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VERSITA

Ecological study of the wood mouse helminth community in a burned Mediterranean ecosystem in regeneration five years after a wildfire

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Abstract

Parasites are used as biological tags in environmental impact studies. However, terrestrial systems in general and small mammals in particular are rarely considered in these ecological studies. Based on the effects of a wildfire which occurred in the Spanish Serra Calderona Natural Park – a typical Mediterranean ecosystem – the regeneration process of the wood mouse population and its helminth community is analysed. A total of 217 individuals of *Apodemus sylvaticus* were studied in a five year period, from the second to the fifth post-fire year: 152 mice originating from the burned area and 65 from the control – non-burned – area. The helminth community for both burned and non-burned areas as well as the effect of intrinsic (host age and sex) and extrinsic (site, period and season of capture) factors on helminth prevalences and abundances were analysed. Taking into account the most important results of this study, various aspects of the helminth community dynamics of the wood mouse are postulated as biological tags of the environmental impact of a wildfire, such as the changes in the frequency distribution of the helminth species, the higher diversity in the burned area, and the prevalences of helminth species having biological cycles directly affected by climatic conditions and the vegetal regeneration process. Consequently, the helminth species of *A. sylvaticus* should be considered suitable biological tags of environmental perturbations, such as a wildfire, and the wood mouse/helminth model can be applied to predict the consequences for helminth species in general.

Keywords

Helminth community, *Apodemus sylvaticus*, post-fire, Mediterranean ecosystem, Serra Calderona, Spain

Introduction

The strict dependence of the parasite on its host and the exploitation of the latter by the former provide a useful research model in the fields of ecology and evolutionary biology. The close relationship which links parasites to their hosts has led to their use as biological tags. Parasites are excellent indicators concerning certain aspects of their hosts' biology, including diet, population biology and phylogeny (Williams *et al*. 1992). Parasites are also used in environmental impact studies. Lafferty (1997) reviewed those aspects related to parasites which provide information about human impacts on the environment.

Parasite communities may prove to be excellent indicators of environmental stress and biodiversity (Marcogliese and Cone 1997). In this sense, the vast majority of these investigations have focused on the effects of pollution on fish parasites, and, to a lesser degree, larval digeneans in gastropods. Lafferty and Kuris (1999) provided a number of examples of the interaction between parasites and other stressors in aquatic environments.

Comparisons in terrestrial systems are relatively uncommon but include studies on insects (Ehler 1989, Ehler and Kinsey 1991, Boggs *et al*. 1991, Torres 1992), helminths of marsupials (Spratt 1987), small mammals (Boggs *et al*. 1991; Boren *et al*. 1993; Galán-Puchades *et al*. 1998) and rabbits (Boggs *et al*. 1990). Therefore, studies concerning the interactive effects of both intrinsic (host age and sex) and extrinsic factors (site, season and year of capture) in the helminth community of small mammals have been carried out in various European countries. The effect of these factors as well as other interactions have been well analysed in the helminth community of the wood mouse, from the first studies of Lewis (1968) to those of Abu-Madi *et al*. (2000) and Behnke *et al*.

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(2005) in the UK or, more recently, that of Eira *et al*. (2006) in Portugal. However, none of these studies considered any extrinsic effects concerning ecosystem perturbations, as produced, for example, by a wildfire and the consequent regeneration process.

The study of the dynamics of helminth parasite populations in small mammals (insectivores and rodents) captured in Mediterranean ecosystems affected by fire represents a new source of information about scarring processes of the affected areas. The host's dissemination strategy after the fire has repercussions upon its parasitic fauna, which can thus be used as an indicator of recolonization (Galán-Puchades and Fuentes 1996; Galán-Puchades *et al*. 1998, 1999; Fuentes *et al*. 2005).

The aim of this paper, following the methodology proposed by Galán-Puchades *et al*. (1999), is to explore the effect of a great wildfire on the wood mouse *Apodemus sylvaticus* (Rodentia, Muridae) population biology and the repercussions of this extreme environmental perturbation on its helminth community in the Spanish Serra Calderona Natural Park – a Mediterranean ecosystem in regeneration 5 years after a wildfire. These conditions provide a test of the parasites' ability to tolerate environmental stressors and the effects on their transmission strategies. The specific aims of the investigation are: to compare the prevalence, mean abundance, aggregation and diversity of helminthiasis among mice captured from control (non-burned) and impact (burned) sites; to correlate changes in host population in perturbed zones with possible changes in the structure of its helminth community; to determine how affected sites recover carrying out an 'impact level-by-time' study; and the possible use of helminths as biological tags in this regeneration process.

Material and methods

The study area, the Serra Calderona Natural Park, is a Spanish Mediterranean ecosystem located between the provinces of Castelló and València-Comunitat Valenciana (39°35′–39°51′N, 0°15′–0°43′W). This mountain-range, with a total surface of approximately 52000 ha, suffered a large wildfire at the end of the summer of 1992 affecting a total of 9500 ha including forests and cultivated land which had been left untended.

A multidisciplinary project concerning the post-fire recolonization dynamics of small mammals and the study of their helminth parasites as biological tags in the process of post-fire regeneration was initiated in February 1994, the winter of the second post-fire year. Throughout the study area three trapping stations were established for annual-seasonal follow-up, two in burned areas and one in a control area, which presented the same ecological conditions as the burned areas before the fire. A comprehensive description of the trapping method and study procedures were previously described by Fuentes *et al*. (1998, 2000) and Galán-Puchades *et al*. (1999). The trap method used to capture hosts is based on the square plot (quadrate) technique, using the live-trapping and capture-mark-release methods. On a seasonal basis (four times annually at intervals of no longer than three months), 110 traps were placed at night in each of the three population study enclaves. The traps were left in place for 48 hours and checked in the morning. The captured animals were identified at species level and weighed; sexual activity was determined and the animals were then marked and released at the place of capture to record data on host population sizes. The parasitological study was, in turn, based on those animals that died during capture. In the event that no such death occurred, no more than 10% of the captured specimens were dissected.

The present article includes the study of 217 individual wood mice, *A. sylvaticus*, captured prior to September 1997, the summer of the fifth year after the fire. One hundred and fifty two individual hosts originated from the burned area and 65 from the control area. The capture year of the hosts, their age and sex structure for the burned and the control areas are summarized in Table I.

The host dynamic recolonization and population study for the current period was analysed by Fuentes *et al.* (1998), who revealed that the wood mouse turns into an efficient recolonizer of the burned area, mainly because of male subadult

Table I. The number of *Apodemus sylvaticus* analysed in Serra Calderona from the burned and control areas, from the second to the fifth post-fire year

	Juvenile		Subadult		Adult		
Post-fire year	male	female	male	female	male	female	total
Burned area							
Second	–	1	5	8	4	3	21
Third	2	2	4	5	6	–	19
Fourth	5	8	12	18	10	8	61
Fifth	1	2	20	14	11	3	51
Control area							
Second	–	–	4	2	5	–	11
Third	1	1	8	5	9	3	27
Fourth	1	–	1	2	3	1	8
Fifth	2	1	2	5	4	5	19

individuals. The burned area is successfully recolonized by the wood mouse during the period between the spring of the fourth and the autumn of the fifth post-fire year.

Helminths were collected as previously described by Fuentes *et al*. (2000). Trematodes and cestodes were preserved in 70% ethanol, stained with Grenacher's boracic and alcoholic chlorhydric carmine, respectively, differentiated with acidified ethanol, dehydrated in an alcohol series, cleared with xylene and mounted in Canada balsam. Nematodes were preserved in ethanol 70% and cleared in Amann lactophenol.

All helminths were specifically identified based on their morphology and morphometry, and employing the most relevant literature on each of the species involved. A number of specimens could not be specifically classified, due to their limited development within the host (as in some catenotaeniid cestodes), or the detection of larval stages or immature nematodes.

The study was carried out comparing the burned area with the control area globally. The analysis of the helminth community compositions and structures for both burned and unburned areas was carried out considering each particular biological cycle and calculating the prevalence, mean abundance, median intensity and range according to Bush *et al*. (1997). The study of the helminth biological cycles was carried out differentiating between helminth species which have one or more free-environmental stages (FES helminth species) and those helminth species which have one or more invertebrate intermediate hosts (no-FES helminth species), and not using the more common classification between heteroxenous and monoxenous helminths (Fuentes *et al.* 2006).

The analysis of the helminth community components was carried out calculating the frequency of occurrence of the number of helminth species, the abundance index (Bush 1973), excluding those parasite species for which the wood mouse acts as an intermediate host, as well as the frequency distribution of helminths and distinguishing between "component" species (prevalence $\geq 10\%$) and "rare" species (prevalence $<10\%$) (Bush *et al*. 1990). This frequency distribution was calculated by means of the Lefkovitch index (L), by which $L = (1/45)\text{tang}^{-1}$ (variance/mean)–1 ranging from –1 (positive binomial or uniform distribution), 0 (Poisson or random distribution) and +1 (negative binomial or aggregated distribution).

The diversity/uniformity analysis of the helminth community was completed by using the Shannon index (Pielou 1975, Magurran 1988), Simpson index (D) (Simpson 1949) expressed as 1–D (Magurran 1988), Berger-Parker index (Berger and Parker 1970, May 1975, Magurran 1988) and Shannon evenness index (Pielou 1969, Magurran 1988).

The helminth infracommunity structure study was established through the analysis of the number of helminths, number of helminth species, the Brillouin index (Pielou 1975, Magurran 1988), Brillouin index for infected hosts only and percentage of hosts infected.

Where possible, standard non-parametric tests – chi-squared (x^2) and Mann-Whitney (U) tests – were applied (Sokal and Rohlf 1981), and statistical significance was established at $P<0.05$.

The role played by intrinsic (host age and sex) and extrinsic (site, season and year of capture) factors in determining helminth prevalences, species richness, helminth diversity and worm burden for component species of the wood mouse were studied. The season of capture was considered as a variable linked with the year of capture, namely period of capture, as the effect of season is strongly related to each post-fire year. Moreover, in order to compare the influence of the other factors on each site, the analysis was carried out separately for the burned and the control area, respectively. The analysis for helminth prevalences, as the dependent variable, was carried out using a binary logistic regression (infected = 1; uninfected = 0) and the intrinsic and extrinsic factors as independent variables. The analysis of species richness (expressed by the number of helminth species), helminth diversity (expressed by the Brillouin index) and worm burden (expressed by helminth abundance) was carried out using a multifactorial general linear model (GLM). As the number of helminths was highly aggregated, the helminth abundance of each species was normalized by the ln (x + 1) transformation for this GLM analysis.

StatView 5.0 – SAS Institute Inc. – and SPSS 13.0 – SPSS Inc. – for Windows were the software packages used for statistical analyses.

Results

In the Serra Calderona as a whole, 187 of a total of 217 (86.2%) wood mice analysed were parasitized with 16 species of helminths (Table II). Nine of the helminth species were classified as FES and seven were classified as no-FES; 79.3% of the individuals analysed were infected with FES helminths, and 49.8% were infected with no-FES helminths. This difference was statistically significant ($x^2 = 39.948$, df = 1, $P<0.0001$). The mean species richness (average number of parasite species/host) was 2.18 (SE = 0.12), and the values of the diversity/uniformity index of the helminth community were 1.30 for the Shannon index, 0.63 for the Simpson index, 0.49 for the Berger-Parker index and 0.46 for the Shannon evenness index.

Characteristics of the helminth community of A. sylvaticus *in the burned and control areas*

In the burned area, 136 of a total of 152 individual hosts analysed (89.5%) were parasitized with 15 species: 1 trematode, 6 cestodes and 8 nematodes (Table II). *Syphacia stroma* was the helminth with the highest prevalence, while *S. frederici* was the most abundant helminth overall, presenting the highest individual counts among infrapopulations. 83.6% of the individuals analysed were infected with FES helminths, and 50.0% were infected with no-FES helminths. This difference was statistically significant ($x^2 = 37.068$, df = 1, $P<0.0001$).

Table II. Selected characteristics of the helminth fauna of all wood mice in burned (B) and control (C) areas

Helminth species	Site	LC	Prevalence (95% CI)		Mean abundance (SE)		Median intensity (range)	
			B	C	B	C	B	C
Brachylaima spp.	I	NF	1 (0–4)	2 (0–9)	0.01 (0.01)	0.02 (0.02)	1 (1)	1 (1)
Taenia parva larvae	BC	F	12 (7–18)	18 (10–29)	0.2 (0.04)	0.5 (0.2)	1 (1–3)	2 (1–6)
Taenia martis larvae	BC	F	1 (0–4)	–	0.01 (0.01)	–	1 (1)	–
Mesocestoides sp. larvae	BC	NF	1 (0–4)	2 (0–9)	0.05 (0.04)	0.8 (0.8)	4 (4)	52 (52)
Pseudocatenotaenia matovi	I	NF	8 (4–13)	14 (7–25)	0.3 (02)	0.6 (0.3)	1 (1–29)	2 (1–15)
Skrjabinotaenia lobata	I	NF	5 (2–10)	8 (3–17)	0.7 (0.6)	0.1 (0.08)	2 (1–83)	1 (1–5)
Catenotaeniinae gen. sp.	I	NF	7 (4–12)	8 (3–17)	0.2 (0.08)	0.2 (0.08)	2 (1–11)	2 (1–4)
Hymenolepis straminea	I	NF	1 (0–4)	–	0.03 (0.02)	–	2 (1–3)	–
Trichuris muris	I	F	22 (16–29)	12 (5–22)	0.5 (0.1)	0.4 (0.3)	2 (1–9)	1 (1–16)
Eucoleus bacillatus	S	F	26 (19–34)	15 (8–26)	3.1(1.0)	0.5 (0.2)	5 (1–171)	3 (1–9)
Aonchotheca annulosa	I	NF	37 (29–45)	25 (15–37)	12.5 (3.4)	1.4 (0.5)	8 (1–291)	3 (1–22)
Heligmosomoides polygyrus	I	F	25 (18–33)	25 (15–37)	2.6 (1.0)	2.1 (0.9)	2 (1–113)	3 (1–43)
Syphacia stroma	I	F	38 (30–46)	18 (10–29)	37.5 (1.1)	9.22 (4.5)	33 (1–1140)	14 (2–212)
Syphacia frederici	I	F	30 (23–38)	32 (21–45)	41.9 (18.7)	65.5 (43.9)	21 (1–2646)	47 (1–2846)
Aspiculuris tetraptera	I	F	3 (1–7)	6 (2–15)	0.05 (0.03)	2.4 (2.3)	2 (1–3)	2 (1–152)
Mastophorus muris	I	NF	8 (4–13)	17 (9–28)	0.2 (0.05)	0.6 (0.3)	2 (1–4)	1 (1–14)
Nematoda gen. sp. larvae	I	F	–	2 (0–9)	–	0.02 (0.02)	–	1 (1)

BC – body cavity, CI – confidence interval, F – FES, I – intestine, LC – life cycle, NF – no-FES, S – stomach, SE – standard error.

More than 50% of hosts were parasitized by one and two helminth species, with infracommunities of up to seven species (Table III). Moreover, the frequency in the number of different helminth species in each host corresponds well to a Poisson distribution having a value of L = 0.13.

Analysis of the index of abundance (Table IV) makes it possible to establish the following helminth community structure: *S. frederici*, *S. stroma*, *Aonchotheca annulosa*, *Eucoleus bacillatus* and *Heligmosomoides polygyrus* as dominant species; *Skrjabinotaenia lobata*, *Trichuris muris*, *Pseudocatenotaenia matovi* and *Mastophorus muris* as codominant species; and *Aspiculuris tetraptera*, *Hymenolepis straminea* as well as *Brachylaima* spp. as successful immigrant species. The three cestode larval stages are not considered in this study, as the wood mouse acts as the intermediate host.

Table III. Frequency of occurrence of the number of helminth species present in each specimen of *Apodemus sylvaticus* from Serra Calderona determined by areas of origin, burned (B) and control (C) areas

No. of helminth species	B		C	
	n	%	n	%
0	16	10.5	14	21.5
1	45	29.6	16	24.6
2	37	24.3	16	24.6
3	22	14.5	9	13.8
4	17	11.2	2	3.1
5	8	5.3	5	7.7
6	4	2.6	1	1.5
7	3	2.0	2	3.1

n – number of parasitized hosts, % – frequency of occurrence.

The frequency distributions of the various helminth populations (Table IV) show that all dominant and some codominant species conform to a negative binomial distribution.

The values of the Shannon, Simpson, Berger-Parker and Shannon evenness indices (Table V) reflect the diversity/uniformity of the helminth community.

Table VI shows the diversity of the infracommunities determined by the Brillouin index, and shows values for each infracommunity in the study, including uninfected animals, as well as values for infected hosts alone.

In the control area, 51 of a total of 65 individual hosts analysed (78.5%) were parasitized with 14 species: 1 trema-

Table IV. Abundance index (AI) and Lefkovitch index (L) of all wood mice in the burned (B) and control (C) areas

Helminth species	AI		L	
	B	C	B	C
Brachylaima spp.	0.01	0.02	0.00	0.00
Taenia parva larvae	–	–	0.23	0.62
Taenia martis larvae	–	–	0.00	–
Mesocestoides sp. larvae	–	–	0.69	0.98
Pseudocatenotaenia matovi	0.30	0.60	0.93	0.86
Skrjabinotaenia lobata	0.68	0.14	0.98	0.61
Catenotaeniinae gen. sp.	0.18	0.17	0.77	0.52
Hymenolepis straminea	0.03	–	0.51	–
Trichuris muris	0.51	0.37	0.64	0.88
Eucoleus bacillatus	3.13	0.52	0.98	0.71
Aonchotheca annulosa	12.47	1.43	0.99	0.89
Heligmosomoides polygyrus	2.59	2.05	0.98	0.95
Syphacia stroma	37.53	9.23	1.00	0.99
Syphacia frederici	41.85	65.51	1.00	1.00
Aspiculuris tetraptera	0.05	2.42	0.44	0.99
Mastophorus muris	0.15	0.58	0.49	0.83
Nematoda gen. sp. larvae	–	0.00	–	0.00

Table V. Diversity characteristics of the helminth community of *Apodemus sylvaticus* from Serra Calderona determined by areas of origin, burned (B) and control (C)

	B	C
Shannon index	1.32	0.92
Simpson index	0.66	0.38
Berger-Parker index	0.58	0.22
Shannon evenness index	0.48	0.33

tode, 4 cestodes and 9 nematodes (Table II). The absence of *T. martis* larvae and of *H. straminea* deserve mentioning when compared with the burned area. The global prevalence of parasitism was lower than in the burned area, but this difference was not statistically significant. *S. frederici* was the helminth with the highest prevalence, mean abundance and the highest individual values for infrapopulations. The FES helminth infection rate was 69.2% for the individuals analysed, and 49.20% were infected with no-FES helminths. This difference was statistically significant ($x^2 = 4.587$, df = 1, P = 0.032). When comparing the component helminth species of the two analysed areas, statistically significant differences were found between the prevalences of *S. stroma* ($x^2 = 7.211$, df = 1, P = 0.007) and the mean abundance of *A. annulosa* (U = 4171.5, P = 0.030), *S. stroma* (U = 3916.0, P = 0.004) and *M. muris* (U = 4487, P = 0.046). Moreover, a statistically significant difference was found between the number of wood mice infected with FES helminths in both areas analysed ($x^2 = 4.847$, df = 1, P = 0.028).

Table VI. Diversity characteristics of the infracommunities of helminths of *Apodemus sylvatiucs* (*A.s.*) from Serra Calderona determined by areas of origin

		Burned area	Control area
Mean helminth abundance		99.7	59.5
	SE	16.0	22.9
Mean species richness		2.3	2.0
	SE	0.1	0.2
Brillouin index	X	0.32	0.28
	SE	0.02	0.03
	Max.	1.98	1.39
BI infected *A.s.* only	X	0.35	0.36
	SE	0.02	0.03
% of *A.s.* infected		89.5	78.5

Similar to the burned area, almost 50% of hosts presented between one and two helminth species, with infracommunities of up to seven species (Table III). However, two differences were found: the percentage of non-parasitized mice was clearly higher in the control area than in the burned area, but this difference was statistically non-significant, and the frequency in the number of different helminth species showed a higher value in the control area and cannot be considered as a clear Poisson distribution (L = 0.38).

The analysis of the abundance index values (Table IV) makes it possible to establish a very similar helminth community structure as found in the burned area, while *A. tetraptera* and *E. bacillatus* became dominant and codominant species, respectively.

The analysis of the frequency distributions for the various helminth populations (Table IV) shows changes in the aggregation of various species with respect to the burned area.

The values of the diversity/uniformity indices (Table V) reflect a lower diversity in the control than in the burned area.

The study of the infracommunity diversity (Table VI) reveals a similar species richness and diversity (determined by the Brillouin value index) in the two areas studied but with higher values in the area affected by the fire.

The analysis of wood mouse subpopulations determined by host age showed the highest species richness and helminth diversity in adults and lowest in juveniles in both areas. However, the variation in the subpopulations determined by the period of capture remained very similar in the control area and showed irregular fluctuations in the burned area, reaching its highest values in the second year after the fire. Overall no marked differences were detected between the two sexes.

The multifactorial GLM analysis (Table VII) confirmed the above-mentioned results, showing that host age affected the variation in species richness and helminth diversity in both the burned and control areas. The period of capture influenced helminth diversity but not species richness. However, there was a significant interaction between period of capture and host age on species richness, both in the burned area only.

Table VII. Species richness and helminth diversity in *Apodemus sylvaticus* from Serra Calderona burned and control areas by year and period of capture, host age and host sex, through a multifactorial GLM, expressed by F-statistic values with associated probabilities (P); df – degree of freedom. Only statistically significant values are reported

		Burned area				Control area			
		species richness		helminth diversity		species richness		helminth diversity	
Source of variation	df	F	P	F	P	F	P	F	P
Period of capture	8	–	–	2.716	0.010	–	–	–	–
Host age	2	12.990	<0.0001	4.742	0.011	4.170	0.027	8.372	0.002
Period of capture/host age	2	3.457	0.035	–	–	–	–	–	–

Table VIII. Logistic regression models for prevalences of the helminth component species in *Apodemus sylvaticus* from Serra Calderona burned and control areas by year and period of capture, host age and host sex, expressed by χ^2 values with associated probabilities (P) for the model created including independent variables; df – degree of freedom. Only statistically significant models are reported

		Burned area		Control area	
Helminth species/independent variables included in the model	df	χ^2	P	χ^2	P
Taenia parva larvae					
Year of capture	3	9.787	0.020	13.666	0.003
Trichuris muris					
Host age	2	24.180	<0.0001	–	–
Eucoleus bacillatus					
Year of capture & host age	5	–	–	19.302	0.002
Period of capture & period of capture/host age	21	37.907	0.013	–	–
Aonchotheca annulosa					
Host age	2	–	–	8.899	0.012
Period of capture & period of capture/host age	21	66.122	<0.0001	–	–
Heligmosomoides polygyrus					
Year of capture	3	17.825	<0.0001	–	–
Syphacia stroma					
Period of capture	8	40.878	<0.0001	–	–
Syphacia frederici					
Period of capture	8	23.166	0.003	–	–
Mastophorus muris					
Year of capture	3	–	–	10.238	0.017

Analysis of the helminth infracommunities of A. sylvaticus *determined by host age*, *host sex and site*, *year and period of capture during the post-fire regeneration process*

The role played by extrinsic (site, year and period of capture) and intrinsic (host age and sex) factors in the component species of the helminth community of *A. sylvaticus* are shown in Table VIII in relation to helminth prevalences and in Table IX with respect to helminth abundance. The analysis of the results shows that, in general, the helminth community of the wood mouse in the burned area was more affected by both extrinsic and intrinsic factors, mainly year and period of capture as well as host age. Host sex did not have any important effect on helminth prevalences and abundances.

Taenia parva larvae

Prevalences and abundances of this cestode larval stage were higher in adults than in subadult subpopulations in the burned area only, and no juvenile host was parasitized in either area. The year of capture affected the prevalence of this cestode in both areas although there was no clear predictable pattern in the direction of changes. Moreover, the period of capture, as well as its interaction with host age and sex, determined the worm burden in the burned area only.

Pseudocatenotaenia matovi

Although males and adults were more heavily parasitized than females and subadult subpopulations, respectively, and no juvenile host was parasitized in either area, the only effect detected was related with the period of capture on the worm burden of this cestode in the burned area.

Trichuris muris

Host age affected prevalences in the burned area only, showing a higher prevalence in the adult subpopulation. No juvenile host was parasitized in either area. Moreover, the analysis of the abundance showed the influence of period of capture, host age, and the interaction between host age and sex also in the burned area only.

Eucoleus bacillatus

Year of capture and host age had a strong effect on prevalences and abundances, which showed an irregular interannual fluctuation and higher levels of parasitism always in the adult subpopulation. However, the influence of the year and the period of capture were higher in the burned area, while the influence of the host age was higher in the control area.

Aonchotheca annulosa

As with *E. bacillatus*, the effect of year and period of capture as well as host age on prevalence and abundance were detected in the burned area, but only concerning host age in the control area.

Heligmosomoides polygyrus

The capture year was the only factor which showed a detectable influence on prevalence in the burned area only. Prevalence in this area decreased from the highest values in the

Table IX. Mean abundance of the helminth component species in *Apodemus sylvaticus* from Serra Calderona burned and control areas by year and period of capture, host age and host sex, through a multifactorial GLM, expressed by F-statistic values with associated probabilities (P); df – degree of freedom. Only statistically significant values are reported

		Burned area		Control area	
Helminth species/source of variation	df	F	P	F	P
Taenia parva larvae					
Year of capture	3	–	–	2.777	0.061
Period of capture	8	2.696	0.010	–	–
Host age	2	3.125	0.048	–	–
Year of capture/host age	6	2.407	0.033	–	–
Period of capture/host age	2	10.290	<0.0001	–	–
Period of capture/host sex	3	4.029	0.010	–	–
Year of capture/host age/host sex	1	7.430	0.008	–	–
Pseudocatenotaenia matovi					
Period of capture	8	2.159	0.037	–	–
Trichuris muris					
Period of capture	8	2.956	0.005	–	–
Host age	2	11.973	<0.0001	–	–
Host age/host sex	2	3.609	0.031	–	–
Eucoleus bacillatus					
Year of capture	3	3.798	0.013	–	–
Period of capture	8	4.096	<0.0001	–	–
Host age	2	–	–	4.359	0.023
Year of capture/host age	6	3.204	0.007	–	–
Aonchotheca annulosa					
Year of capture	3	4.486	0.005	–	–
Period of capture	8	3.261	0.002	–	–
Host age	2	5.306	0.007	3.553	0.043
Heligmosomoides polygyrus					
Year of capture	3	8.223	<0.0001	–	–
Period of capture	8	3.599	0.001	–	–
Host age	2	11.663	<0.0001	–	–
Year of capture/host sex	3	3.144	0.029	–	–
Period of capture/host age	2	6.669	0.002	–	–
Syphacia stroma					
Period of capture/host age	8	2.155	0.038	–	–
Syphacia frederici					
Year of capture	3	3.037	0.033	–	–

second to the fourth year after the fire but then rose again after the fifth year. Moreover, helminth abundance in the burned area was affected mainly by the year and period of capture as well as the host age.

Syphacia stroma

The period of capture was the only factor which affected the prevalence of this oxyurid species in the burned area, where prevalences increased from the second to the fifth year after fire. Moreover, an effect of host age together with the period of capture on the worm burden was also detected in the burned area only.

Syphacia frederici

Similar to *S. stroma*, the effect of the period of capture was detected determining prevalences in the burned area only. With respect to the mean abundance, a significant effect of the year of capture was detected in the burned area only and this followed the same pattern as prevalences, but was different from that in the other oxyurid species.

Mastophorus muris

The year of capture was the only factor detected with an effect on prevalence of this nematode species in the control area, but following a similar pattern as in the burned area.

Discussion

According to Fuentes *et al*. (2000), the helminthfauna detected in *A. sylvaticus* in Serra Calderona Natural Park agrees with the results of Feliu *et al*. (1997) for this host species in the Iberian Peninsula. The absence of certain helminths in this enclave may be explained by the limited resources of this mountain range ecosystem in comparison with continental Spain in its entirety. However, the 16 helminth species detected, as well as the prevalence and species richness values are higher than those reported from other enclaves recently studied in the Iberian Peninsula: Albufera de València (Portolés *et al*. 2000) and Serra Espuña (Fuentes *et al*. 2004a), both in Spain, and Dunas de Mira, Portugal (Eira *et al*. 2006). Only

Fuentes *et al*. (2003) in Serra da Malcata, Portugal, Torres *et al*. (2003) in Doñana and Fuentes *et al*. (2004b) in Sierra de Gredos, both in Spain, reported higher prevalences than in the Serra Calderona, but in all three cases based on a very small number of wood mice analysed.

The absence of *T. martis* larvae and of *H. straminea* from the control area and the low prevalences and intensities in the burned areas, was intriguing because this species is generally more common in the Iberian Peninsula. One explanation may simply be the low number of individual hosts analysed in the control area.

Differences detected between the two analysed areas in the terms of the percentages and mean abundances of global parasitism as well as FES helminth species suggest that the changes in these variables might be related to the post-fire regeneration process. The aggregation of hosts in the burned area leads both to the higher prevalence of parasitism in general and to the transmission of helminths with direct life cycle in particular, according to Arneberg *et al*. (1998) and Arneberg (2001).

Mean species richness values and the helminth community components are very similar in both areas without significant differences. However, the higher value of the frequency of uninfected wood mice in the control area stands out, reflecting once again the lower global prevalence in this area.

The analysis of the frequency distribution of helminths revealed that species showed no or little changes in the parameters reflecting aggregation in both areas, namely *S. frederici*, *S. stroma* and *H. polygyrus*. Other species, both dominant and codominant, such as *T. parva* larvae, *P. matovi*, *S. lobata*, *T. muris*, *E. bacillatus* and *M. muris*, showed changed parameters reflecting the repercussions of the environmental impact of the wildfire on the host population. The importance of these changes is related to the capacity for perturbation which each helminth species exercises on their host in the post-fire regeneration area with respect to the control area. A minor aggregation is more damaging for the wood mouse population, because, as Dobson (1988) and Shaw and Dobson (1995) affirmed, a higher aggregation of the parasite population in a small proportion of the host population always increases the stability of the parasite-host relationship. Thus, according to the results obtained in both areas, *P. matovi*, *S. lobata* and *E. bacillatus* do not seem to contribute to the host population destabilization since their aggregation parameters increased in the burned area. *T. muris*, *M. muris* and *T. parva* larvae are the parasite species which suffered a reduction in aggregation, and might therefore be the species causing destabilization in the wood mouse population in the burned areas. This change is particularly relevant as regards the cestode larvae which were randomly distributed among their host. Moreover, *A. tetraptera* underwent a reduction in aggregation in the burned area, but its lower colonization capacity in the burned area suggests that its destabilization capacity ought not to be taken into account until now. Consequently, the changes in the frequency distribution of the helminth species can be considered another potential effect of the environmental impact of a wildfire and related to the post-fire regeneration process.

The analysis of diversity of *A. sylvaticus* in both areas, at the helminth community level (values of various indices) and at infracommunity level (mean helminth abundance, mean species richness and Brillouin index), showed a greater diversity, abundance and species richness in the post-fire regeneration area. The burned area is more destabilized and has, therefore, a greater diversity which itself can also be related to the post-fire succession of this Mediterranean forest ecosystem.

The analysis of the wood mouse infracommunities determined by period of capture revealed a progressive decrease in the diversity of the helminthfauna, with a slow but steady tendency towards a loss in species richness and, therefore, gradually becoming more like the control area. This loss of diversity in the helminth community seems to be related to the progressive increase of the host population, because, as mentioned before and according to Arneberg *et al*. (1998) and Arneberg (2001), the greater size of the host population favours the species with simple biological cycles, mainly those more frequently transmitted directly host-to-host, such as the two species of *Syphacia*, which increase their prevalence and abundance along with regeneration process. However, keeping the same patterns in species richness and helminth diversity in subpopulations determined by host age in both areas at a global level is not surprising and agrees with other studies of this host species, namely Behnke *et al*. (1999) in UK, Fuentes *et al*. (2004a) in Spain and Eira *et al*. (2006) in Portugal, who also reported a higher helminth diversity and species richness in adult subpopulations. This host age effect may be related to two facts. Firstly, with increasing host age there is a corresponding increase in total time for exposure to helminth infections and, secondly, the worm burdens accumulate with time (Gregory 1992, Behnke *et al*. 1999).

Intrinsic and extrinsic factors have different effects on helminth infracommunities of the wood mouse in the two areas analysed. However, host sex does not play a role in determining helminth prevalences and abundances in comparison with the other factors aforementioned. Host sex effects have only occasionally been reported in some species, such as *T. parva* larvae (Eira *et al*. 2006) and *S. stroma* (Behnke *et al*. 1999, Eira *et al*. 2006).

The year-to-year changes in *T. parva* larvae prevalence and abundance in both areas may be related with population changes of its intermediate and definitive hosts, the wood mouse and the genet, respectively. However, the period of capture and host age-sex effects on abundances, detected only in the burned area, may reflect higher seasonal changes of *A. sylvaticus* and *Genetta genetta* populations in the burned area and is likely to be a consequence of the destabilization caused by this cestode due to its aggregation loss.

Variation in abundance of *P. matovi* in the burned area in relation to the period of capture can be explained through the variation of the population of arthropods acting as the intermediate host. Abu-Madi *et al*. (2000) reported similar variations in *Catenotaenia pusilla*, another catenotaeniid cestode, which has very similar biological cycle.

Significant effects of host age and year of capture (Behnke *et al*. 1999) as well as season of capture (Montgomery and

Montgomery 1988) have been reported in *T. muris* parasitizing the wood mouse. However, in our study, host age effect on prevalences and period of capture and host age and sex effects on abundances of this nematode species were only evident in the burned area, reflecting a more stable helminth population in the control area. These effects, as well as the impact of other extrinsic factors linked to the regeneration process, can be related to the hypothesis that *T. muris* destabilizes the wood mouse population in the burned area as a consequence of its loss of aggregation.

Prevalences and abundances of *E. bacillatus* and *A. annulosa* are similarly influenced by all intrinsic and extrinsic factors, with the exception of host sex, in the burned area, but only by host age in the control area. This similarity may be related to the life cycle of these capillariinae species. The life cycle of *A. annulosa* might involve a non-arthropod invertebrate as the intermediate host, while *E. bacillatus* might be transmitted directly, after the egg embrionates in the environment, or may also use a non-arthropod invertebrate as a paratenic host. If both life cycle possibilities are considered, the host age effect in both areas can be explained by the host diet, which increases in non-arthropod invertebrate composition at the same time as host age increases. Moreover, the effect of extrinsic factors in the burned area, with the same interannual variations in both species, may be related to changes in the non-arthropod invertebrates populations between periods of capture (seasons and years) due to the higher susceptibility of this perturbed enclave to climatic changes taking place during the post-fire study years.

The year of capture is the only factor which has an effect on prevalence, but all extrinsic and intrinsic factors, including host sex, and interactions with period and year of capture, have an effect on the abundance of *H. polygyrus* in the burned area only. Similar results were detected in the studies of Montgomery and Montgomery (1988), Abu-Madi *et al*. (1998, 2000), Behnke *et al*. (1999) and Eira *et al*. (2006). The infective larval stage of this nematode species lives in the environment and is also more severally affected by climatic changes, and consequently by the different vegetation cover which protects the free environmental stage, in the burned area than in the control area which remains more stable.

Concerning the two oxyurid species, *S. stroma* and *S. frederici*, only effects of year and period of capture on prevalences and abundances were detected in the burned area, although season and year of capture as well as host age and sex were reported as factors which determine prevalence and abundance of *S. stroma* (Montgomery and Montgomery 1988, Behnke *et al*. 1999, Abu-Madi *et al*. 2000, Eira *et al*. 2006). As the aggregation of the *A. sylvaticus* population in the burned area increased from the second to the fourth year and decreased in the fifth year after the fire in the burned area (Fuentes *et al*. 1998), and the interannual evolution of prevalences and abundances of these oxyurid helminth species has the same pattern, it is clear that these changes in host and helminth population interact positively in the burned area.

The effect of the year of capture on prevalence of *M. muris* in the control area can be related, similarly to *P. matovi*, with interannual changes in the arthropod population that act as the intermediate hosts. The absence of any effect in the burned area, in spite of the loss of aggregation of this nematode species, may be related to the low prevalences detected after the second post-fire year.

Generally speaking, the effect of the wildfire and the regeneration process are reflected in the wood mouse population and in its helminth community. In this sense, the following factors may contribute to regulation of the helminth community after the fire: the direct effect of the fire eliminating the shrub vegetation, which, in turn, alters the soil conditions and decreases the vertebrate and invertebrate populations; changes in the host population dynamics as a consequence of the post-fire regeneration process, which itself is clearly influenced by climatic conditions; changes in the infection pressure of certain parasite species having altered epidemiological patterns; and, lastly, a certain loss of immunity in the hosts caused by the aforementioned changes in the helminth infection pressure, that possibly alter the host/parasite relationship. These changes, which occurred during the four study years and affected the burned area more severely and caused changes in the wood mouse helminth community, have to be considered as biological tags of the regeneration process after a wildfire in Mediterranean ecosystems. These biological tags are mainly the increase of global prevalences and abundances, the increase of the helminth diversity as well as the dominance of helminth species transmitted directly host-to-host as a consequence of a higher host aggregation, and changes in the helminth frequency distribution, loss of aggregation, in the burned area. Moreover, dietetic deficiencies, potential loss of the host immunity, and the characteristics of helminth biological cycles enable us to consider individually the regeneration process in each of the helminth species included as component species in the helminth community of the wood mouse. These facts should make it possible to postulate, as proposed by Galán-Puchades and Fuentes (1996) and Galán-Puchades *et al*. (1998, 1999) after their studies in the Eastern Pyrenees, that the component species of the wood mouse helminth community are suitable biological tags of environmental perturbations, such as wildfires, their effects and consequences. Moreover, future studies, after the analysis of the host dynamics in the burned and control areas and more helminthological material from the following post-fire years, should allow us eventually to create a helminth/mammal model, based on one or more species or one or more types of biological cycles, capable of shedding light on the state of regeneration of wildlife following major perturbations such as fires in Mediterranean ecosystems.

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