Burkina-Faso, these ecological indicators will be used together with vegetation follow-up to monitor the impact of various conservation strategies proposed at a local scale to protect the relic forests of the Banfora cliff. They will also be used in Tsetse control programmes to monitor the impact of the elimination of African Animal Trypanosomosis, associated with an increase in cattle production and crop surfaces, on natural ecosystems.

Acknowledgements

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Appendix

Comparison of the apparent densities of *Charaxes epijasius*, *Hamanumida daedalus*, *Pachnoda marginata*- and *P. cordata*-complexes in the landuse units of the northern (Burkina Faso) and southern (Bénin) transects, W Regional park. Results of the Steel-type non-parametric multiple comparisons test (TC, traditional crops, OCC, old cotton crops, RCC, recent cotton crops, F, fallow, G, gathering, B, Buffer, H, hunting area and P, Park). The groups were ordered according to increasing mean apparent densities for each site and species. The results of the one-sided npmc tests, which reject if group with smaller index has larger values due to the calculation of the relative effect-estimators, are summarized in the first column of each table.

Compared groups	Sum of both sample-sizes	Statistic	One-sided p value	Two-sided p value
Northern transect (Burkina-Faso)				
C. epijasius				
TC–F***	149	4.2079700	5.5500975e−05	1.639361e−04
TC–H***	184	9.1547543	0.000000e+00	0.000000e+00
TC–P***	174	9.1310788	0.000000e+00	0.000000e+00
F–H***	175	7.0455448	1.857712e−12	4.135652e−12
F–P***	165	7.0010799	2.575048e−12	6 907808e−12
H–P	200	0.3438669	5.760321e−01	9.963233e−01
P. marginata				
TC–F***	148	1.9942480	1.110648e−01	1.956774e−01
TC–H***	182	8.0080310	1.110223e−15	2.220446e−15
TC–P***	164	9.2520392	0.000000e+00	0.000000e+00
F–H***	164	6.4222658	1.376212e−10	6.575316e−10
F–P***	146	7.5633654	3.952394e−14	8.948398e−14
H–P	180	0.3484829	8.669662e−01	9.920862e−01
H. daedalus				
TC–F	149	1.859276	1.488937e−01	2.585386e−01
TC–H***	184	8.238816	2.220446e−16	4.440892e−16
TC–P***	174	8.546823	0.000000e+00	0.000000e+00

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Appendix – *continued*

Compared groups	Sum of both sample-sizes	Statistic	One-sided *p* value	Two-sided *p* value
F–H***	175	6.909118	5.830336e−12	1.034761e−11
F–P***	165	7.408734	1.255635e−13	3.073097e−13
H–P	200	2.158665	7.754709e−02	1.412943e−01
P. cordata				
TC–F	148	0.18353338	9.205863e−01	9.993759e−01
TC–H***	182	5.91723609	5.136443e−09	1.049771e−08
TC–P***	164	5.33059678	1.191876e−07	3.826230e−07
F–H***	164	5.20483413	2.815632e−07	1 048459e−06
F–P***	146	4.69382573	5.228875e−06	1.209836e−05
H–P	180	0.06790126	9.441528e−01	9.999754e−01
Southern transect (Bénin)				
C. epijasius				
OCC–RCC	120	0.9230210	9.024329e−01	9.854791e−01
OCC–F	90	2.7213180	5.350214e−02	9.820381e−02
OCC–TC***	130	5.5952628	7.481118e−08	2.029646e−07
OCC–G***	80	4.4644924	3.864854e−05	1.720501e−04
OCC–P***	120	6.0560171	4.386924e−09	8.191158e−09
OCC–B***	100	6.3091666	6.556076e−10	1.638512e−09
RCC–F	90	1.9731891	2.978106e−01	4.645613e−01
RCC–TC**	130	4.9042880	3.847651e−06	7.464288e−06
RCC–G**	80	3.8356977	1.158524e−03	2.600783e−03
RCC–P***	120	5.3619157	2.894843e−07	5.783857e−07
RCC–B***	100	5.7943459	6.667309e−06	4.521197e−08
F–TC	100	2.1645009	2.063935e−01	3.396880e−01
F–G	50	1.8605173	3.621309e−01	5.421493e−01
F–P	90	2.6209541	7.240037e−02	1.268066e−01
F–B**	70	3.4665500	5.303781e−03	9.205083e−03
TC–G	90	0.2325026	9.983490e−01	9.599599e−01
TC–P	130	0.5744210	9.800095e−01	9.995998e−01
TC–B	110	1.9839096	2.931833e−01	4.553877e−01
G–P	80	0.2368460	9.983116e−01	9.999999e−01
G–B	60	1.3397955	6.940204e−01	8.738250e−01
P–B	100	1.3799530	6.655524e−01	8.543130e−01
P. marginata				
RCC–OCC	120	1.0231206	8.633234e−01	9.731307e−01
RCC–P*	120	2.7650869	4.868814e−02	9.001472e−02
RCC–F	90	2.5068462	9.505232e−02	1.679579e−01
RCC–G***	80	5.2304683	6.713502e−07	1.371849e−06
RCC–B***	100	7.3084747	5.682121s-13	1.033507e−12
RCC–TC***	130	7.1505575	2.404077e−12	4.158007e−12
OCC–P	120	1.9243335	3.257418e−01	5.000784e−01
OCC–F	90	1.7903850	4.026006e−01	5.562550e−01
OCC–G***	80	4.7360841	1.094290e−05	3.026069e−05
OCC–B***	100	6.9142362	1.170442e−11	2.779887e−11
OCC–TC***	130	6.7230649	4.380130e−11	9.065065e−11
P–F	90	0.2169766	9.554451e−01	1.000000e+00
P–G**	80	3.3896493	6.020668e−03	1.277458e−02
P–B***	100	5.4716044	1.785253e−07	9.042856e−06
P–TC	130	5.2445652	7.430505e−07	2.537347e−05
F–G*	50	2.7669457	4.595235e−02	8.814559e−02
F–B***	70	4.2056603	2.751642e−04	3.3749789-04
F–TC**	100	3.9038185	1.080354e−03	1.921341e−03
G–B	60	1.0505790	8510527e−01	9.6800419e−01
G–TC	90	0.6578377	9.6271 37e−01	9.5847659e−01
B–TC	110	−0.5849355	1.000000e+00	9.5962049-01
H. daedalus				
OCC–RCC	120	2.1736369	2.070842e−01	3.338973e−01
OCC–F***	90	5.1790111	1.149138e−06	1.861374e−06
OCC–TC***	130	5.8346398	1.353210e−07	4.106885e−08
OCC–G***	80	6.0263723	6.019115e−09	1.074937e−08
OCC–B***	100	7.0426499	4.657941e−12	9.050316e−12
OCC–P***	120	7.8108300	1.267559e−14	2.742251e−14

(*continued on next page*)

Appendix – *continued*

Compared groups	Sum of both sample-sizes	Statistic	One-sided *p* value	Two-sided *p* value
RCC–F***	90	3.9453993	7.669654e−04	1.518192e−03
RCC–TC***	130	4.5190543	4.650141e−05	6.352051e−05
RCC–G***	80	54105254	3.354514e−07	4.902150e−07
RCC–B***	100	6.3106720	8.251124e−10	1.927052e−09
RCC–P***	120	7.2663675	7.560619e−13	1.503242e−12
F–TC	100	0.4619559	9.902803e−01	9.955624e−01
F–G*	50	2.9174161	3.185027e−02	5.939746e−02
F–B**	70	3.5092513	4.589782e−03	7.261001e−03
F–P***	90	4.5161733	7.306412e−05	2.441490e−04
TC–G	90	2.4603450	1.071339e−01	1 .882935e−01
TC–B**	110	3.6307571	2.542402e−03	5.078304e−03
TC–P***	130	4.9899002	2.331206e−06	5.007029e−06
G–B	60	1.1892166	7.547061e−01	9.351765e−01
G–P	80	2.2986106	1.546937e−01	2.558373e−01
B–P	100	1.1702106	7.942435e−01	9.406955e−01
P. cordata				
RCC–OCC	120	1.0122143	8.561337e−01	9.661796e−01
RCC–F*	90	2.9453615	2.767620e−02	5 067838e−02
RCC–P***	120	4.2962334	2.115920e−04	3.543273e−04
RCC–TC***	130	6.1677281	1.913422e−09	3.644095e−09
RCC–B***	100	6.1730856	1.815092e−09	3.664041e−09
RCC–G***	80	6.7627137	2.553282e−11	6.304479e−11
OCC–F	90	1.9549123	3.023423e−01	4.610860e−01
OCC–P**	120	3.5208115	3.964752e−03	7.035831e−03
OCC–TC***	130	5.5451023	9.169366e−06	2.226583e−07
OCC–B***	100	5.5211643	1.096255e−07	1.967065e−07
OCC–G***	80	6.0995407	2.526839e−09	6.781435e−09
F–P	90	1.3339703	6.871457e−01	8.610716e−01
F–TC*	100	3.2141371	1.219350e−02	2.123154e−02
F–B**	70	3.4041659	5.558772e−03	1.208294e−02
F–G***	50	4.2352361	2.455253e−04	5.329698e−04
P–TC	130	2.4345461	1.133434e−01	1.507577e−01
P–B	100	2.6552962	6.402801e−02	1.139645e−01
P–G**	80	3.5567417	3.735694e−03	7.744685e−03
TC–B	110	0.5651358	9.779120e−01	9.993221e−01
TC–G	90	1.7574789	4.144005e−01	6.008733e−01
B–G	60	1.2007872	7.633639e−01	9.151344e−01

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

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