

Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests

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Abstract Changes in ecosystem functions following disturbances are of central concern in ecology and a challenge for ecologists is to understand the factors that affect the resilience of community structures and ecosystem functions. In many forest ecosystems, one such important natural disturbance is fire. The aim of this study was to understand the variation of resilience in six functional groups of invertebrates in response to different fire frequencies in southern Switzerland. We measured resilience by analysing arthropod species composition, abundance and diversity in plots where the elapsed time after single or repeated fires, as determined by dendrochronology, varied. We compared data from these plots with data from plots that had not burned recently and defined high resilience as the rapid recovery of the species composition to that prior to fire. Pooling all functional groups showed that

they were more resilient to single fires than to repeated events, recovering 6–14 years after a single fire, but only 17–24 years after the last of several fires. Flying zoophagous and phytophagous arthropods were the most resilient groups. Pollinophagous and epigeic zoophagous species showed intermediate resilience, while ground-litter saprophagous and saproxylophagous arthropods clearly displayed the lowest resilience to fire. Their species composition 17–24 years post-burn still differed markedly from that of the unburned control plots. Depending on the fire history of a forest plot, we found significant differences in the dominance hierarchy among invertebrate species. Any attempt to imitate natural disturbances, such as fire, through forest management must take into account the recovery times of biodiversity, including functional group composition, to ensure the conservation of multiple taxa and ecosystem functions in a sustainable manner.

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1 Introduction

Forest ecosystems are affected by different kinds of disturbance, including wildfire. Fires often lead to changes in environmental conditions, biomass, species diversity, and ecosystem function (see Peterson et al. 1998; Bengtsson et al. 2000 for reviews). Ecological theory predicts that repeatedly and moderately disturbed ecosystems are likely to have the greatest species richness and to be highly resilient to disturbance (Connell 1978; Walker 1995; Bengtsson 1998). Local

changes in environmental conditions after disturbance tend to switch the competitive balance between species, allowing a redistribution of dominance among species (Begon et al. 1999).

There is growing recognition that classifying species based on their functional types, rather than their higher taxonomic identity, is a promising approach for tackling ecological questions relating to ecosystem stability, on the scale of ecosystems, landscapes or biomes (e.g. Koricheva et al. 2000). Moreover, focusing on functional groups allows comparisons of distinct biogeographical areas even if the species assemblages are different.

Few studies have explored the effects of disturbance on functional groups of invertebrates, and even fewer have considered many different taxonomic groups concurrently. Findings to date indicate differential responses of various taxa to fire: litter- and soil-dwelling zoophagous and saprophagous species show a high resilience to fire (Wikars 2001; Hanula and Wade 2003; Parr et al. 2004), whereas pollinators are negatively affected in the phrygana ecosystem of Greece (Ne'e-man et al. 2000; Potts et al. 2003). On the other hand, saproxylic insects (Similä et al. 2002; Hyvarinen et al. 2005) generally seem to profit from fires, particularly in boreal forests, similar to all highly mobile groups that recolonize quickly (e.g. Holliday 1991; Moretti et al. 2002).

In our approach using space-for-time substitution, resilience to fire was defined as the time needed for the species composition in a site to return to its original state after a disturbance (Begon et al. 1999). Resistance to fire, on the other hand, was measured as the degree of similarity in species composition immediately after a fire (<1 year).

Resistance and resilience to fire are closely related to the fire history of the ecosystem and to the taxa referred to (Bengtsson 2002). In fire-prone regions, resistance and resilience are generally positively correlated with fire frequency (e.g. Parr et al. 2004), while ecosystems free of fire or affected by an increase in fire frequency are highly sensitive to fire (e.g. Rowell and Moore 1999).

In this paper we investigate the resilience of different functional groups of arthropods to fire, analysing community similarity, the number of species and individuals, and changes in the dominance of species within communities at different time intervals following single or repeated fires.

We expect resilience to be highest in mobile groups, and single fires to allow for a faster recovery of functional groups and dominance distributions than repeated fires.

2 Materials and methods

2.1 Study area

The study area is located on the southern slope of the Swiss Alps in the hilly and mountainous belt dominated by coppice stands of sweet chestnut (*Castanea sativa* Miller). The study area has a moist, warm temperate climate, which differs from the more southern regions with a Mediterranean climate. Rainfall in summer is about twice as high as in winter (June–September, about 800 mm; November–February, about 400 mm). The area is prone to anthropogenic, fast-spreading surface fires of low or medium intensity during the period of vegetation dormancy (December–April; Moretti et al. 2002).

In our study area fire regimes changed substantially with the introduction of agriculture ca. 7,500 years ago. Reconstruction of fire history by means of charcoal deposited into sediment archives of different sites (Tinner et al. 1999) revealed that anthropogenic fires became much more abundant during the Neolithic (7,500–4,200 years ago) and reached highest frequencies during the Iron Age (2,800–2,000 years ago), when fires were about 3–5 times more frequent than during the past 70 years (Tinner et al. 1998). Pollen and charcoal studies suggest that these anthropogenically increased fire frequencies lead to the transformation of entire vegetation communities in the southern Alps (e.g. Tinner et al. 2005), thus profoundly altering important ecosystem properties. Only with the introduction of chestnut (*C. sativa*) cultivation by the Romans 2,000 years ago, was slash and burn agriculture abandoned and fire frequencies returned to lower levels. However, these intermediate levels, which are still characteristic for today, are still well above the natural fire frequencies known from prehistoric soil profiles (Tinner et al. 2005).

The study sites were chosen on a south-facing slope (450–850 m a.s.l.), extending over 15 km near Locarno (08°44'E, 46°09'N). The sampling design was based on a space-for-time substitution (Pickett 1989). For this purpose the slope was divided into six sectors of approximately 1 km², in which a total of 22 study sites (three to four per sector) were selected. The sites were grouped into three categories of fire frequency: the first, the control plots, were defined as unburnt sites, where no fire had occurred for at least 30 years. The records of older fires are less reliable with regard to fire intensity and impacted area. In single-fire sites a fire had occurred only once in the previous 30 years, while in sites of repeated fires, fires have occurred at least 3 times in the previous 30 years. Because each sector had

a different fire history, it was not possible to have consistent replicate sites with the same fire regime in each sector. However, at least one unburnt (control) site was defined in each sector.

The sites were similar to each other in aspect, slope, soil and plant species composition, but differed in terms of fire frequency and time elapsed since the last fire. The fire history of each site was assessed using dendrochronological methods (Moretti et al. 2002). Based on dendrochronology, the sites were also attributed to four successional stages (<1, 1–3, 6–14, 17–24 years since the last fire; Table 1). The successional stages differed in tree and grass cover, as well as in forest structure (Moretti et al. 2002). Forest canopies were more open and the grass more luxuriant at burnt sites (especially at recently burnt sites) than at unburnt sites. Because of the stump resprouting and the high shoot mortality following fire, sites which had burned repeatedly were more dense than unburned sites and those which had burned only once. The dominant trees at repeatedly burned sites had a smaller diameter at 1.5 m height than those at unburned sites and those at sites burned only once (Moretti and Barbalat 2004).

2.2 Invertebrates

Invertebrates were collected using three different standard methods: pitfall traps, surface eclectors (emergence traps), and combination traps, (Duelli et al. 1999). Together, these methods allowed sampling of ground-dwelling arthropods, as well as flying and flower-visiting species. The pitfall traps consisted of plastic funnels recessed into the soil (with openings 15 cm in diameter) and mounted on top of a plastic bottle containing 2% formaldehyde solution. A roof 10 cm above the traps provided protection from rain.

Surface eclectors (Brunhes 1981) consisted of a pyramid-like construction (50×50 cm at the base) fixed on the ground and covered with a fine black wire-mesh (mesh width <0.5 mm) in order to preserve the microclimatic conditions. Emerging insects were trapped in collection vials on top of the dark pyramid, where

they tried to escape to the light. Combination traps, consisting of a non-directional window (interception) trap combined with a yellow pan, filled with water and detergent to reduce its surface tension, were placed at a height of 1.5 m above the ground. Detailed descriptions of the trapping characteristics of the traps used are available in Obrist and Duelli (1996), Duelli et al. (1999), Martikainen et al. (2000) and Moretti et al. (2002).

At each of the 22 sites, we installed three trap triplets (a pitfall trap, a combination trap, and an eclector), resulting in a total of 66 traps of each type (Table 1). The minimum distance between traps of the same type at each site was 10 m, while the average distance between the sites was 301±128 m. The traps were emptied weekly from March to September 1997. Collecting took place during 28 sampling periods, covering the main activity season of most taxa.

Totally, 111 families from seven taxonomic orders of invertebrates [Isopoda (two), Aranea (22), Coleoptera (59), Hemiptera (14), Neuroptera (four), Hymenoptera (nine), Diptera (one)] were identified to species level. These orders comprise the main terrestrial invertebrate groups for which there is good systematic and ecological knowledge available in Switzerland. Each species was assigned to one (or two, if larvae and adults belong to different groups) of six functional groups, determined by taxonomic experts. These were ground-litter saprophagous species (decomposers on the ground and litter layer), flying zoophagous, epigeic zoophagous (surface-dwelling predators), phytophagous (sucking and leaf-eating species), pollinophagous (pollinators and flower-visiting insects), and saproxylophagous arthropods (wood-eating species).

2.3 Data analysis

First of all we analysed the spatial auto-correlations among the sites for each functional group by applying a multivariate Mantel correlogram based on the normalized Mantel statistic (r_M). Significance was assessed by using Monte Carlo randomization (999 permutations)

Table 1 Trap sites grouped into the three categories of fire frequency. *Unburnt* Sites which had not burnt in the last 30 years, *Single fire* sites with one fire in the last 30 years, *Repeated fires* sites with three to four fires in the last 30 years

Fire frequency	Unburnt	Time since last fire				Total
		<1 Year	1–3 Years	6–14 Years	17–24 Years	
Unburnt (control)	18					18
Single fire		3	6	6	9	24
Repeated fires		3	6	12	3	24
Total trap triplet locations	18	6	12	18	12	66

and Bonferroni correction. The method is designed, in particular, to describe the spatial structure of species assemblages (Legendre and Legendre 1998).

For each functional group and for all groups pooled, we then calculated the number of species and individuals caught at each of the 66 trap locations. Mean values (\pm SD) were calculated per successional stage following single and repeated fires, and for the plots without fire. The mean values of normally distributed data sets (Lilliefors test, Systat 10.0; SPSS, Chicago, Ill.) were analysed by ANOVA and a subsequent Scheffé post hoc test using Systat (SPSS). When the homogeneity of variances was not achieved, the data were $\log(x+1)$ -transformed. Non-parametric Kruskal–Wallis ANOVA by rank and the by Mann–Whitney U -test with Bonferroni correction between two groups were applied if normality was not achieved (Zar 1984).

For all pairs of trap locations we calculated van der Maarel similarity coefficients for abundance data (Wildi and Orloci 1996) and statistically compared community similarity with ANOVA.

The Van der Maarel similarity coefficient is given by:

$$S_{jk} = \frac{\sum_i x_{ij} x_{ik}}{\sum_i (x_{ij} - x_{ik})^2 + \sum_i x_{ij} x_{ik}}$$

where x_{ij} = number of individuals of species i in site j ; i = species; j, k = sites. $S_{jk} = 1$ if $x_{ij} = x_{ik}$ for every species i ; $S_{jk} = 0$ if sites j and k do not share any species.

For this analysis, we only considered those species for which the total number of all individuals sampled was at least five. The number of individuals was $\log(x+1)$ -transformed in order to reduce the weight of very abundant species. Because all data were normally distributed, we used ANOVA with a subsequent Scheffé post hoc test to compare the mean values (\pm SD) of the similarity indices between the communities at each successional stage with those of the unburnt sites (control).

Numerical dominance (relative abundance) was divided into four categories (<1%, 1.0–3.1%, 3.2–9.9%,

$\geq 10\%$) (Mühlenberg 1993) and is referred to as “dominance” throughout the text. We analysed the changes in species dominance distribution in burned and unburnt sites by comparing the median values of the relative abundance of dominant ($\geq 10\%$) and sub-dominant (3.2–9.9%) species for each post-burn stage.

Finally, the degree to which species changed dominance was analysed by selecting species sampled with more than ten individuals per study site in any of the following categories: unburnt sites, freshly burnt sites (<1 year after the fire; first successional stage) and sites burnt 17–24 years ago (last successional stage). Any species that varied at least tenfold before and after the fire was tested for significance of dominance change by ANOVA, or by the equivalent Kruskal–Wallace rank ANOVA if normality was not achieved. Lacking standards, we arbitrarily chose a tenfold change (1 order of magnitude) as critical since it seems severe enough for most invertebrate groups.

3 Results

A total of 1,085 species were identified from a total of 110,482 individuals; 284 species (26%) were observed exclusively at one sample site, while at least five individuals were sampled of each of 486 species (53%). The latter were attributed to one or more functional groups: 42 (8.6%) were assigned to ground-litter saprophagous species, 146 (30.0%) to epigaeic zoophages, 166 (34.2%) to flying zoophages, 66 (13.6%) to phytophages, 262 (53.9%) to pollinophages, and 136 (28.0%) to saproxylophages (Table 2). As a species may be attributed to more than one functional group (see Materials and methods), the sum of the percentages of the different groups is higher than 100%.

All analyses were conducted treating the 22 sites as independent replicates (Hurlbert 1984), after checking for non-significant spatial autocorrelation of each functional group (multivariate Mantel correlogram).

Table 2 Total number of species and individuals (*in parentheses*) of six functional groups from the seven selected orders (Isopoda, Aranea, Coleoptera, Heteroptera, Neuroptera, Hymenoptera, Diptera)

Functional groups	Isopoda	Aranea	Coleoptera	Heteroptera	Neuroptera	Hymenoptera, Aculeata	Diptera, Syrphidae	Total species	Total individuals
Ground-litter saprophages	12 (1,147)		17 (458)			13 (9,118)		42	10,723
Epigaeic zoophages		70 (7,956)	45 (15,611)			31 (19,650)		146	43,217
Flying zoophages			12 (232)	24 (1,222)	23 (2,578)	80 (4,075)	27 (2,110)	166	10,217
Phytophages			33 (9,214)	27 (1,454)		3 (175)	3 (101)	66	10,793
Pollinophages			54 (9,063)			171 (52,375)	37 (2,704)	262	64,142
Saproxylophages			126 (14,383)	4 (53)		1 (95)	5 (437)	136	14,968

The herbivores, flying and epigeaic predators were very marginally affected by spatial autocorrelation (i.e. only one out of 24 distance classes), probably due to the spatial arrangement of burns in the study area and thus to the location of the sample sites.

3.1 Effect of fire frequency on species richness and abundance

Fires tended to affect the various taxa and functional groups rather differently. Some showed no observable effects, whereas others had not returned to their initial state even 17–24 years after the fire.

Single fires did not affect the overall number of species or individuals during the four successional stages following burning (Fig. 1a, left). A similar pattern was observed for phytophagous species (Fig. 1c, left). The species richness increased <1 year and 1–3 years after fire in flying zoophagous (Fig. 1b, left; ANOVA, $F_{4,42}=5.81$, $P<0.001$) and in pollinophagous species (Fig. 1d, left; ANOVA, $F_{4,42}=5.92$, $P<0.001$). The number of individuals of the epigeaic zoophagous species, on the other hand, decreased immediately after the fire (ANOVA, $F_{4,42}=4.45$, $P=0.004$), while numbers of ground-litter saprophagous species were still less than in sites 17–24 years following burning (ANOVA, $F_{4,42}=10.29$, $P<0.001$) (Fig. 1e, f, left).

Repeated fires affected the overall number of species (ANOVA, $F_{4,42}=5.01$, $P=0.003$) and the number of individuals significantly ($F_{4,42}=4.20$, $P=0.007$). While the number of species increased gradually until the second successional stage (1–3 years after the last fire) and decreased slightly during the next two stages (6–14 and 17–24 years), a higher number of individuals was observed only 1–3 years after the last fire. A similar pattern was found for the flying zoophagous species (Fig. 1b; $F_{4,42}=6.72$, $P<0.001$) and for pollinophagous species (Fig. 1d; ANOVA, $F_{4,42}=6.09$, $P<0.001$). While the species richness of the ground-litter saprophages did not change after repeated fires (Fig. 1f, left), the number of species of the epigeaic zoophages increased significantly 1–3 and 6–14 years after the last fire (Fig. 1e, left) (ANOVA, $F_{4,42}=11.11$, $P<0.001$). The number of individuals of both groups (Fig. 1g, left), on the other hand, decreased dramatically immediately after the fire (ANOVA, $F_{4,42}=7.78$, $P<0.001$ for the saprophages; $F_{4,42}=7.60$, $P<0.001$ for the epigeaic zoophages) as did, to a lesser extent, the number of saproxylophagous individuals ($F_{4,42}=10.56$, $P<0.001$). During the following successional stages the abundance of all three groups did not recover, not even by the last successional stage (17–24 years after the last fire).

3.2 Resilience to fire

Single and repeated fires significantly (Fig. 1a, right) affected the similarity of the overall species assemblage (ANOVA, $F_{4,42}=245.65$, $P<0.001$ for single fires and $F_{4,42}=180.75$, $P<0.001$ for repeated fires). After a single fire the overall species composition changed more strongly (the community was less resistant) than after repeated events, but showed higher resilience to single fires than to repeated ones (Fig. 1a, right). After repeated fires, the sites had overall only recovered partially, even at the last successional stage. In a Scheffé post hoc test this difference was significant, especially during the first two successional stages (<1 and 1–3 years after the fire).

For single fires a similar pattern of similarity was observed for most of the functional groups. The phytophagous and the flying zoophagous arthropods (Fig. 1c, b, right) were the most resistant groups and showed the highest resilience to fire, while the epigeaic zoophages (Fig. 1e, right; ANOVA, $F_{4,42}=33.47$, $P<0.001$), the ground-litter saprophages (Fig. 1f, right; ANOVA, $F_{4,42}=242.28$, $P<0.001$), and the saproxylophages (Fig. 1g, right; ANOVA, $F_{4,42}=219.71$, $P<0.001$) were the least resilient groups, recovering only 6–14 years after the first fire.

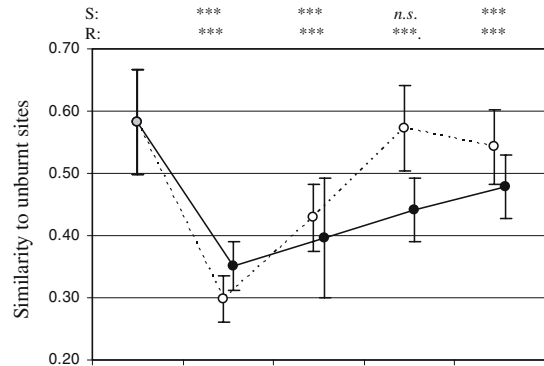
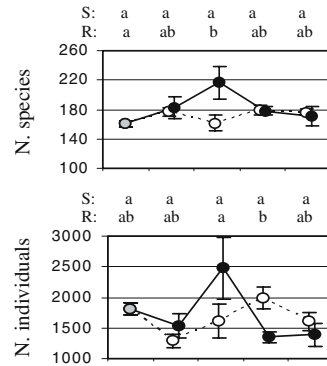
In the case of repeated fires, long-term major changes in species assemblage were observed for the epigeaic zoophagous (ANOVA, $F_{4,42}=132.54$, $P<0.001$), ground-litter saprophagous (ANOVA, $F_{4,42}=242.09$, $P<0.001$), and saproxylophagous (ANOVA, $F_{4,42}=163.65$, $P<0.001$) species. Resistance and resilience to repeated fires were lowest in these three groups. After repeated fires their communities were different from those at the pre-burn stage, even in the last successional stage after burning.

3.3 Dominance distribution after the fire

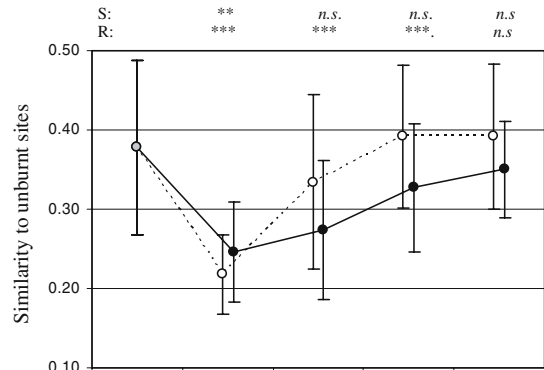
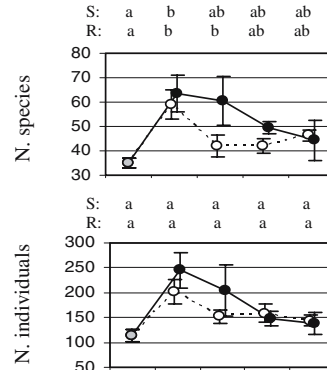
At unburnt sites the number of dominant ($\geq 10\%$) and subdominant (3.2–9.9%) species varied from a maximum of six epigeaic zoophagous and flying zoophagous species, to a minimum of three saproxylophagous species (Table 3). The functional groups that underwent major changes in dominance after a fire were the epigeaic and flying zoophagous, as well as the saproxylophagous species. More than 60% of the species with dominance $\geq 3.2\%$ were replaced by minor species (dominance $< 3.2\%$) during the first two successional stages after the fire. For the other groups, only 30% of the dominant and subdominant species were replaced shortly after fires. In the third successional stage (6–14 years after the last event), the dominant and sub-

Fig. 1a–g Mean number of species and individuals (\pm SE), and mean of similarity coefficient (\pm SD) (van der Maarel) for species assemblages at the different successional stages (< 1, 1–3, 6–14, 17–24 years) after single (S; open circle) and repeated (R; filled circle) fires versus species assemblages at the 18 unburnt sites as controls. Data points with different letters are significantly different. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. not significant

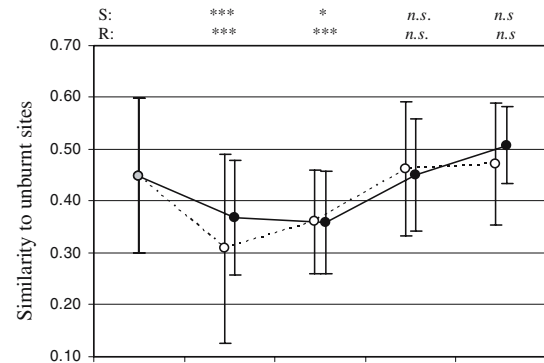
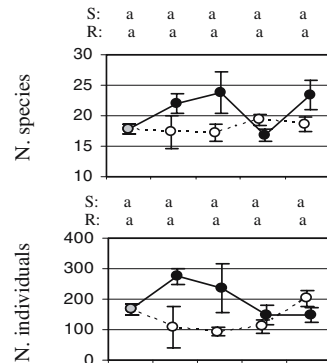
a) Overall functional groups



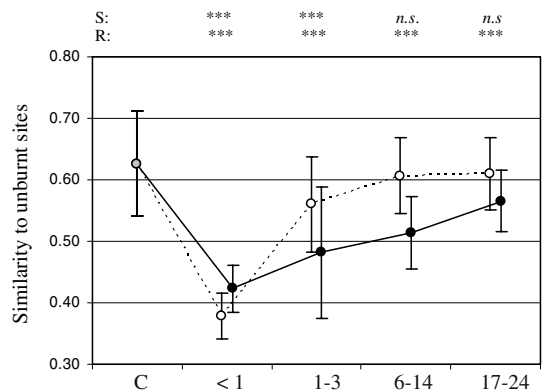
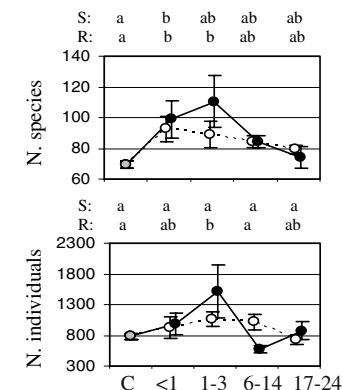
b) Flying zoophages



c) Phytophages



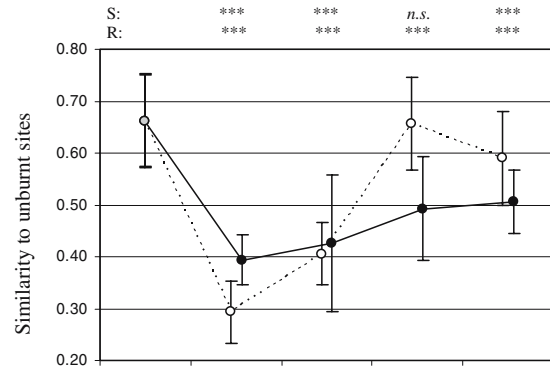
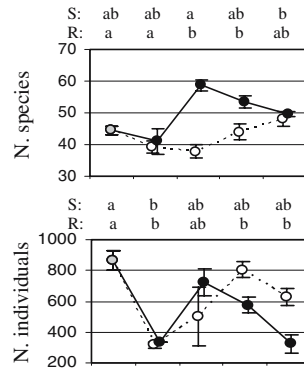
d) Pollinophages



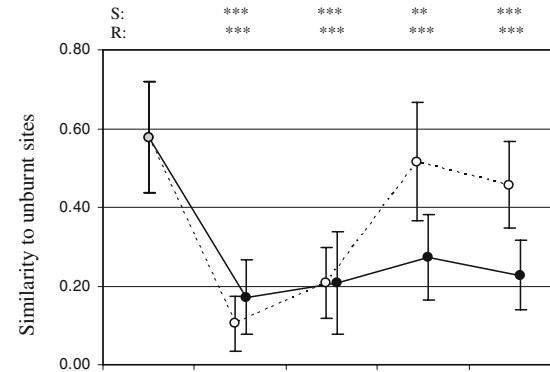
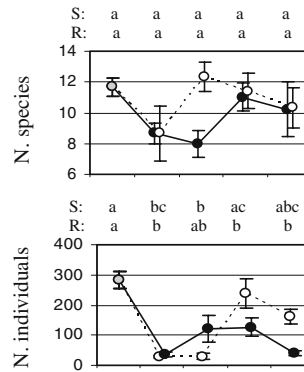
Time elapsed since the last fire (years)

Fig. 1a–g continued

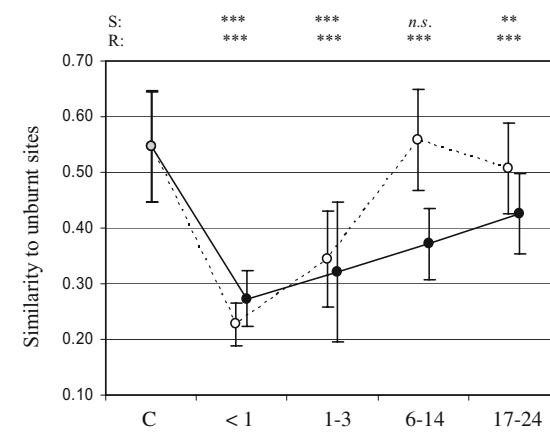
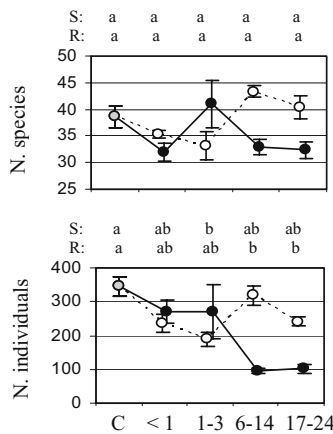
e) Epigeaic zoophages



f) Ground-litter saprophages



g) Saprophylophages



Time elapsed since the last fire (years)

dominant species of most functional groups recovered completely after repeated fires. Exceptions were the flying zoophages and the ground-litter saprophages.

Such processes of dominance redistribution after fire increase the proportion of newly dominant or subdominant species about threefold (from five to 16 species) during the first two successional stages, reaching nearly 4 times as many (from five to 19 species) at the last stage (Fig. 2). On the other hand, the dominant and subdominant species in the unburnt

forests decreased by half during the first year following a fire, but they recovered almost completely 6–14 years after the fire.

3.4 Species most affected by fire

Among the species sampled with an average of at least ten individuals per study site at unburnt or freshly burnt sites, 24 species increased at least tenfold at freshly burnt sites, but only three of them were sig-

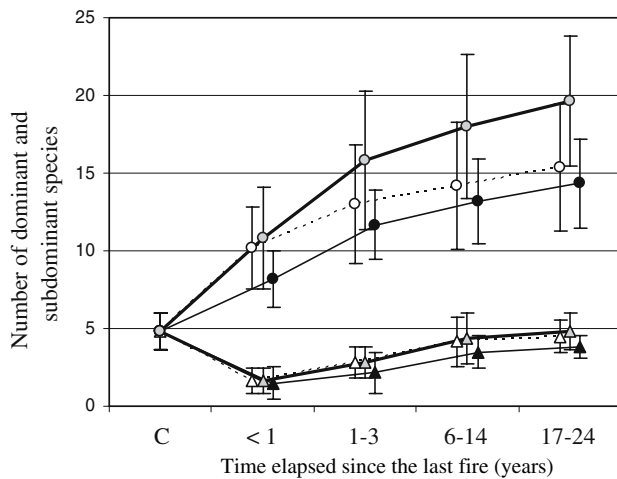


Fig. 2 Changes in the number of dominant and subdominant species after the fire. Cumulative number of new dominant and subdominant species (circles), and those remaining intact (triangles) during the successional stages (<1, 1–3, 6–14, 17–24 years) after single (black symbols) and repeated (empty symbols) fires. The grey symbols and the thicker line indicate the overall variation of dominant and subdominant species after fire

nificantly more abundant at the last successional stage compared to unburnt sites (Table 4). The most favoured species belonged to the pollinophagous taxa (+47.4% after a single fire and +45.0% after repeated fires) such as *Hylaeus communis*, *Lasioglossum rufitarse*, *Lasioglossum pygmaeus* (Hymenoptera), *Sphaerophoria scripta* (Diptera) and *Oedemera flavipes* (Coleoptera). Similarly some saproxylophagous taxa increased their abundance (+31.6% after a single fire and +35.0% after repeated fires), e.g. *Anthrenus museorum*, *Corticarina similata*, and *Orius horvathi* (Coleoptera). Three species were still significantly more abundant at the last successional stages: the pollinophagous *Hylaeus gibbus*, *Lasioglossum morio* (Hymenoptera), and the saproxylophagous *Harpocera thoracica* (Hemiptera).

On the other hand, 28 species disappeared or decreased to one-tenth their number shortly after the fire. Fourteen of them remained significantly less abundant at the last successional stage compared to the unburnt sites (Table 4). The most negatively affected species belonged to the epigeic zoophagous group (–45.0% after a single fire and –50.0% after repeated fires), e.g. the ants *Stenamma striolatum*, *Aphaenogaster subterranean*, *Leptothorax parvulus* and *L. nylanderii* (Hymenoptera), *Pterostichus micans* (Coleoptera), and *Lepthyphantes flavipes* (Aranea). The abundance of some pollinophagous species decreased in a similar way (–30.0% after a single fire and –21.4% after repeated fires), as in *Lasioglossum politum* (Hymenoptera), or in the saproxylophagous

Ptinus bidens (Coleoptera). Fourteen species did not recover at this stage, particularly at repeatedly burnt sites: the epigeic zoophagous *Coelotes mediocris* (Aranea), *Aphaenogaster subterranea*, *Leptothorax nylanderii*, *L. parvulus*, *Stenamma striatum* (Hymenoptera Formicidae), the pollinophagous *Andrena fulvata*, *A. nigroaenea*, *Lasioglossum politum* (Hymenoptera), the ground-litter saprophagous *Dienerella clathrata*, *Enicmus minutus*, *Lathridius nodifer* (Coleoptera), and the saproxylophagous *Ptinus bidens* (Coleoptera).

4 Discussion

4.1 Species composition and functional groups

To assess ecological resilience we can either focus on the taxonomic level and measure the time it takes after an event to return to the original species composition, or we can focus on the functional level, where it is ecologically relevant whether a species accomplishes one or several ecological functions in a lifetime. Here we advocate the latter approach. Accordingly, we assigned every species to one or two of six functional groups, depending on its life history traits as larvae or adults. Out of the 1,085 identified species, 281 were counted twice in the analysis of the functional groups. As the double-counting species were equally distributed among the six functional groups, we judge a potential bias in the analysis of the entity of all functional groups as negligible.

In the analysis of single functional groups this bias was not involved as every species only contributed once to a specific group.

4.2 Abundance, diversity and resilience to fire

The response of invertebrates to fire results from both direct mortality and post-fire succession. Direct mortality depends on the fire regime, but also on the biotic conditions during the fire, such as the particular habitat occupied by a species, its developmental stage, and its mobility during the fire (e.g. Niwa and Peck 2002; Hoffmann 2003).

Post-fire succession depends on the new environmental conditions, on the rate at which differences in competitive abilities are expressed in space and time (Huston 1979, 1994), and on the potential for immigration, i.e. on the composition and structure of the surrounding habitats. The species compositions before a fire, particularly the presence of minor species that are able to take advantage of post-burn conditions, are

important for the development of the community during post-fire succession. The surviving and quickly immigrating species are the ones that have the greatest advantage in early stages of the succession. Our results for all functional groups at burned sites, particularly after repeated fires, corroborate the observation of several other authors that disturbances promote species richness in forests (e.g. Haydon et al. 2000; Similä et al. 2002; Sippola et al. 2002).

The long-term dynamics of space and the heterogeneity of structure and resources result in a variety of more or less temporary habitats for a large number of species (e.g. Reed et al. 2000; Debinski et al. 2001; Mielikainen and Hynynen 2003). This is predicted by the mosaic concept (e.g. Forman and Gordon 1986; Duelli 1997) and the patch-dynamics model (Tilman 1982). Epigeic predators provide evidence of these dynamics through an increase in species richness and a change in species composition in a diverse environmental microhabitat (Moretti et al. 2002). This was to be expected as we observed a general increase in the number of invertebrates as potential prey after the fires in our study.

The winter fires of the contemporary chestnut forests in the southern Alps tend to be of low or medium intensity (Marxer 2003). In order to link our results with the intermediate disturbance hypothesis (Connell 1978), we have to be able to sample and quantify a broad spectrum of disturbance intensities. Since there are no records of fires of high intensity, the frequency of repeated fires or the time elapsed since the last fire can also be measures of disturbance intensity (Collins et al. 1995; Li et al. 2004). But even then, the fact that our data show a tendency of species richness increasing with fire frequency suggests that these chestnut communities are still in the increasing phase of the hump predicted by the intermediate disturbance hypothesis (Huston 1979).

Post-fire changes in species composition vary according to fire frequency. In several functional groups we found higher resilience to single rather than to repeated fires. The temporary increase in the number of pollinophagous, phytophagous and flying zoophagous individuals and species in burnt areas and their high resilience to fire is very likely due to their high mobility. The increase observed in these flying arthropods arises from their opportunistic exploitation of suitable resources on a large spatial scale in a landscape mosaic created by previous fires, forest clearings, natural gaps, fire residuals, and intact patches of forest (e.g. Moretti et al. 2004). Most ecological processes and interactions depend on spatial scales much larger than a single habitat. Flying invertebrate

groups may therefore benefit more from ecological processes related to disturbances on a landscape scale (Steffan-Dewenter et al. 2002).

The pollinophagous species in our study did not show the long-term decline after fire in the Mediterranean due to post-fire floral resource quality as reported by other authors (e.g. Ne'eman et al. 2000; Potts et al. 2003), but rather a complete recovery of the pre-fire situation 17–24 years after the fire. This can be explained by the quick recovery of the chestnut trees, which are known to be a high-quality nectar source for wild and honey bees (e.g. Crailsheim 1992). This also confirms the findings of Potts et al. (2005) that nesting resource availability for bees varied markedly across habitats in different stages of post-fire regeneration in the Mediterranean, thus influencing the bee community structure and species richness.

The ground-litter saprophagous and saproxylophagous arthropods, on the other hand, showed the lowest resilience to repeated fires of all the groups. The species richness of both was not significantly affected by fire, but the number of individuals decreased dramatically. The main reasons for the long-term changes in species composition observed following repeated disturbances are probably the change in the post-fire ground-habitat conditions (Siemann et al. 1997; Wikars 2001) and in the coarse woody debris diversity (Stephens and Moghaddas 2005), as well as the high specialisation and sensitivity to habitat changes of many saproxylophagous species (Dajoz 2000; Wermelinger et al. 2002).

4.3 Dominance shifts

Many authors emphasise that disturbance plays a major role in driving evolutionary adaptations (e.g. Walker et al. 1999; Nyström and Folke 2001; Peterson 2002), but responses to disturbance vary between species. Whereas certain species benefit from a particular type of disturbance, others suffer and decrease, depending on their specific adaptation. According to Huston (1979, 1994), the species diversity found at any location is the result of a dynamic equilibrium between competitive displacement and disturbance. In our case changes in resources could account for the change in species composition, particularly in the case of repeated fires and fires that occurred <1 and 1–3 years before the investigation. Our results suggest that changes and fluctuations in environmental post-fire conditions altered the species composition among all functional groups. This resulted in a redistribution of the species dominance among the community groups whereby some formerly inferior competitors

became dominant. Our results show that the species favoured by disturbance were already present in the community and had survived exogenic and anthropogenic disturbances in the past. They either survived during the fires or immigrated from the surrounding area. This result could explain the high resilience to fire observed in our study by most functional groups. According to the resilience hypothesis (Ludwig et al. 1997), dominant and minor species may respond differently even when they are functionally similar. In the majority of the functional groups in our study, dominant species were primarily affected negatively by disturbances, whereas some minor species (<3.1% of dominance) seem to have benefited from new opportunities and increased, thus becoming dominant or subdominant.

4.4 Responses of the species most affected by fire

The pollinivorous and, in particular, mobile saproxylophagous species were positively affected by fire. They exploit open habitats and forest edges, such as gaps created by fires or clearings, as well as rocky sites, on a large spatial scale (i.e. *Lasioglossum rufitarse*, *L. pygmaeus* (Hymenoptera), *Sphaerophoria scripta* (Diptera), and *Oedemera flavipes* (Coleoptera)). Some of those species depend on dead wood for a certain period of their development. Examples are *Hylaeus gibbus* and *Lasioglossum morio* (Hymenoptera), which nest in the galleries of xylophagous beetles (Westrich 1989), and *Xylota segnis* (Diptera), which has a xylophagous larval stage (Röder 1990). For these species, as well as for saproxylophagous taxa like *Leptura maculata*, *Stenopterus rufus*, *Corticarina ferruginea* and *C. similata* (Coleoptera) (Bense 1995), fire is likely to play an important role as it creates new structural elements and habitats such as gaps and dead wood.

The epigeic zoophagous and, to a lesser extent, the ground-litter saprophagous species suffered most from the fire. Species associated with old-growth forests were particularly affected, e.g. *Leptothorax parvulus*, *L. nylanderi*, *Aphaenogaster subterranea*, *Stenammina striatulus* (Hymenoptera Formicidae), *Pterostichus micans*, *Dienerella clathrata*, *Enicmus minutus* and *Lathridius nodifer* (Coleoptera). Many of them are small and sedentary, and therefore potentially vulnerable to fire (Koch 1989; Seifert 1996). Many pollinivorous species, like the wild bees *Lasioglossum politum*, *Andrena haemorrhoa*, *A. nigroaenea* and *A. fulvata*, were also negatively affected by fire. These species are particularly vulnerable to fire because they nest on the ground, in the litter layer, under stones and wood (Seifert 1996).

4.5 Implications for forest management

In the forests of the southern Alps, it seems that most invertebrate species have adapted to past disturbance regimes created by fire and human exploitation. There is good evidence (e.g. Tinner et al. 1999) from which to assume that disturbance of ecosystems by fire has led to strong selective processes not only among plants, but also among invertebrates, since the intermediate fire levels which are characteristic for today are still well above the natural fire frequency. Although these forest communities appear to be quite resilient to fire, prescribed burning cannot be advocated as a preventative measure to avoid intensive crown fires. Most fires occur in the springtime, when the deciduous broadleaved trees have no leaves, limiting the risk of crown fires. However, even low intensity fires increase the risk of more run-off erosion, which is a highly undesirable effect in the densely inhabited and steep hilly region south of the Alps (Marxer 2003; Conedera et al. 2003).

The cultivation of chestnut forests as coppice for timber production started in most parts of Europe with the Romans, who also introduced the tree species itself. Thus, coppices of chestnut forests were managed intensively for about 2,000 years. In most countries with a long tradition of chestnut cultivation, chestnut coppices were cut in a 15- to 20-year rotation for pole, firewood and charcoal production (Conedera et al. 2004a, b). However, in southern Switzerland the traditional chestnut coppices have mostly been abandoned since the 1960s (Conedera et al. 2001). We suggest reconsidering coppicing chestnut forests on small areas and leaving part of the dead wood in the field to mimic frequent disturbances of low intensity. The conservation of tracts of intact forests should provide suitable biotopes for late successional organisms, which require dead and old wood and generally stable conditions.

Informed management of chestnut forests requires an understanding of ecosystem resilience. While Baker et al. (2004) found little difference between the beetle fauna after logging or wildfire treatments in Tasmanian forests, Buddle et al. (2000) and Saint-Germain et al. (2005) observed a significant divergence in spiders' and carabid beetles' responses to such disturbances in boreal forests. Could patch-wise clearfelling and harvesting be a way of preserving a fire-adapted biodiversity without the negative effects of forest fires (emissions and erosion), and at the same time allow for the production of valuable chestnut timber? If attempts are made to imitate a natural disturbance such as a forest fire through forest management and interventions, like harvesting timber in small-scale coppice groves, they must take into account the recovery times of func-

tionality and biodiversity to allow for a multifunctional, but still sustainable, form of management.

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Appendix (Tables 3, 4)

Table 3 a–f Transient or non-transient changes in dominance at the species level. Median value of relative abundance (dominance) in the different functional groups at the unburnt site (control) and the successional stages (<1, 1–3, 6–14,

17–24 years) after single and repeated fires (dominance: (big filled circle) ≥10%, (big open circle) 3.2–9.9%, + 1.0–3.1%, (small filled circle) <1%, -0%)

10a) Epigaic zoophages

Species	Systematic group	Unburnt	Single fire				Repeated fires			
			< 1	1-3	6-14	17-24	< 1	1-3	6-14	17-24
<i>Dienerella clathrata</i>	Col	●	○	●	●	●	●	+	○	○
<i>Lasius emarginatus</i>	For	●	●	●	○	●	○	●	●	○
<i>Leptothorax nylanderi</i>	For	●	-	+	●	○	●	●	+	●
<i>Pterostichus micans</i>	Col	○	-	+	○	○	●	●	○	●
<i>Abax continuus</i>	Col	○	+	+	○	○	+	●	+	○
<i>Aphaenogaster subterranea</i>	For	○	-	+	●	+	●	+	○	●
<i>Corticaria ferruginea</i>	Col	●	●	●	-	●	●	●	●	-
<i>Stenammina debile</i>	For	●	○	+	-	+	○	●	●	●
<i>Lepthyphantes pall. pallidus</i>	Ara	●	○	+	+	+	+	●	+	+
<i>Tegenaria fuesslini</i>	Ara	+	○	+	+	+	+	+	+	+
<i>Lasius platythorax</i>	For	+	○	●	●	●	+	○	+	-
<i>Carabus glabratus</i>	Col	●	+	○	-	●	●	●	●	-
<i>Diplostyla concolor</i>	Ara	●	●	○	●	●	●	●	●	●
<i>Leptothorax parvulus</i>	For	+	-	●	●	○	●	●	●	●
<i>Carabus problematicus</i>	Col	+	+	-	○	○	+	+	●	+
<i>Pardosa saltans</i>	Ara	+	●	●	○	○	●	○	○	○
<i>Forica fusca</i>	For	+	+	○	+	○	●	○	+	○
<i>Abax baenningeri</i>	Col	+	+	●	+	○	+	●	●	+
<i>Myrmica ruginodis</i>	For	●	-	-	●	+	-	○	●	-
<i>Lasius psammophilus</i>	For	●	●	+	-	●	●	+	●	○
<i>Amaurobius jugorum</i>	Ara	●	●	+	+	+	+	●	+	○
<i>Leptothorax unifasciatus</i>	For	●	-	-	+	+	-	●	●	○
Total dominant species	●	3	2	2	4	2	2	2	3	1
Total subdominant species	○	3	5	3	5	8	2	4	4	8

b) Saproxylrophages

Species	Systematic group	Unburnt	Single fire				Repeated fires			
			< 1	1-3	6-14	17-24	< 1	1-3	6-14	17-24
<i>Dienerella clathrata</i>	Col	●	○	●	●	●	●	○	●	●
<i>Ptinus bidens</i>	Col	●	●	●	●	●	-	○	+	○
<i>Lathridius nodifer</i>	Col	○	●	○	+	○	+	+	○	○
<i>Xyleborinus saxesenii</i>	Col	●	●	○	●	●	●	+	●	+
<i>Coxelus pictus</i>	Col	●	●	●	●	●	●	●	○	○
<i>Magdalis cerasi</i>	Col	●	●	+	●	+	●	○	●	+
<i>Xyleborus dispar</i>	Col	●	-	+	●	+	-	+	+	○
<i>Corticaria ferruginea</i>	Col	●	●	●	-	●	●	●	●	-
<i>Xylota segnis</i>	Syr	●	○	●	●	●	○	○	●	-
<i>Oedemera flavipes</i>	Col	●	○	●	●	●	+	●	●	+
<i>Isomira murina</i>	Col	●	-	-	+	○	●	●	●	+
<i>Leptura maculata</i>	Col	●	+	+	●	●	+	○	+	●
<i>Chlorophorus figuratus</i>	Col	-	●	-	-	-	●	○	●	-
<i>Acalles roboris</i>	Col	+	●	●	+	+	+	●	○	○
<i>Aneurys laevis</i>	Het	●	-	-	●	●	-	●	●	○
Total dominant species	●	2	1	2	2	2	2	1	1	1
Total subdominant species	○	1	3	2	0	2	1	6	3	6

Table 3 continued

c) Ground-litter saprophages

Species	Systematic group	Unburnt	Single fire				Repeated fires			
			< 1	1-3	6-14	17-24	< 1	1-3	6-14	17-24
<i>Leptothorax nylanderi</i>	For	●	-	●	●	●	+	+	○	+
<i>Leptothorax parvulus</i>	For	○	-	+	●	●	•	+	○	+
<i>Stenamamma striatulum</i>	For	○	+	+	•	○	•	○	•	•
<i>Trichoniscus alemannicus</i>	Iso	○	○	-	+	+	○	+	+	●
<i>Stenamamma debile</i>	For	+	●	●	-	+	●	+	+	•
<i>Tiroloscia exigua</i>	Iso	•	●	•	-	•	●	-	•	-
<i>Cylisticus bieliensis</i>	Iso	•	○	○	•	•	●	•	•	+
<i>Lepidoniscus pruinosus</i>	Iso	+	○	-	•	+	+	•	●	○
<i>Lasius umbratus</i>	For	•	○	+	-	•	•	•	•	-
<i>Tetramorium caespitum</i>	For	•	○	+	-	•	•	+	•	-
<i>Pseudophonus rufipes</i>	Col	-	○	•	-	-	-	•	•	-
<i>Notiophilus biguttatus</i>	Col	•	+	○	-	•	○	-	-	-
<i>Cryptophagus sp.</i>	Col	•	-	○	+	•	-	•	•	+
<i>Nicrophorus vespilloides</i>	Col	•	-	○	•	•	-	+	•	+
<i>Geotrupes niger</i>	Col	•	+	○	•	•	-	•	•	-
<i>Nicrophorus humator</i>	Col	•	+	○	•	•	•	•	•	-
<i>Nicrophorus investigator</i>	Col	•	-	○	•	•	-	○	•	○
<i>Leptothorax unifasciatus</i>	For	+	-	-	○	○	-	○	○	●
<i>Myrmica ruginodis</i>	For	•	-	-	+	○	-	●	●	-
<i>Orthometopon planum</i>	Iso	+	+	•	+	+	•	+	○	●
<i>Myrmica sabuleti</i>	For	•	-	-	+	•	•	○	○	+
<i>Myrmecina graminicola</i>	For	+	-	•	•	•	-	○	•	•
<i>Sciodrepoides watsoni</i>	Col	-	-	-	-	-	-	○	-	-
Total dominant species	●	1	2	2	2	2	3	1	2	3
Total subdominant species	○	3	5	7	1	3	2	6	5	2

5d) Phytophages

Species	Systematic group	Unburnt	Single fire				Repeated fires			
			< 1	1-3	6-14	17-24	< 1	1-3	6-14	17-24
<i>Attelabus nitens</i>	Col	●	●	●	●	●	●	●	●	●
<i>Polydrusus marginatus</i>	Col	●	●	-	○	●	●	○	○	●
<i>Kleidocerys resedae</i>	Het	●	•	○	○	•	•	•	+	○
<i>Strophosoma melanogrammum</i>	Col	○	•	•	○	+	•	○	●	○
<i>Otiorhynchus difficilis</i>	Col	○	•	+	○	○	-	•	○	○
<i>Polydrusus cervinus</i>	Col	+	○	○	○	○	●	+	+	○
<i>Phyllobius argentatus</i>	Col	+	●	○	○	+	●	•	○	-
<i>Homorhynchus hirticornis</i>	Col	+	○	○	○	+	+	•	•	+
<i>Dicyphus errans</i>	Het	•	○	○	-	•	+	•	-	-
<i>Magdalis cerasi</i>	Col	+	•	○	•	+	•	○	•	+
<i>Magdalis flavicornis</i>	Col	•	•	○	+	•	•	+	+	+
<i>Dicyphus flavoviridis</i>	Het	-	-	○	-	-	•	-	-	-
<i>Scolopostethus cognatus</i>	Het	•	-	-	○	•	-	-	•	-
<i>Rhynchaenus rusci</i>	Col	•	•	•	-	○	+	+	•	+
<i>Lasiornychites sericeus</i>	Col	•	•	•	-	•	○	+	•	•
Total dominant species	●	3	3	1	1	2	4	1	2	2
Total subdominant species	○	2	3	8	7	3	0	3	3	4

Table 3 continued

e) Pollinophages

Species	Systematic group	Unburnt	Single fire				Repeated fires			
			< 1	1-3	6-14	17-24	< 1	1-3	6-14	17-24
<i>Andrena minutula</i>	Apo	●	○	●	●	●	○	●	●	●
<i>Dienerella clathrata</i>	Col	●	+	○	○	●	○	+	○	○
<i>Apis mellifera</i>	Apo	●	+	○	○	○	+	○	○	○
<i>Lasioglossum minutulum</i>	Apo	○	○	○	○	○	+	○	○	+
<i>Andrena fulvata</i>	Apo	○	•	+	•	○	+	•	•	•
<i>Lasioglossum morio</i>	Apo	+	●	○	●	○	●	●	○	●
<i>Hylaeus communis</i>	Apo	•	●	○	•	•	●	+	○	•
<i>Corticaria ferruginea</i>	Col	•	●	•	-	•	●	•	•	-
<i>Lasioglossum laticeps</i>	Apo	+	○	+	•	+	○	+	•	+
<i>Lasioglossum pygmaeum</i>	Apo	•	○	•	•	•	○	•	•	•
<i>Melangyna lasiophthalma</i>	Syr	+	-	○	+	+	•	•	+	•
<i>Lasioglossum fulvicorne</i>	Apo	+	•	+	○	+	•	+	+	+
<i>Bombus pascuorum</i>	Apo	+	+	+	○	+	•	+	+	+
<i>Andrena helvola</i>	Apo	+	•	+	•	○	+	●	•	+
<i>Forica fusca</i>	For	+	•	+	+	○	•	○	+	○
<i>Lasioglossum politum</i>	Apo	+	-	•	+	+	•	○	○	●
<i>Oedemera flavipes</i>	Col	•	+	•	•	•	•	○	•	•
<i>Andrena dorsata</i>	Apo	+	•	+	+	+	•	+	○	+
<i>Lasius psammophilus</i>	For	•	•	•	•	•	•	+	•	○
Total dominant species	●	3	3	1	2	2	3	3	1	3
Total subdominant species	○	2	4	5	5	6	4	5	7	4

5f) Flying zoophages

Species	Systematic group	Unburnt	Single fire				Repeated fires			
			< 1	1-3	6-14	17-24	< 1	1-3	6-14	17-24
<i>Melangyna lasiophthalma</i>	Syr	●	-	●	○	●	•	+	○	+
<i>Panorpa communis</i>	Neu	●	+	○	●	○	+	+	●	●
<i>Semidalis aleyrodiForis</i>	Neu	○	•	-	●	○	•	•	+	○
<i>Vespula vulgaris</i>	Hym	○	+	+	○	○	+	+	+	○
<i>Deraeocoris lutescens</i>	Het	○	•	+	●	+	•	•	•	+
<i>Chrysoperla carnea</i>	Neu	○	○	○	○	+	+	+	+	•
<i>Crossocerus quadrimaculatus</i>	Hym	+	○	+	○	○	○	○	+	○
<i>Orius horvathi</i>	Het	-	○	+	•	•	●	•	-	•
<i>Sphaerophoria scripta</i>	Syr	•	○	+	-	-	+	+	•	•
<i>Hemerobius humulinus</i>	Neu	•	○	+	•	•	+	+	+	+
<i>Hemerobius micans</i>	Neu	+	○	+	+	+	+	•	+	+
<i>Passaloecus corniger</i>	Hym	•	○	•	•	•	+	•	+	•
<i>Passaloecus insignis</i>	Hym	+	○	•	•	+	○	+	○	•
<i>Spilomena troglodytes</i>	Hym	+	○	+	○	+	+	○	+	+
<i>Dicyphus errans</i>	Het	•	+	○	-	•	+	•	-	-
<i>Crossocerus annulipes</i>	Hym	•	+	○	-	•	-	•	•	-
<i>EpiSyrus balteatus</i>	Syr	+	+	○	•	+	○	+	+	○
<i>Harpocera thoracica</i>	Het	+	•	•	+	○	○	○	•	○
<i>Priocnemis perturbator</i>	Hym	+	+	•	•	+	•	○	+	○
<i>Psenulus pallipes</i>	Hym	•	+	+	+	•	•	+	○	+
<i>Trypoxylon minus</i>	Hym	•	+	-	•	•	•	+	○	•
<i>Syrus torvus</i>	Syr	+	•	+	•	+	+	+	○	•
<i>Vespula rufa</i>	Hym	•	•	•	•	+	•	•	•	○
Total dominant species	●	2	0	1	3	1	1	0	1	1
Total subdominant species	○	4	9	5	5	5	4	4	5	7

Changes by the dominant ($\geq 10\%$) and subdominant (3.2–9.9%) species have to be interpreted as major/important change/alteration within a community

Systematic groups: *Ara* Aranea, *Col* Coleoptera, *For* Formicidae, *Het* Heteroptera, *Iso* Isopoda, *Neu* Neuroptera, *Syr* Syrphidae

Table 4 Species whose abundances were significantly affected in the short or long term by single or repeated fires. Mean number of individuals per trap site of fire-affected species varied tenfold either shortly after the fire (< 1 year) or at the last successional

stage (17–24 years after the last fire). The mean values were tested by ANOVA or non-parametric Mann–Whitney U-test if homogeneity of variance was not achieved

Functional group	Species	Systematic group	Total ind.	Unburnt > 30 years	Single fire			Repeated fires					
					< 1 year	17–24 years		< 1 year	17–24 years				
Species favoured by fire													
Pollinophages	<i>Hylaeus communis</i>	Hym	1,489	0.5	132.0	***	1.8	n.s.	121.7	***	0.3	n.s.	
	<i>Hylaeus gibbus</i>	Hym	183	0.2	3.7	***	0.6	n.s.	2.7	**	2.3	*	
	<i>Lasioglossum morio</i>	Hym	4,738	18.4	108.3	*	21.4	n.s.	118.3	*	223.0	***	
	<i>Lasioglossum pygmaeum</i>	Hym	592	2.3	75.7	***	1.8	n.s.	65.7	***	1.0	n.s.	
	<i>Lasioglossum rufitarse</i>	Hym	92	0.2	7.3	**	0.4	n.s.	5.0	*	0.0	n.s.	
	<i>Melanostoma scalare</i>	Syr	49	0.2	6.0	**	0.7	n.s.	3.7	**	0.7	n.s.	
	<i>Platycheirus scutatus</i>	Syr	70	0.4	6.0	**	1.3	n.s.	6.3	**	0.0	n.s.	
	<i>Sphaerophoria scripta</i>	Syr	103	0.2	13.3	**	0.0	n.s.	7.7	*	0.3	n.s.	
	<i>Xylota segnis</i>	Syr	393	0.7	16.0	***	1.0	n.s.	14.7	***	0.0	n.s.	
	<i>Oedemera flavipes</i>	Col	437	0.3	8.7	**	0.1	n.s.	3.3	**	1.0	n.s.	
	Saproxylophages	<i>Anthrenus museorum</i>	Col	24	0.0	0.3	*	0.0	n.s.	7.7	***	0.0	n.s.
		<i>Corticaria ferruginea</i>	Col	579	0.7	86.7	***	1.0	n.s.	92.7	***	0.0	n.s.
		<i>Corticarina similata</i>	Col	20	0.0	2.3	*	0.0	n.s.	3.7	*	0.0	n.s.
		<i>Leptura maculata</i>	Col	142	0.3	4.3	**	0.7	n.s.	3.0	n.s.	0.7	n.s.
<i>Stenopterus rufus</i>		Col	79	0.0	4.7	*	0.0	n.s.	3.7	*	0.0	n.s.	
<i>Dicyphus errans</i>		Het	70	0.1	4.0	*	0.1	n.s.	3.0	*	0.0	n.s.	
<i>Harporera thoracica</i>		Het	286	1.4	1.3	n.s.	14.1	**	14.0	***	6.7	n.s.	
<i>Orius horvathi</i>		Het	179	0.0	16.0	***	0.1	n.s.	32.3	***	0.3	n.s.	
<i>Passaloecus corniger</i>		Hym	104	0.5	6.7	**	0.1	n.s.	7.0	**	0.3	n.s.	
<i>Passaloecus gracilis</i>		Hym	58	0.2	4.7	**	0.4	n.s.	1.7	n.s.	0.3	n.s.	
Flying zoophages	<i>Passaloecus insignis</i>	Hym	207	1.2	7.3	**	2.1	n.s.	12.0	**	0.7	n.s.	
	<i>Pemphredon inornata</i>	Hym	75	0.1	2.0	**	0.4	n.s.	5.0	***	0.7	n.s.	
	<i>Lasiorrhynchites sericeus</i>	Col	97	0.7	3.7	*	1.4	n.s.	11.7	**	1.0	n.s.	
	<i>Phyllobius argentatus</i>	Col	523	3.8	46.0	***	3.1	n.s.	52.3	***	0.0	n.s.	
Species negatively affected by fire													
Epigaeic zoophages	<i>Coelotes mediocris</i>	Ara	136	4.2	0.0	*	1.2	n.s.	0.0	*	0.0	**	
	<i>Lepthyphantes flavipes</i>	Ara	556	11.9	1.0	*	8.9	n.s.	1.7	*	5.0	n.s.	
	<i>Tapinocyba maureri</i>	Ara	229	5.8	0.3	n.s.	6.1	n.s.	0.0	n.s.	4.3	n.s.	
	<i>Trochosa hispanica</i>	Ara	525	5.5	0.0	*	4.3	n.s.	0.3	*	6.7	n.s.	
	<i>Aphaenogaster subterranea</i>	Hym	1,768	41.3	0.0	*	19.6	n.s.	0.7	**	1.7	*	
	<i>Leptothorax nylanderi</i>	Hym	5,066	206.1	0.0	*	57.9	*	0.7	***	1.0	***	
	<i>Leptothorax parvulus</i>	Hym	1,404	17.5	0.0	*	50.3	n.s.	0.3	*	0.7	*	
	<i>Leptothorax unifasciatus</i>	Hym	426	7.3	0.0	n.s.	15.3	*	0.0	n.s.	12.0	n.s.	
	<i>Myrmecina graminicola</i>	Hym	147	4.6	0.0	*	1.2	n.s.	0.0	*	0.3	*	
	<i>Stenammina striatulum</i>	Hym	342	11.7	0.3	*	7.1	n.s.	0.3	*	0.3	*	
	<i>Pterostichus micans</i>	Col	2,328	52.0	0.0	**	58.6	n.s.	2.3	*	50.0	n.s.	
	Pollinophages	<i>Andrena dorsata</i>	Hym	962	12.4	0.3	*	9.2	n.s.	2.0	*	19.0	n.s.
		<i>Andrena fulvata</i>	Hym	1,018	28.6	1.7	*	21.8	n.s.	20.7	n.s.	0.3	*
		<i>Andrena haemorrhhoa</i>	Hym	380	5.7	0.3	*	5.0	n.s.	0.3	*	3.3	n.s.
		<i>Andrena nigroaenea</i>	Hym	248	5.5	0.3	**	1.9	**	0.0	**	2.7	n.s.
		<i>Apis mellifera</i>	Hym	4,588	132.9	13.3	n.s.	27.8	n.s.	18.3	n.s.	38.0	n.s.
<i>Bombus hypnorum</i>		Hym	224	4.0	0.3	*	3.0	n.s.	0.7	*	2.7	n.s.	
<i>Lasioglossum fulvicorne</i>		Hym	732	10.4	4.3	n.s.	8.4	n.s.	1.0	*	11.3	n.s.	
<i>Lasioglossum politum</i>		Hym	1,993	15.0	0.0	**	8.8	n.s.	0.7	*	97.7	**	
<i>Melangyna lasiophthalma</i>		Syr	864	15.8	0.0	*	14.9	n.s.	2.0	*	2.3	n.s.	
<i>Dienerella clathrata</i>		Col	5,065	156.1	11.0	*	68.2	*	33.0	**	22.0	**	
Ground-litter saprophages	<i>Enicmus minutus</i>	Col	81	3.8	0.0	*	0.2	n.s.	0.0	*	0.0	*	
	<i>Lathridius nodifer</i>	Col	467	10.4	0.7	**	8.1	n.s.	2.3	*	4.0	n.s.	
	<i>Orthometopon planum</i>	Iso	237	3.9	0.3	n.s.	3.7	n.s.	0.3	n.s.	5.3	n.s.	
	<i>Kleidocerys resedae</i>	Het	679	31.4	1.0	n.s.	1.0	n.s.	0.3	n.s.	5.0	n.s.	
Phytophages	<i>Otiorrhynchus difficilis</i>	Col	347	6.6	1.0	*	8.3	n.s.	0.0	*	3.7	*	
	<i>Semidalis aleyrodiforis</i>	Neu	405	8.9	0.3	*	8.3	n.s.	0.7	*	5.7	n.s.	
Flying zoophages	<i>Semidalis aleyrodiforis</i>	Neu	405	8.9	0.3	*	8.3	n.s.	0.7	*	5.7	n.s.	
Saproxylophages	<i>Ptinus bidens</i>	Col	1,293	37.3	0.3	**	33.9	n.s.	0.0	*	3.0	*	

* $P \leq 0.5$, ** $P \leq 0.01$, *** $P \leq 0.001$, n.s. not significant

Total ind. Total number of individuals sampled in the 66 trap sites, Hym Hymenoptera, Syr Syrphidae, Col Coleoptera, Het Heteroptera, Ara Aranea, Iso Isopoda, Neu Neuroptera

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