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The study of unburned savanna sections serving as temporary refuges for insects. An experiment in a tropical humid savanna in Côte d'Ivoire

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ABSTRACT
Objective: Fire is a significant factor in the Lamto savanna where it is considered as the major cause of disturbance. Although previous studies have very well shown its role in the creation of spatial heterogeneity in the vegetation, few reliable data exist on its effects on biodiversity in general and on insects in particular. In the context of biodiversity conservation in protected areas in Côte d'Ivoire, an investigation was conducted in the Lamto reserve to study the effects of fire on insect's movements.
Methodology and results: Using different trapping methods (pitfall trap, Malaise trap and movable cage), data were collected on insects between and within two plots of savanna differing in their fire-treatment in order to examine the effect of fire on the insects movement and community composition. The results showed intensive movements of flying insects between plots during the fire while ground-dwelling insects seemed to find refuge in the ground and grass tufts in the burned area; this strategy being mostly used by individuals of small size. The unburned plot played a dual function in biodiversity conservation. On the one hand, it provided a refuge for flying insects during the fire, and on the other hand, it served as a retreat for many species that eventually resettled the burned plot offering new and attractive living conditions for insects some months after the fire via the new growth of grasses.
Conclusion and Application: In the framework of biodiversity management in Lamto reserve, such a study can be used for guiding further research on the interaction between biodiversity and savanna fires.
Key words: Biodiversity, conservation, fire, insects, refuge, savanna

INTRODUCTION
Fire is a major disturbance in many biomes throughout the world and particularly in the tropics where it plays a key role in savanna dynamics (Goldammer, 1990; Andersen *et al.*, 2003). The fires are largely ignited by humans, and occur annually due to the rapid growth of grass in the wet season, which dries up rapidly to produce large fuel loads in the dry season. In recent times, fire is widely used for conservation management in extensive savanna landscapes but there is a lack of reliable data on its role in the framework of biodiversity conservation (Andersen, 1996; Brockett *et al.*, 2001; Van Wilgen *et al.*, 2004; Parr & Anderson, 2006). The application of fire management in savanna systems often lacks a well

established and unequivocal scientific foundation (Andersen, 2003; Parr & Chown, 2003).

At Lamto, fire modifies plant abundance and distribution, creates spatial heterogeneity, and thus maintains a mosaic pattern of the vegetation. Therewith, it plays a crucial role in determining the system's structure and also some of its functional properties (Abbadie *et al.*, 2006; Ménaut & Abbadie, 2006). While the effects of fire on the vegetation are well known (Mordelet, 1993; Gignoux et al. 1997; Ménaut & Abbadie, 2006), very few studies focused on animals in general and invertebrates in particular and these produced controversial results (Gillon & Pernès, 1968; Lamotte, 1975; Gillon, 1983). Indeed, the effects of fire on fauna are diversely argued, notably in insects on which it is assumed to cause direct mortality (Miller *et al.*, 1955; Reichert & Reeder, 1972; Bock & Bock, 1990), forced emigration (Gillon, 1970) and even the immigration of pyrophilous species (Komarek, 1970). The limited understanding of the effect of fire is of particular concern as it is also regularly used as a management tool in the Lamto savanna against uncontrolled fires and for presumed biodiversity conservation. Arthropods in general and insects in particular are a major component of biodiversity playing key roles (pollination, predation) in savanna ecosystems. Despite this fact, the impact of fire on the diversity and spatio-temporal dynamics of insects is still a mostly open issue constituting a major knowledge gap for a better understanding of the functioning of the Lamto ecosystem and savannas in general (Parr *et al.* 2004; Andersen *et al.* 2007; Yarnell *et al.* 2007). Improved knowledge on the response of insect guilds to fire could have important implications for the management of Lamto protected area and comparable areas.

This paper assessed the abundance and composition of the insect community between and inside two savanna plots before, during and up to three months after setting fire. Specifically, it aimed at (i) exploring how insect guilds responded to the burning event, and (ii) showing the role unburned savanna sections play in biodiversity conservation.

MATERIAL AND METHODS

Study site: This study was carried out within the Lamto reserve (6°13 N, 5°02 W) located in central Côte d'Ivoire. The annual rainfall of the region is about 1200 mm. Interrupted by a short dry season in August; the rainy season lasts from February to November and is followed by a dry season in December and January. Lamto represents the wettest end of the West African aridity gradient and is located at the bottom end of the "V Baoulé" which is a region where one would expect Guinea savannas to border rainforests. Fire is the main cause of the unexpected presence of savannas where climate and water availability should allow sustaining rainforests (Monnier, 1968). Different experiments of fire exclusion have been conducted and have proven the decisive role of fire in preventing this savanna from massive tree invasion on long time scales, thus freezing the forest-savanna boundary in a historical position (Abbadie *et al.,* 2006). The mosaic pattern of the vegetation in this area offers habitat variability, among which some (e.g. forest islands, savanna woodlands, unburned savannas) can provide a refuge for animals during the occurrence of fire.

Sampling, identification and data analysis: The investigation took place during the dry season, mid January, during the time span where the unplanned man-made bush fires occur in the Lamto reserve. The samplings were carried out on an experimental site consisting of a pair of savanna plots (each 60 x 60 m), with one plot burned and the second protected against fire. This experimental site was located in a part of the savanna where tree cover ranges between 7 % and 36 % (Gautier, 1990). Three days before starting the experiment, a fire-break of 10 m width was cleared and burned between the two plots. All traps were set within this fire-break and one of plots was then burned by setting its vegetation on fire perpendicularly taking into account the prevailing wind direction. To avoid high humidity due to dew falling during the night, the fire was lit around midday, and it burned up the entire plot during 18 minutes having an epigeous biomass of 1.36 $Kg.m^{-2}$ dry matter. Biomass determination was carried out within a 1 x 1-m quadrat, at four points distributed over the plot by following Koné *et al.* (2008). The average height of grass equaled 54.75 cm on the day before the fire.

Samplings were executed on: the day before the fire, the day of the fire, one day after the fire, one month, two months and three months after the fire. Ground-dwelling and flying insects migrating through the fire-break were caught respectively with 10 pitfall traps and 3 Malaise traps; each trap being set at equal distance to the other (6.67 m between pitfall traps and 20 m between Malaise traps). Pitfall traps consisted of plastic cups having an inner diameter of 6.8 cm at the top, an inner diameter of 4.9 cm at the bottom and a depth of 10.3 cm. The cups were placed in holes dug with sharp machetes to minimize the impact on the surrounding area. They were filled, approximately half, with a mixture of glycerin and 70 % ethanol. As these traps only allowed assessing temporal variations in the abundance and activity of insects, Malaise traps (Malaise, 1937; Gressitt & Gressitt, 1962), 2 m high and 1.8 m wide, were modified in such a manner to detect the direction of flying insect's movements by using two collecting jars with opposite orientation at the two open sides (Figure 1). The traps were left active for 24 hours on each catching day (from 8 am to 8 am next day).

Figure 1: A model of bidirectional Malaise trap used for the catch of flying insects

On all sampling days (except, the day of the fire), the insect community composition was assessed within each plot using a movable cage (2 m x 2 m wide and 1.5 m high) at three random locations. This method was standardized by engaging two people who collected insects with flexible forceps thoroughly searching the enclosed volume for 30 min. Apart from the downward side; all other sides of the cage were covered with a wire mesh of 1-mm diameter to prevent trapped insects from escaping. Opportunistic catches were done over the entire plot areas using sweep nets. However, these data were not included in the statistical analyses and served only to complete the list of taxa found inside the plots. All insects collected were classified to order by referring to different identification keys e.g. Villiers (1952), Roth (1980), Delvare & Aberlenc (1989) and Leraut (2003).

Statistical analyses were made with the software STATISTICA 7.1. After testing the homogeneity of variances, variations in insect abundances across sampling dates were examined using the one-way analysis of variance (ANOVA 1) and LSD (Least Significant Difference) post hoc comparison tests served to detect differences between abundances. In case of non-homogeneity, non-parametric tests (ANOVA of Kruskal-Wallis and U-test of Mann Whitney) were used to make analyses. Changes in the insect community composition were analyzed by quantifying the abundance of taxa and comparing the total abundances of insects either between plots or between sampling dates. Although the use of bidirectional Malaise traps did not imply true replication, these data served to explain insect directional movements.

RESULTS

Abundance of ground-dwelling insects: In all, 594 ground-dwelling insects were caught in migration through the fire-break. The number of caught insects varied significantly between samplings (ANOVA 1, $F = 35.51$, $p = 0.0001$) (Table 1). Significantly more insects were caught between the plots on the day before the fire than on the day of the fire (LSD test, p = 0.02, n = 10) and on the following day (LSD test, p = 0.0001, n = 10). Compared to these latter dates, the abundance of insects strongly increased one month (LSD test, p = 0.02 and 2.10^{-4}, n = 10 respectively) and two months later (LSD test, p = 0.04 and 10^{-4}, n = 10 respectively). Still more insects were caught three months after the fire, their abundance being higher than the day before the fire (LSD test, p = 0.01, n = 10).

Table 1: Comparisons of insect abundances between sampling dates

	One day before	Fire day	One day after	One month after	Two months after	Three months After
Ground-dwelling insects	11.4±2.4[a]	5±1.2[b]	1.4±0.5[c]	11.9±2.7[a]	10.6±2.6[a]	19.1±2.7[d]
Flying insects	23±1.5[a]	36±1.2[be]	22±1[a]	27.7±4.5[ae]	70.7±2.2[c]	50±4.5[d]

For each line, values having the same letters (a, b, c, d and e) did not differ significantly at p = 0.05 level (LSD post comparison tests or U-test of Mann Whitney)

Of all taxa, only Hymenoptera were consistently caught during the entire sampling period (Figure 2). The Coleoptera were caught in small numbers before the fire and one month to three months after the fire. They were not caught on the day of and the day following the fire. The Orthoptera were caught in increased numbers one month, two months and three months after the fire. Other taxa such as Dictyoptera, Heteroptera and Isoptera were caught rarely and variably between sampling dates.

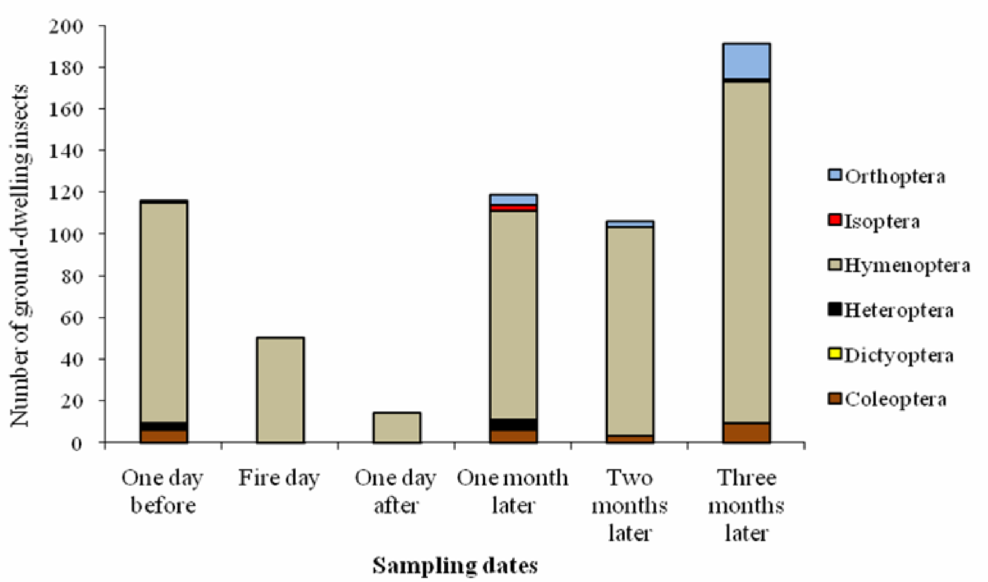

Figure 2: Temporal variation in the total abundance of ground-dwelling taxa caught between the two plots.

Abundance of flying insects: In total, 692 flying insects were caught between the burned and unburned savanna plots. Their mean abundance varied between the sampling dates (ANOVA of Kruskal-Wallis, F = 14.81, p = 0.01) (Table 1). Significantly more insects were trapped on the day of the fire than the day before (U-test, p = 0.04, n = 3) and the day following the fire (U-test, p = 0.04, n = 3). Compared to the latter dates, the influx of flying insects increased significantly two months (U-test, p = 0.04, n = 3) and three months later (U-test, p = 0.04, n = 3). The analysis of captures on the two sides of Malaise traps showed clear variation in insects' directional movements on the day of the fire and one month later (Table 2). At the latter date, more insects were caught flying towards the burned savanna than towards the opposite side.

Of the eight flying taxa identified, six (Coleoptera, Diptera, Homoptera, Hymenoptera, Lepidoptera and

Orthoptera) were caught at all sampling dates (Figure 3).

Table 2: Comparisons of flying insect abundances between their directions of flight.

	One day before	Fire Day	One day After	One month after	Two months after	Three months After
Towards Unburned	11±1.3[a]	23.7±0.4[be]	11.3±3.8[ac]	7.7±2.9[c]	29.7±3.8[b]	22.3±0.4[e]
Towards Burned	12±2.7[a]	12.3±1.1[a]	10.7±4.2[a]	20±4.7[ad]	41±4[b]	29±5.3[ed]

Values having the same letters (a, b, c, d and e) did not differ significantly at p = 0.05 level (LSD post comparison tests).

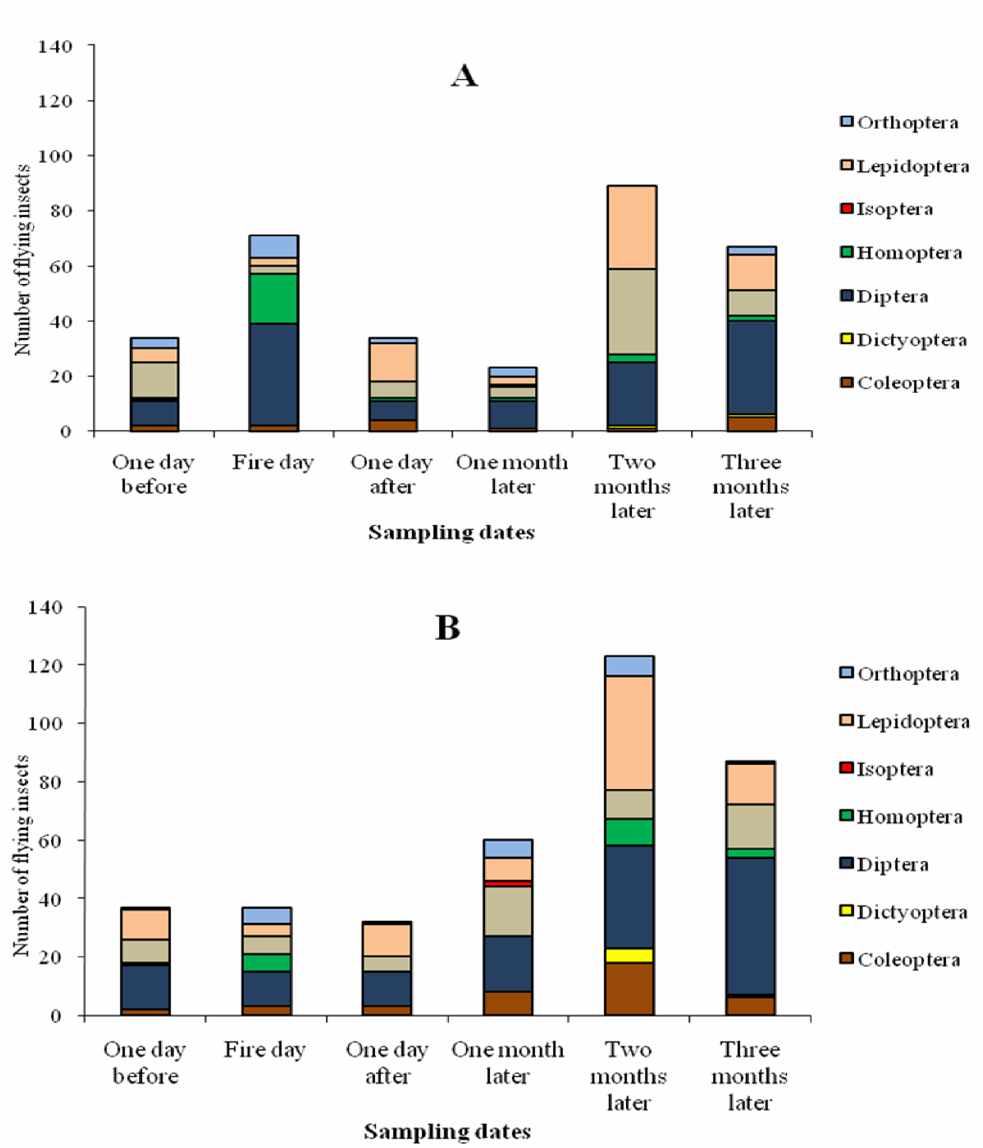

Figure 3: Temporal variation in the total abundance of flying taxa caught between the two plots (A: movement towards the unburned plot; B: movement towards the burned plot)

They were trapped in varying numbers and differing preferential movement directions across sampling dates. Among individuals moving towards the unburned savanna plot, Diptera, Homoptera and Orthoptera were the most abundant on the fire day while Coleoptera, Hymenoptera and Lepidoptera were mostly caught only after this day. All taxa caught moving in the opposite direction were significantly more abundant one month, two months and three months after the fire than at the preceding sampling dates. Except Lepidoptera and Orthoptera, the abundances of other taxa did not vary significantly between the three first sampling dates. The number of Lepidoptera decreased on the day of the fire contrary to Orthoptera that were caught in moderately increased numbers.

Changes in the insect community composition within plots: Whatever the plot, the total abundance of insects collected varied significantly between samplings (unburned plot: $F = 6.15$, $p = 0.009$; burned plot: $F = 24.26$, $p = 4.10^{-5}$). The number of insects caught within the unburned plot one day after the fire increased by 20 % compared to the day before. This number decreased significantly one month and two months later and it greatly re-increased in the third month (Table 3). As shown on figure 4, the mostly caught taxa were, in decreasing order: Orthoptera (113 specimens), Hymenoptera (111 specimens), Homoptera (63 specimens), Heteroptera (59 specimens), Lepidoptera (34 specimens), Coleoptera (23 specimens) and Dictyoptera (21 specimens). The Homoptera were similarly caught on the day before and the day following the fire where they represented 19.8 % and 18.3 % of all insects caught respectively. Apart from one month after the fire, the Hymenoptera were caught in relatively high numbers during all samplings. As for Orthoptera, they were consistently collected during the whole sampling period, with especially elevated proportions one month (45 %), two months (28 %) and three months (32 %) after the fire. The Lepidoptera were abundant on the day before and the day following the fire, with 13 % and 14 % of the insects caught respectively. Although collected during all samplings, Coleoptera and Dictyoptera were in our samples no abundant groups of the insect community. Contrary to the unburned plot, the burned one was significantly less populated on the day following the fire compared to the day before; only 43 % of insects caught were found. In addition, significantly more insects were caught within this latter plot one month, two months and three months after the fire (Table 3).

Table 3: Comparison of the abundances of insects caught within the two plots

	One day before	One day after	One month after	Two months after	Three months after
Within Unburned	$33.7±4.1^{ac}$	$40.7±4.1^{a}$	$9.7±1.5^{b}$	$22.3±3.7^{c}$	$41±9.9^{ae}$
Within Burned	$33±4.4^{a}$	$14±0.6^{b}$	$50.7±3.2^{cd}$	$56±3.5^{d}$	$76.7±8.6^{e}$

Values having the same letters (a, b, c, d and e) did not differ significantly at p = 0.05 level (t-test and U-test of Mann Whitney).

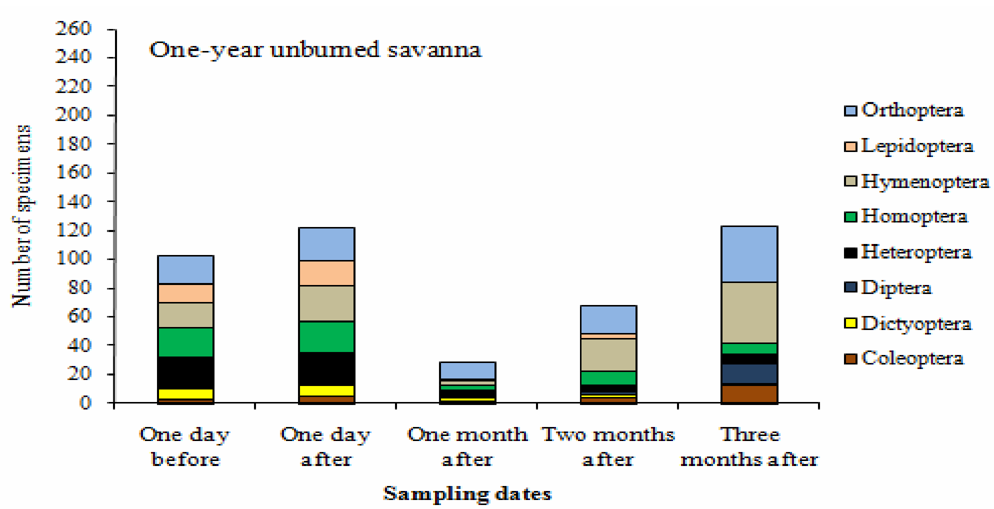

Figure 4: Temporal variation in the abundances of taxonomic groups within the one-year unburned savanna plot.

The number of insects caught during these months respectively went up 53 %, 69 % and 132 % over that of the day before the fire. As shown on figure 5, the mostly caught taxa were Coleoptera, Heteroptera, Hymenoptera and Orthoptera. The abundance of Heteroptera was reduced by more than half one day after the fire and to a quarter one month later before increasing two months after the fire. The abundance of Hymenoptera did not appreciably vary between the day before and the day following the fire.

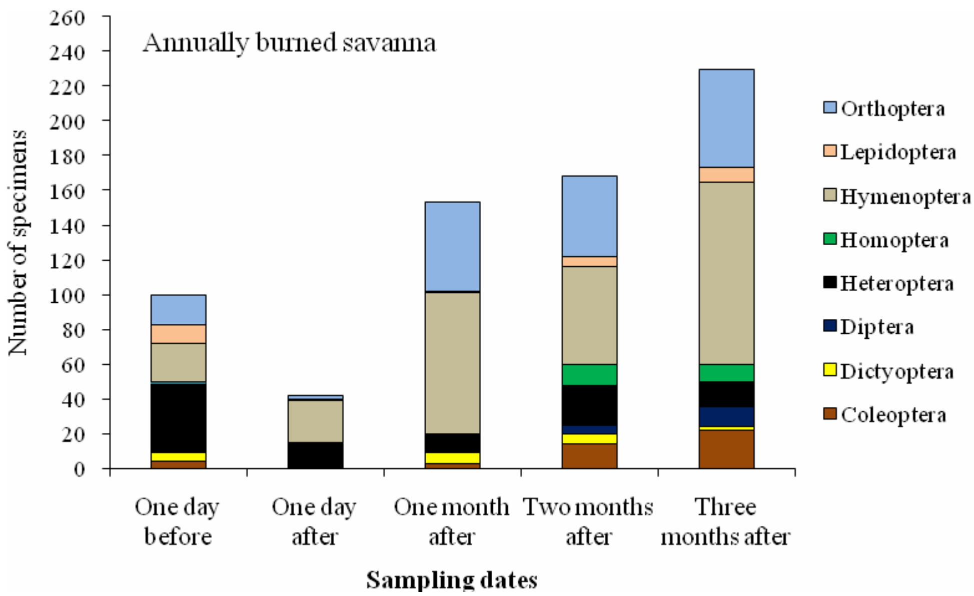

Figure 5: Temporal variation in the abundances of taxonomic groups within the annually burned savanna plot

However, they were by far the most dominant group on this latter day with 57 % of all insects caught. They were mostly caught one month, two months and three months after the fire even if their proportions did not increase (53 %, 33 % and 46 % respectively) in regard to other groups. The Orthoptera were caught in moderate numbers before the fire (17 %), rarely one day after the fire (less than 1 %) and in much larger amounts one month, two months and three months after the fire where represented 34 %, 27 % and 25 % of all insects caught respectively. Although caught during the whole sampling, Coleoptera, Dictyoptera, Diptera and Lepidoptera were absent one day after the fire. Except the Coleoptera whose number increased markedly two months and three months after the fire, the abundances of other less represented taxa did not vary appreciably between sampling dates. Not caught from the day before to one month after the fire, the Homoptera appeared two months and three months after the fire.

DISCUSSION

These study findings can only be interpreted in general terms, given the broad classification of taxa caught and the limited temporal resolution of the samples. However, they can be used as a basis to guide further research to achieve a much deeper understanding of fire impacts on the community of savanna-dwelling insects. During the samplings, only individuals active on and above the ground were caught, representing the "operating population" (Roth 1968). Our data allowed analyzing variations in the abundances of ground-dwelling and flying insects that were moving through the fire-break separating the experimental plots over the time span for this study. Changes in the insect community composition were assessed inside the plots in order to better understand the variations in insect's movements.

Migrations of ground-dwelling insects between plots: Significantly fewer ground-dwelling insects were caught in migration through the fire-break on the fire day than the day before. This decrease in the insect abundance might be partly due to high mortality (Rice, 1932; Buffington, 1967; Lamotte, 1975; Miller, 1979; Force, 1981; Warren *et al.,* 1987; Ditlhogo *et al.*, 1992;

Wright, 1993; Swengel & Swengel, 1999). The quantitative changes observed in the community composition reminded this mortality since the insects caught inside the burned plot one day after the fire represented only 42 % of those caught the day before the fire. Such findings matched those of Gillon (1970; 1983) on ground-living arthropods in the grass layer of this fire-prone savanna. During the same period of time, this author estimated the loss to reach 12 to 36 % of the arthropods caught before burning. Otherwise, the insects would have taken refuge in the unburned plot, waiting for the grass layer to re-grow before they return in the formerly burned plot. The Hymenoptera (mostly ants) were the only group caught between the two plots on the day of and the day following the fire. This result mirrored that of Ahlgren (1974) who had stated that many ground-living ant species have subterranean nests allowing them to survive the combustion phase. None of other ground-dwelling taxa was consistently caught inside the burned plot (except the Heteroptera) and in migration through the fire-break, neither on the fire day nor on the day following the fire. This finding may be explained by the mortality, sheltering under soil surface and flight during the burning.

One month after the fire, significantly more insects were caught between plots than on the day of and the day following the fire. This result agreed with other authors such as Rice (1932), Hurst (1971), Nagel (1973), Winter (1984) who noticed that ants increase in abundance some weeks following bush fires. It also may be explained by intensive movements of insects towards the burned plot becoming more attractive and by the appearance of new mobile adults after metamorphosis. The recolonization of the burned area coincided with an increase of the abundance of insects caught (by 53 %), reflecting the restoration of their community. Our finding differed a little from that of Gillon (1983) who found one month after the fire 35 to 39 % of the arthropods collected on the day before burning. On the other hand, the moderate influx of ground-dwelling insects through the fire break at this date might reflect a late return of some species to the burned plot (Pippin & Nichols, 1996) or probably, it was just a moving around in search for resources. Indeed, fresh grasses still offer a very limited set of micro-habitats and food resources, and in addition some insects remain more visible and are thus more vulnerable to visually hunting predators than they would be in the unburned area. This aspect-limited set of micro-habitats and partly unsuitable habitats might lead to an increased mobility of those insects searching for suitable habitats. Two months and three months after the fire, the influx of insects was strongly intensified. At these dates, insects were caught in such abundance inside the burned area that it equaled the double of that found inside the unburned plot. Contrary to this latter plot dominated by a thick layer of old dry vegetation, the vegetation in the fire-impacted plot was dominated by fresh and higher grasses and some flowering plants, offering a spectrum of different nourishments and shelter to escape predators.

Migrations of flying insects between plots: Compared to before and after the fire, the trend observed in the abundance of flying insects caught on the day of the fire suggested massive emigrations of individuals from the burned plot. As to be expected, more insects were caught flying away from the burning front, e.g. 108 individuals were caught on the fire day against 69 and 66 before and after the fire respectively. However, the two opposite fluxes were similar on the day following the fire without clear orientation in their migration. This finding might be partly explained by the fact that survivors were still searching for suitable habitats.

One month, two months and three months after the fire, the abundance of flying insects caught increased continuously and more individuals were caught moving from the unburned to the burned plot. Pollet (1972) had also noticed intensive movements of insects resettling the burned savanna after having taken refuge in the adjacent unburned areas. Many insects were caught one month after the fire, certainly because several species flew towards the open sun-shone plot or larvae living in the unburned plot massively flew out to the open savanna after their metamorphosis. Thus, the unburned plot played a double role of refuges for insects that had fled from the burning front and later, of sources for resettlement of the regenerating burned savanna plot.

Through the time of the study, flying-insect abundances fluctuated variably. Such a result suggests that each taxonomic group has its own way of reacting to the burning and following re-growth of the vegetation (Gillon, 1983). For instance, only three taxa (Diptera, Homoptera, Lepidoptera and Orthoptera) were caught in remarkable amounts between plots on the fire day. In agreement with Duviard & Pollet (1973), they returned earliest to the burned plot where they became relatively very abundant. From one month to three months after the fire, taxa such as Coleoptera inhabiting the lower stratum of the grass layer became abundant. This finding agreed with the observation of Warren *et al.* (1987) who noticed that most species resettling the burned areas during the months following the fire are plant feeders. Re-establishment of the insect community composition was rather closely linked to the regeneration of the vegetation. Although caught in lesser numbers between the plots after the fire, the Orthoptera were particularly abundant in the burned savanna. Most of their species may have had already laid eggs at the time of the fire and the new generation had probably partly developed in the burned area. Consistent with Branson & Vermeire (2007), the success of their species would depend on species-specific oviposition characteristics that mediate the negative effects of the fire on egg mortality.

The Homoptera (mostly bugs) were neither consistently nor abundantly caught while moving between the plots; however, they were abundant inside the plots. Our direct observations suggest that bugs (e.g. shade-loving adults) living near ground level took refuge in the center of grass clumps where they were able to survive the fire.

CONCLUSION

The findings of this study indicated that finding refuges in the ground or in grass tufts, and flying away from burning front are strategies for the adaptation of insects in the Lamto savanna. It also appeared that the unburned plot was a refuge for flying insects during the fire while there was no evidence of increased movement of ground-living insects between the two plots (except some ants). Otherwise, the study revealed the increase in numbers of insects as well as the increased diversity of insect guilds in the burned savanna area, which was apparent from one month to three months after the fire. Thus, it appears that unburned areas can provide a refuge for different subsets of the insect community while burned areas offer new and desirable habitats for a range of insect guilds via the new growth of grasses. Thus, we suggest to the managers of this protected area to harmonize the occurrence of the fire and protect some savanna patches in order to maximize biodiversity.

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