Fire disturbance disrupts co-occurrence patterns of terrestrial vertebrates in Mediterranean woodlands

3 authors, including:

Maurizio Sarà

Università degli Studi di Palermo

99 PUBLICATIONS   926 CITATIONS

Some of the authors of this publication are also working on these related projects:

Practical actions for preserving the main European population of Lanner falcon' View project

ORIGINAL ARTICLE

Fire disturbance disrupts co-occurrence patterns of terrestrial vertebrates in Mediterranean woodlands

Maurizio Sarà*, Enrico Bellia and Andrea Milazzo

Dipartimento di Biologia Animale, University of Palermo, Palermo, Italy

ABSTRACT

Aim This paper uses null model analysis to explore the pattern of species co-occurrence of terrestrial vertebrate fauna in fire-prone, mixed evergreen oak woodlands.

Location The *Erico–Quercion ilicis* of the Mediterranean belt (50–800 m a.s.l.) in the Madonie mountain range, a regional park in northern Sicily (37°50′ N, 14°05′ E), Italy.

Methods The stratified sampling of vertebrates in a secondary succession of recent burned areas (BA, 1–2 years old), intermediate burned areas (INT, 4–10 years old) and ancient burned areas (CNB, > 50 years old), plus forest fragments left within burned areas (FF, 1–2 years old) permitted the comparison of patterns of species co-occurrence using a set of separate presence/absence matrices. First, the breeding avifauna derived from standardized point counts was analysed using Stone & Roberts' *C*-score, and by a null model algorithm (fixed/equiprobable). Secondly, the analysis was repeated using all vertebrate species recorded in the succession.

Results Sixty-five species were recorded in the 2-year study period in the four sample treatments. Birds were found to make up the largest component (63%) of the recorded assemblage. The BA treatment had the lowest species richness, followed in order by the small, medium and large FFs, and then by the CNBs. For both analyses (birds and total vertebrates), the *C*-scores were quite small and not significantly different from those that could be expected by chance in the BA and INT burned areas; this indicates a random co-occurrence among vertebrates of those assemblages. Contrariwise, for both analyses in the CNBs, the *C*-scores were large and significantly different from the simulated indices, thereby indicating a non-random co-occurrence pattern (segregation) of vertebrates in the undisturbed woodlands. In addition, *C*-score values for the surviving FFs show a significant aggregation of species.

Main conclusions The null model analyses highlighted a new aspect of fire disturbance in Mediterranean woodland ecosystems: the disruption in patterns of co-occurrence in the terrestrial vertebrate community. Wildfire alters community organization, inducing, for at least 10 years, a random aggregate of species. Communities re-assemble themselves, showing the occurrence of species segregation at least 50 years after fire.

*Correspondence: Maurizio Sarà, Dipartimento di Biologia Animale, University of Palermo, Via Archirafi 18, 90123 Palermo, Italy. E-mail: mausar@unipa.it

INTRODUCTION

The temporal dynamics of a landscape pattern are driven by disturbances that alter habitats and create a constantly changing mosaic of disturbed and undisturbed patches (Sousa, 1984; Pickett & White, 1985). Disturbances, which are almost never truly random, 'reset' succession processes and alter the distribution of organisms and their resources within the landscape (Huston, 1994). Different types of disturbances lead to specific regional regimes and vary in character in different regions of the globe. In Mediterranean climate zones, fire is a pervasive disturbance process that creates fire-dependent communities with a continuous cover of fire-adapted woody vegetation (Di Castri, 1981). Fire use, as a tool for forest opening and transformation, has been widespread in the Mediterranean area since early Neolithic times (Liacos, 1973; Prodon, 1987; Naveh, 1990), and, as a consequence, wildfire is one of the major determinants of landscape modification. Over longer time-scales, wildfire has affected both population ecology and species evolution and has created resilient and resistant communities (Trabaud & Prodon, 1993; Blondel, 1995).

In spite of the alleged role of fire in the functioning and shaping of terrestrial Mediterranean ecosystems (Huston, 1994; Blondel & Aronson, 1999; Aber & Melillo, 2001), existing research regarding the Mediterranean Basin is limited and has addressed only specific taxa in some countries (Prodon & Pons, 1993). Specifically, Mediterranean fire-prone landscapes are characterized by a succession of secondary habitats from grasslands/garrigues to forests, which replace each other in time and space with specific dynamics along environmental gradients (see models in Di Castri, 1981; Blondel, 1995). Population density, species richness and assemblage composition of small mammals (Arrizabala et al., 1993; Fons et al., 1993; Haim, 1993; Haim et al., 1996, 1997; Haim & Izhaki, 2000) and birds (Prodon & Lebreton, 1981; Prodon et al., 1984, 1987; Izhaki & Adar, 1997; Izhaki, 2000) vary concomitantly. To date, the effect of fire upon the whole terrestrial vertebrate community has not been investigated (but see Prodon et al., 1984, 1987) and little attention has been paid to the various aspects of the fire-prone community ecology.

In general terms, fire perturbation can be referred to as the displacement of some property of a community, such as total biomass, density or reproductive rate, away from a value generally considered to represent an equilibrium value or a steady state for that specific parameter (Huston, 1994). In this regard, one of the first and most basic questions is whether general assembly rules (Diamond, 1975; Connor & Simberloff, 1979; Wiens, 1989; Gotelli & Graves, 1996) still apply and determine the non-random structure (see Gotelli & McCabe, 2002) of vertebrate communities that are frequently exposed to fire. In order to test this hypothesis, null model analysis was applied to the vertebrate community of an area of c. 1200 ha of Mediterranean woodland and shrubland destroyed by an accidental fire in 2001 to check the pattern of species co-occurrence. Since several small patches of wood within the completely burned matrix had escaped the fire, their pattern of species richness and co-occurrence was also investigated to ascertain whether and to what extent vertebrate fauna surviving in these fragments contributed to the maintenance of ecological diversity.

MATERIALS AND METHODS

Study areas

The study area is located in the Madonie mountain range, a regional park of some 40,000 ha in northern Sicily (37°50′ N, 14°05′ E). The vegetation of these dolomite massifs is arranged along several altitudinal belts, commencing with the high-altitude (1300–2000 m a.s.l.) beech forests (Anthrisco–Fagetum aceretosum) of the Subatlantic belt and extending down to the low-altitude (50–800 m a.s.l.) mixed evergreen oak wood (Erico–Quercion ilicis) of the Mediterranean belt (Pignatti, 1997; Raimondo, 1998). The latter, extending for approximately 4000 ha, plus a further 6500 ha of low and high shrubland and degraded woods in the Regional Park, falls within the meso-Mediterranean life-zone (Blondel, 1995). The woodland is dominated by cork oaks (Quercus suber), intermingled with deciduous oaks (Q. virgiliana, Q. amplifolia and Q. delechampi), ashes (Fraxinus ornus) and pines (Pinus pinea). The undergrowth layer is mainly composed of Erica arborea, Arbutus unedo, Cistus creticus, C. monspeliensis, C. salvifolius, and Calicotome infesta (Raimondo, 1998).

Human-induced fires periodically hit the Mediterranean belt of the Regional Park, which falls within five administrative counties. 28% of the surface area (n = 27,210 ha) of these counties, either within or outside the Park boundaries, burned or re-burned from 1980 to 2002, and these areas are classified as high or very high risk (USSAB, 2003).

Three valleys, equivalent to about 1200 ha of Erico–Quercion ilicis vegetation, which were struck by fire on 11 November 2001, defined our study area. Within this burned Park territory, three burned replicates of 100 ha (BA1–3) and 20 fragments of vegetation (FF1–20) were selected for a study of species richness and the composition and co-occurrence of terrestrial vertebrate fauna. Furthermore, five 100-ha replicates of Mediterranean mixed evergreen oak woods, which had not burned for at least 50 years and which are isolated from the burned areas and from each other, were chosen as control areas (CNB1–5). The age of the last fire in these areas was determined by asking local people and forestry officers, and it corresponded well to the time interval of spontaneous fires occurring in similar dry ecosystems of the Mediterranean Climate Zone (Sousa, 1984). The terrestrial vertebrate fauna living in the CNBs was, therefore, considered as the mature community living in a less disturbed ecosystem; that is, chronologically the farthest from the disturbance.

The secondary succession

To reconstruct, at least partially, the secondary succession of such a Mediterranean fire-prone area (Table 1), two other

Table 1 The secondary successions reconstructed according to a diachro-synchronic approach for applying null model analysis to vertebrate communities in the Mediterranean belt (*Erico–Quercion ilicis*) in the Madonie Regional Park. Twenty vegetation fragments (FF) and various replicates of 100-ha sample areas of recently burned (BA) and control areas (CNB) were considered. Intermediate post-fire areas (INT1 and INT2) were not replicated because of the absence of suitable areas, and this meant their exclusion from the null model analysis for the entire vertebrate community (see Table 4)

| Treatment | Year of census | | N | Year of fire | Previous fires |
	2002 (age of 1st succession)	2003 (age of 2nd succession)			
Diachronic			*Synchronic*		
BA	1	2	3	2001	1973 (BA1); 1981 (BA2–3)
FF	1	2	20	2001	1973 or 1981 according to localization within BA1–3
INT1	4	5	1	1998	1981
INT2	9	10	1	1993	Not known
CNB	> 50	> 50	5	*c.* 1950	Not known

100-ha sample areas in two large, adjacent woodland territories (400 and 800 ha), burned in 1993 and in 1998 respectively, were considered. In the 2002 census, they represented the two intermediate recovery stages of fire after 4 years (INT1) and 9 years (INT2). In the 2003 census, these became 5-year-old and 10-year-old stages, and the BAs and FFs became 2 years old. In both cases, the CNBs were considered as > 50 years old. The sampling design followed in this research was the diachrosynchronic schedule, using both diachronic sampling (i.e. in 2002 and 2003) of the same burned areas, and synchronic sampling of different areas burned at different dates (i.e. at different post-fire ages), to gain an idea of long-term changes (Table 1). This mixed approach is a useful compromise often used for reconstructing a secondary succession when the period of field sampling is brief (Prodon & Pons, 1993). Disadvantages, however, include not being able to consider the heterogeneity of the areas under consideration, their variation in past fire histories, and the possible variation in species detection arising from the two years of the census.

Species records

A checklist of terrestrial vertebrate species (excluding Chiroptera) was created using a stratified sampling (Morrison *et al.*, 2001) of the four treatments (FFs, BAs, INTs and CNBs). The available literature (Casamento & Sarà, 1993; Lo Valvo *et al.*, 1993; Sarà & Casamento, 1993, 1995; Sarà, 2000; Milazzo *et al.*, 2003; Sarà *et al.*, 2005) provided further information regarding the presence of species in the CNBs. Surveys were carried out during 2002 and then repeated in 2003, in accordance with the activity pattern and breeding phenology of species. Monthly bird censuses were performed from 15 March to 15 June in 2002 (median value of the post-fire recovery time = 5.5 months after the fire in November 2001) and throughout the same period in 2003 (median value = 17.5 months). *Muscardinus avellanarius* colonized nest-boxes each year from October to January (median values = 12.5 and 25 months), and *Glis glis* from July to

December (median values = 10.5 and 21 months). For reasons of brevity, the 2002 census will hereafter be referred to as '1 year after fire' and that for 2003 as '2 years after fire' in all the treatments.

Singing birds were censused in accordance with the point count technique (Bibby *et al.*, 1992). 300 (78 in FFs + 71 in BAs + 36 in INT1 + 29 in INT2 + 86 in CNBs) random-point counts in a period of 10 min (Fuller & Langslow, 1984) were carried out in spring 2002, and 278 (65 in FFs + 60 in BAs + 42 in INT1 + 42 in INT2 + 69 in CNBs) in 2003. A laser range-finder was used to fix the radius (50 m) of each station in order to avoid double counts and the detection of birds singing outside every point count. This improved sample accuracy, especially for the smallest FFs.

The presence of dormice was assessed by locating natural nests (*M. avellanarius*) and by making nocturnal listening and track (opened oak acorns) records (*G. glis*). In addition, 54 small (20 × 15 × 15 cm; hole size: 32 mm) and 22 large (20 × 20 × 30 cm; hole size: 50 mm) artificial nest-boxes were mounted in those FFs that possessed a suitable habitat for *M. avellanarius* ($n = 10$) and *G. glis* ($n = 8$); see Sarà (2000), Sarà *et al.* (2000, 2001), Milazzo *et al.* (2003). The number of nest-boxes was proportional to the fragment size area (e.g. for *M. avellanarius*: $r = 0.73$, $P = 0.04$). From 1999 to 2001, 46 small nest-boxes for dormice were active in an area, which later burned during the 2001 fire (defined as CNB0). A further 159 (127 small + 32 large) small nest-boxes were mounted and controlled in the BAs, INTs and CNBs during the period 2002 to 2003.

In addition, nest-boxes yielded information about the presence of various other species: three reptiles (*Podarcis sicula* and *P. wagleriana*, *Tarentola mauretanica*), three passerines (*Parus major*, *P. caeruleus*, *Certhia brachydactyla*), and three rodents (*Rattus rattus*, *Mus domesticus*, *Apodemus sylvaticus*). Trapping sessions (two fixed grids of 1 ha containing 60 traps, and 5 samples with groups of 8 to 10 traps) in autumn and spring increased the sampling of small terrestrial mammals in an already well-explored area (see Casamento & Sarà, 1993;

Sarà & Vitturi, 1996; Goüy de Bellocq et al., 2003). Two or three groups of researchers, each with two or three people, looked contemporaneously for dens, nests and tracks, and recorded seen (or collected dead) individuals of species during diurnal and nocturnal excursions in the FFs, BAs, INTs and CNBs. This enabled the detection of amphibians, reptiles and medium-size mammals.

Statistical analysis of species co-occurrence

Null model analysis (Gotelli & Graves, 1996; Gotelli, 2000) was used in order to test for non-random patterns of species co-occurrence. Null models are pattern-generating models that deliberately exclude a mechanism of interest, thereby allowing for the randomization tests of ecological and biogeographical data (Gotelli, 2001). They are used to address specific hypotheses about patterns in nature, by creating artificial data sets that would be expected if a given null hypothesis were true and comparing this with observed patterns derived from survey work.

In our case, the null model tested whether species-specific and/or habitat-specific interactions led to non-random co-occurrence patterns (through species segregation) or, alternatively, whether community composition was determined randomly (through progressive species aggregation). A set of separate presence/absence matrices for each replicate within each treatment (see Table 1) was created to compare the co-occurrence patterns of recent (BA, 1–2 years old), intermediate (INT, 4–10 years old) and ancient (CNB > 50 years old) burned areas, plus those of the forest fragments (FF, 1–2 years old). First, the breeding avifauna was analysed. The entries in the matrices were, therefore, the breeding bird species (rows) recorded, by the given n of point counts (columns) in each treatment. Since the n of point counts and the breeding n of species varied, the sizes of the derived matrices also varied. Next, the statistical analysis for avifauna was repeated, excluding the summer breeding (migratory) species and hence considering only the year-round resident breeding species.

C-score of Stone & Roberts (1990 in Gotelli, 2000) was used as a quantitative index of bird community organization. This index quantifies the average number of checkerboard units for each unique pair of species (see Gotelli, 2000; Gotelli & Entsminger, 2004 for more details). When compared with that simulated from a null distribution, a large index value suggests that there is a lower degree of pairwise species co-occurrence than would be expected by chance. If the index is unusually small, the converse is the case. The observed C-scores were tested statistically against an expected null distribution using a randomization procedure of 5000 iterations, which reshuffled the presence/absence matrix, starting from a random seed number.

The so-called 'fixed/equiprobable' or SIM2 (Gotelli, 2000) module in the Ecosim 7.70 software (Gotelli & Entsminger, 2004) was used to create an appropriate null model algorithm for lists of species derived from standardized samples (i.e. the EFP point counts) within relatively homogeneous sample areas

(i.e. the treatments). According to the algorithm used, the occurrences of species (row totals in a studied matrix) were kept fixed but sample plots (column totals) were considered as equally likely to be represented and were left to vary accordingly (Gotelli, 2000). This simulation algorithm has an effective statistical power (type I and type II errors) in detecting patterns in noisy data sets (Gotelli, 2000), such as those deriving from census methods.

Secondly, all vertebrate species censused in the treatments were analysed, also including the possible breeding species and those (e.g. Vulpes vulpes, Falco tinnunculus) regularly feeding in and visiting various FFs or 100-ha replicates within the treatments. This second block of data formed separate matrices in which the entries were the vertebrate presences/absences (rows), which were recorded in each considered replicate (columns). In this case also, the sizes of the derived matrices varied, according to the n of recorded species and to the n of considered fragments or replicates within a treatment. The two single-column matrices (INT1 and INT2 in both years) were not processed. The null model analysis of vertebrate matrices was performed again, using C-scores and SIM2.

For a meaningful comparison of the different tests, all the null model results among independent sampling periods and treatments were scaled to standard effect sizes (SES), which were calculated as (observed index − mean of simulated indices)/SD of simulated indices. Assuming a normal deviation distribution, a SES that is greater than 2 or less than −2 is statistically significant, with a tail probability of less than 0.05 (Gotelli, 2000).

To explore further whether the co-occurrence structure had changed in response to fire disturbance, the matrices were tested to ascertain the existence of patterns by analysing the treatments in pairs or as a single group (i.e. the four treatments all together). The 'guild structure' module in the Ecosim software was used.

ANOVA and other statistical analyses were run using STATISTICA 6.0 or calculated by macro routines in Microsoft Excel (e.g. Sorensen's Similarity Index). In some cases, the 20 FFs were grouped into three classes: small (1000–7500 m², $n = 9$), medium (7501–25,000 m², $n = 6$) and large (> 25,000 m², $n = 5$), in order to reduce the effect of the species–area relationship and to obtain a sample comparable to those in the other treatments.

RESULTS

Species richness and taxonomic composition

In total, 65 species of terrestrial vertebrates were recorded in this 2-year study period and in the four Erico–Quercion ilicis treatments of the Mediterranean belt. They represent exactly 50% of the terrestrial fauna listed throughout the lowland Madonie Range (M. Sarà, pers. obs.). Eliomys quercinus and Bufo viridis, formerly recorded as present in the lowland Madonie (Sarà, 2000; Lo Valvo & Longo, 2001), may have been
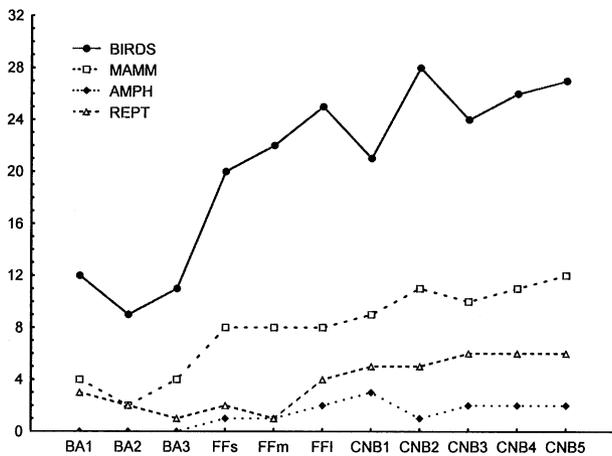
Figure 1 Plot of the average species richness per taxonomic group, for both census years (2002 and 2003), with treatment (BA, FF and CNB) as the main effect. BA: burned areas; FF: forest fragments; CNB: control areas not burned for 50 years. Here and in Fig. 2 the FFs have been grouped into three classes: small (1000–7500 m^2, $n = 9$); medium (7501–25,000 m^2, $n = 6$); and large (> 25,000 m^2, $n = 5$).

Figure 2 Box & Whisker plot (mean ± SD ± SE) of Sorensen's similarity index among the terrestrial vertebrate species recorded in the three treatments one year after fire (2002). Abbreviations are as in Fig. 1. BA vs. FF: $t_{(2)} = 3.29$, $P =$ n.s.; BA vs. CNB: $t_{(2)} = 20.79$, $P = 0.002$; FF vs. CNB: $t_{(7)} = 3.35$, $P =$ n.s.

omitted from the census. As only two burned carapaces of *Testudo hermanni* were found, this species was excluded from our calculations. These three species, endangered or vulnerable in Sicily, may be very rare or on the verge of extinction in the Mediterranean belt of Madonie.

In order to compare the taxonomic composition of the community, the recorded vertebrates were divided into the four largest taxonomic groups. The 2-way MANOVA produced significant results for both fixed and general effects: (1) treatment [Wilks' $\lambda_{(8,22)} = 0.201$, $P < 0.001$], and (2) year [Wilks' $\lambda_{(4,11)} = 0.361$, $P = 0.017$], but their interaction, treatment × year [Wilks' $\lambda_{(8,22)} = 0.342$, $P = 0.102$] was not significant. Post hoc comparisons revealed specific effects among taxa in the treatments and in the 2-year sample periods. For the taxa, all differences were significant except for those regarding the amphibians in FFs vs. CNBs and the reptiles in BAs vs. FFs. The species richness of mammals, birds and reptiles recorded in 2002 were significantly lower than that recorded in 2003, whereas the species richness of amphibians was not.

Figure 1 shows the mean for four taxonomic groups, with the treatments (INTs not considered) as the main effect. Birds make up the largest component of the assemblage (63% of total species recorded), followed by mammals, reptiles and amphibians. The BAs have the lowest species richness, followed in ascending order by the small, medium and large FFs, and later by the CNBs. Furthermore, the similarity of species was checked (Fig. 2): one year after fire, the average intra-BA similarity was at its lowest point with respect to FFs and CNBs. The CNB communities proved to be the most homogeneous (0.85 ± 0.04, $n = 6$) in terms of faunal similarity, while those of the BAs were relatively more heterogeneous (0.67 ± 0.04, $n = 3$), and those of the three FF classes were intermediate
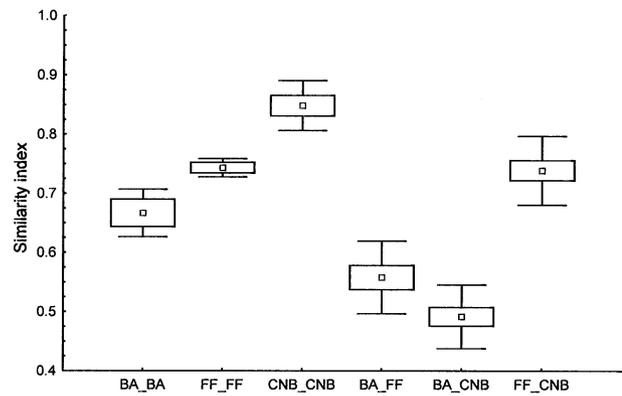
(0.74 ± 0.02, $n = 3$). Accordingly, the similarity comparisons showed that the vertebrate assemblage for BAs was less similar than that for CNBs, whereas the communities in FFs and CNBs were quite similar (Fig. 2).

The vertebrates of forest fragments

There were two origins of the FFs: (1) natural FFs were created by ground morphology, slopes or wind – the latter turned the direction of the fire and left behind unburned patches with a characteristic concave or 'cradle' shape, and (2) 'anthropogenic' FFs created by either the work of firefighters and/or recent forestry management (i.e. clearing the undergrowth, which stops the crown fire). In our sample, 70% of FFs proved to be anthropogenic in origin, characterized by a vertical vegetation coverage, which was less dense and poorer in plant species than in the natural FFs [Wilks' $\lambda_{(5,93)} = 0.724$, $P < 0.001$]. Post hoc comparisons (Tukey HSD test for unequal n) produced statistically significant differences for the coverage at the 0–1 m layer ($P = 0.003$); 1–2 m ($P = 0.0002$); and > 4 m ($P = 0.0002$), in addition for the average plant species richness ($P = 0.012$). There was no statistical significance for the coverage at the 2–4 m layer ($P = 0.306$), area size ($P = 0.626$) and shape of the fragments ($P = 0.786$), as compared with their origin.

In total, 50 vertebrate species were present in 20 FFs 1 year after the fire, and four new vagile species (birds and medium-size mammals) were added in the second year. The species richness for each FF correlated well with FF area in both years ($R_{2002} = 0.64$; $P < 0.05$ and $R_{2003} = 0.70$; $P < 0.05$), and regression slopes (the z-value of Preston, 1960) indicated a high degree of insularity ($z_{2002} = 0.396$ and $z_{2003} = 0.431$). Only FFs larger than 25,000 m^2 displayed species richness and taxonomic similarity values comparable to those of the CNBs. In addition, the taxonomic similarity of species among the FFs and the BAs was relatively low (Fig. 2).

Species co-occurrence

Null model analysis has enabled us to explore the pattern of species co-occurrence in the fire-prone woodland ecosystems of the Madonie Regional Park. In both census years, there was evidence for a non-random co-occurrence pattern (segregation) of breeding birds in the CNB woodlands but not for the other treatments (Table 2). In recent and intermediate burned areas, the observed C-scores were not significantly different from the indices simulated by chance. This, therefore, indicated a random average co-occurrence among bird species for those assemblages. The INT1 stage of 4 years after fire was an exception to this general pattern, because it showed a non-random co-occurrence pattern. On the other hand, the breeding birds found in FFs showed C-scores that were significantly smaller than those expected by chance ($P < 0.001$), thereby indicating an aggregation of breeding species within these unburned patches of habitat.

Figure 3 plots the null model results for the avifauna matrices, scaled to SES values. In both years the breeding

Table 2 Patterns of species co-occurrence for the breeding bird community in the post-fire secondary successions under consideration. Summer breeding species were excluded in (b) in order to check for their role in the co-occurrence pattern of INT1(4 years). Statistically significant P-values for observed C-scores less than simulated are in italics

Treatment (years post-fire)	Observed C-score	Mean of simulated C-score	Variance of simulated C-score	P
(a) *SIM2 model, with summer and resident breeding bird species*				
2002 census				
FF (1 year)	82.275	91.702	4.588	1.000
BA (1 year)	14.890	16.724	0.514	0.990
INT1 (4 years)	23.886	22.147	0.897	*0.023*
INT2 (9 years)	14.117	14.158	0.625	0.545
CNB (50 years)	145.602	140.938	6.736	*0.028*
2003 census				
FF (2 years)	54.428	57.033	1.654	0.971
BA (2 years)	29.873	28.882	0.803	0.131
INT1 (5 years)	27.693	27.533	1.131	0.455
INT2 (10 years)	24.910	25.309	1.392	0.643
CNB (50 years)	87.603	83.413	3.674	*0.007*
(b) *SIM2 model, with resident breeding bird species*				
2002 census				
FF (1 year)	87.724	97.241	0.000	1.000
BA (1 year)	12.808	13.603	0.415	0.885
INT1 (4 years)	22.935	21.852	1.260	0.170
INT2 (9 years)	14.524	14.232	0.820	0.393
CNB (50 years)	180.344	173.624	13.617	*0.025*
2003 census				
FF (2 years)	61.451	65.932	3.170	0.990
BA (2 years)	30.053	29.432	1.127	0.291
INT1 (5 years)	30.735	29.307	1.945	0.151
INT2 (10 years)	28.595	28.609	1.998	0.521
CNB (50 years)	93.490	89.965	5.427	*0.050*

avifauna of the FFs displayed negative SES values, that is, a more significant aggregated pattern than could be expected by chance alone. In the first year after fire, the BAs revealed a negative SES, but in the second year the SES values were positive. In both years, the breeding avifauna of the CNBs displayed positive SES values, thereby highlighting a segregation of co-occurrence patterns at the end of the secondary succession. The SES values for the intermediate post-fire stages of 4–5 years and 9–10 years did not fit neatly into the sequence, as the co-occurrence pattern of INT2 proved to be more random than that of the previous younger INT1 stage.

The results of the null model tests that analysed pairs/groups of data matrices taken together and not independently as in the earlier case (Table 2, Fig. 3), confirmed that the observed C-scores significantly increased, passing from the first to the 50th years after fire (i.e. from BA to CNB in Table 3).

Results for the vertebrate community are shown in Table 4. In both census years, a non-random co-occurrence pattern (segregation) of vertebrates in the CNBs was found. Within the FFs the community displayed an aggregated pattern, while the pattern was random within the BAs.

DISCUSSION

Wildfires in areas of the Mediterranean contribute to the fragmentation of original forest habitats and to their destruction, thereby reducing their size, increasing the isolation of forest patches, and producing a heterogeneous landscape, with woodland archipelagos located in open or shrubby matrices with different post-fire ages (Trabaud & Prodon, 1993; Blondel, 1995; Forman, 1995). Within this scenario, the stochastic extinction of small and slowly dispersing populations (Bright, 1993; Andrén, 1994; Meffe & Carrol, 1997) is attributable to the temporal and spatial isolation of forest fragments and increasing edge effects (Hinsley et al., 1995; Bellamy et al., 1996; Diaz et al., 1998). Furthermore, bird and mammal communities react to fire with species turnover and changes in population density at every stage in the post-fire succession (Prodon et al., 1984, 1987; Haim et al., 1996, 1997; Izhaki & Adar, 1997).

The results of this study indicate that wildfires influence species richness in Mediterranean woodland ecosystems, as three formerly present species were not recorded and species richness was much lower in the BAs than in the CNBs (Fig. 1). Furthermore, in such areas, rarity, of at least six species (*Hyla intermedia*, *Parus caeruleus*, *Turdus viscivorus*, *Oriolus oriolus*, *M. avellanarius*, *G. glis*), can be attributed to fire, which affected population densities (M. Sarà, A. Milazzo, E. Belleva, unpubl. data).

The application of a null model analysis to the phenomenon of wildfires has suggested that their effects influenced the community structure in the studied system, reorganizing the co-occurrence patterns of communities and resulting in changes that occurred over several consecutive years following burning. As depicted by the bird community data in Fig. 3, the assemblage was reorganized during the secondary succession,

Figure 3 The displacement of co-occurrence patterns in breeding avifauna emerging by the standardized effect size (SES) of the matrices and ordered according to post-fire time and study period. Larger SES values were cut at the 2.0 and −2.0 significant SES boundaries. The SES values have been calculated for summer and resident breeding birds in 2002 (S + R_02) and in 2003 (S + R_03); and only for resident breeding birds in 2002 (R_02) and 2003 (R_03).
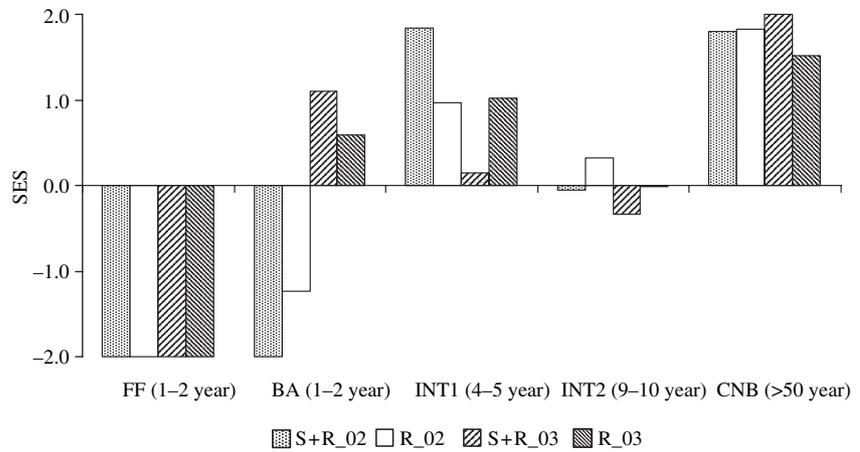
Table 3 Co-occurrence patterns of breeding avifauna recorded in 2002 among the post-fire stages considered all together. In the first BA stage, the observed C-scores were smaller than the mean of simulated C-scores; then this ratio was reversed until the observed C-scores became much larger than the simulated C-scores. The observed variances were significantly larger than the simulated variances both for the four treatments considered as a single group and for their pair-wise comparisons. These values (at the bottom of the table) indicate that co-occurrence structures were significantly different between the post-fire stages with respect to the control areas

Treatment (years post-fire)	N	Observed C-score	Mean of simulated C-score	Variance of simulated C-score	Observed variance	Simulated variance	P
BA (1 year)	71	14.890	54.529	49.001	2986.335	256.888	< 0.001
BA (4–9 years)	65	59.644	46.653	41.801			
FF (1 year)	78	76.343	65.220	60.315			
CNB (50 years)	86	146.484	77.700	86.322			

Pair-wise variance test (P of observed vs. simulated variance)

	BA (1 year)	BA (4–9 years)	FF (1 year)
CNB (50 years)	< 0.001	0.006	< 0.001

Table 4 Patterns of species co-occurrence, by SIM2 model, of the vertebrate community in the post-fire secondary successions under consideration. Intermediate post-fire stages (INT1 and INT2 in Table 1) were not considered owing to the absence of replicates. P-values are the same as in Table 2

Treatment (years post-fire)	Observed C-score	Mean of simulated C-score	Variance of simulated C-score	P
2002 census				
FF (1 year)	4.413	6.944	0.025	1.000
BA (1 year)	0.312	0.347	0.001	0.875
CNB (50 years)	0.498	0.475	0.000	*0.087*
2003 census				
FF (2 years)	5.873	8.931	0.000	1.000
BA (2 years)	0.369	0.367	0.000	0.549
CNB (50 years)	0.294	0.275	0.000	*0.004*

shifting from aggregation to random in the second year after fire, tending towards random/segregation in the following INT1 years, and definitely structuring in a non-random segregated pattern in the CNBs.

This trend is, however, not perfectly ordered, since the more mature post-fire stage of 9–10 years proved to be more random that the previous younger 4–5 year stage, which also had an unexpected non-random co-occurrence pattern (Table 2). This latter atypical value could be partly attributable to the presence of three summer breeding species (*Sylvia cantillans*, *Luscinia megarhynchos*, *Cuculus canorus*), owing to the fact that, when the model was repeated in the absence of these species, the random pattern re-appeared. Apparently, bird phenology in some intermediate post-fire stages – for example the arrival of a migratory stock only in a given breeding area and/or in a given breeding season – may play a role in influencing point-count records and hence checkerboard units for every species pair. As a general consideration, the unexpectedly varying results in the INT1 and INT2 stages merit more investigation, because they may depend on both the absence of replicas and limits of the mixed diachro-synchronic sampling design, which was followed in reconstructing the secondary succession.

The entire vertebrate community also was a random aggregate of species until 10 years after the fire, and species segregation re-appeared in unburned woodlands at least 50 years after the fire (Table 4).

The present application of null models to fire-prone vertebrate communities suggests, therefore, that assembly rules contribute to organizing community living in the Mediterranean woodland ecosystem, which is the farthest from the disturbance. The vertebrates of such woodlands are likely to be structured by competitive interactions, as species coexist less than could be expected by chance. Diamond's otherwise controversial (Connor & Simberloff, 1979; Wiens, 1989; Gotelli & Graves, 1996) assembly rules (1975) have predicted that competitive interactions between species lead to non-random co-occurrence patterns, and a recent analysis (Gotelli & McCabe, 2002) has supported this model. Although the latter work did not clarify the processes underlying these assembly rules, it showed that the observed co-occurrences in the natural communities reviewed were, in general, statistically less than could be expected by chance.

Given that wildfires disrupt assembly rules in Mediterranean woodland vertebrate communities, we can infer some underlying mechanisms that cause such a displacement from segregation to randomness. First, fire might have a differential impact on species survival and density (see, for example, Prodon *et al.*, 1987; Haim *et al.*, 1997; and references in Trabaud & Prodon, 1993). More vagile, densely distributed species or habitat generalists (e.g. *Lacerta bilineata*, *Sylvia melanocephala*, *P. major*, *Turdus merula*, *M. domesticus*, etc.) might suffer a relatively lower mortality rate than the less vagile, rarer or habitat specialist species (e.g. *H. intermedia*, *Discoglossus pictus*, *P. caeruleus*, *T. viscivorus*, *M. avellanarius*, etc). As only the first group of species could persist in or colonize early in recently burned habitats – where the second group of species could not – co-occurrence patterns among species might be altered. That is to say, the most resistant and resilient species would be more likely to be found than the others, by chance, in the burned habitats (Haim, 1993; Izhaki, 1993, 2000), and this would produce a community with a higher degree of co-occurrence than would otherwise be expected.

Moreover, fire intensity and frequency might affect the structure of the fire-prone community in a differential way, since both these factors and, consequently, their effects vary spatially and temporally (see USSAB, 2003 for the studied area; and references in Trabaud & Prodon, 1993; Aber & Melillo, 2001). The overall outcome would then be a random co-occurrence of species in a patchwork of areas hit in the past with different fire intensities and frequencies.

The surviving community of vertebrates in the forest fragments merits a final consideration. It was an impoverished sample of undisturbed woodlands, as revealed by the strong area–species relationships, and null model analyses produced strongly aggregated assemblages. This species aggregation may depend on the significantly different habitat structure of the unburned fragments, which shelters, by chance, the presence of slow-dispersing species; and favours the arrival, soon after the fire, of vagile species attracted by parcels of suitable habitat. Wood fragments, in this view, might act as species reservoirs, which contribute both to relax the extinction process of species

less resistant to fire (*M. avellanarius*, *H. intermedia*, etc.), and later to re-start the colonization process in the nearby areas. Nevertheless, the current investigation did not provide information regarding the quality of individuals (Wiens, 1989), the persistence time (Quinn & Hastings, 1987; Ovaskainen, 2002; Reed, 2004), or the loss of the genetic diversity of populations (Fahrig & Merriam, 1994; Debinski & Holt, 2000) that live in such forest fragments and in general in the fire-prone ecosystems.

CONCLUSION

The species co-occurrence patterns for both birds and total vertebrates changed after the advent of fire in the *Erico–Quercion ilicis* woodland. Where the time since fire exceeded 50 years, there was a significantly lower degree of species co-occurrence than could be expected by chance. On the other hand, where fire occurred between 1 and 10 years previously, co-occurrence patterns in the series of regenerating areas did not differ significantly from random. The forest fragments behaved differently, by displaying more species aggregation than could be expected by chance alone.

In addition, this case study has suggested that the recolonization of burned areas essentially proceeds by: (1) the permanence and early arrival from surrounding, old post-fire stages of vagile colonizers and habitat generalists; and (2) the minor contribution of less vagile and specialist species surviving by chance, especially in the largest forest fragments present in the burned matrix. These fragments are, therefore, implicated in the persistence of various previously mentioned rare species. The ecological attributes of species and their order of arrival from minor and major sources, together with a shared long-term regional fire regime of selection, are likely to be the ultimate factors responsible for such a marked co-occurrence pattern of species in these fire-prone ecosystems.

ACKNOWLEDGEMENTS

REFERENCES

Aber, J.D. & Melillo, J.M. (2001) *Terrestrial ecosystems.* Academic Press, London.

Andrén, H. (1994) Effect of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitats: a review. *Oikos*, **71**, 355–366.

Arrizabala, A., Montagud, E. & Fons, R. (1993) Post-fire succession in small mammal communities in the Montserrat

Massif (Catalonia, Spain). *Fire in Mediterranean ecosystems* (ed. by L. Trabaud and R. Prodon), pp. 281–292. Ecosystem Research Report no. 5. Commission European Communities, Brussels.

Bellamy, P.E., Hinsley, S.A. & Newton, I. (1996) Factors influencing bird species numbers in south-east England. *Journal of Applied Ecology*, **33**, 249–262.

Bibby, C.J., Burgess, N.D. & Hill, D.A. (1992) *Bird census techniques*. Academic Press, London.

Blondel, J. (1995) *Biogeographie: approche ecologique et evolutive*. Masson et Cie, Paris.

Blondel, J. & Aronson, J. (1999) *Biology and wildlife of the Mediterranean Region*. Oxford University Press, Oxford.

Bright, P. (1993) Habitat fragmentation – problems and predictions for British mammals. *Mammal Review*, **23**, 101–111.

Casamento, G. & Sarà, M. (1993) Distribuzione dei Mammiferi delle Madonie (Mammalia). *Naturalista siciliano*, **17**, 169–179.

Connor, E.F. & Simberloff, D. (1979) The assembly of species communities: chance or competition? *Ecology*, **60**, 1132–1140.

Debinski, D.M. & Holt, R.D. (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology*, **14**, 342–355.

Di Castri, F. (1981) Mediterranean-type shrubland of the world. *Ecosystems of the world*, Vol. 11 (ed. by F. Di Castri, D.W. Goodall and R.L. Specht), pp. 1–52. Elsevier, Amsterdam.

Diamond, J.M. (1975) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, **7**, 129–146.

Diaz, M., Carbonell, R., Santos, T. & Telleria, J.L. (1998) Breeding bird communities in pine plantations of the Spanish plateaux: biogeography, landscape and vegetation effects. *Journal of Applied Ecology*, **35**, 562–574.

Fahrig, L. & Merriam, G. (1994) Conservation of fragmented populations. *Conservation Biology*, **8**, 50–59.

Fons, R., Grabulosa, I., Feliu, C., Mas-Coma, S., Galan-Puchades, M.T. & Comes, A.M. (1993) Post-fire dynamics of a small mammal community in a Mediterranean forest (*Quercus suber*). *Fire in Mediterranean ecosystems* (ed. by L. Trabaud and R. Prodon), pp. 259–270. Ecosystem Research Report no. 5. Commission European Communities, Brussels.

Forman, R.T.T. (1995) *Land mosaics: the ecology of landscapes and regions*. Cambridge University Press, Cambridge.

Fuller, R.J. & Langslow, D.R. (1984) Estimating number of birds by point counts: how long should counts last? *Bird Study*, **31**, 195–202.

Gotelli, N.J. (2000) Null model analysis of species co-occurrence patterns. *Ecology*, **81**, 2606–2621.

Gotelli, N.J. (2001) Research frontiers in null model analysis. *Global Ecology & Biogeography*, **10**, 337–343.

Gotelli, N.J. & Entsminger, G.L. (2004) *ECOSIM, null models software for ecology*. Acquired Intelligence Inc., Kesey-Bear Jericho. http://garyentsminger.com/ecosim.

Gotelli, N.J. & Graves, G.R. (1996) *Null models in ecology*. Smithsonian Institution Press, Washington, DC.

Gotelli, N.J. & McCabe, D.J. (2002) Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. *Ecology*, **83**, 2091–2096.

Goüy de Bellocq, J., Sarà, M., Casanova, J.C., Feliu, C. & Morand, S. (2003) A comparison of the structure of helminth communities in the woodmouse *Apodemus sylvaticus*, on islands of the western Mediterranean and continental Europe. *Parasitology Research*, **90**, 64–70.

Haim, A. (1993) Resilience to fire of rodents in an east-Mediterranean pine forest on Mount Carmel, Israel: the effect of different managements. *Fire in Mediterranean ecosystems* (ed. by L. Trabaud and R. Prodon), pp. 293–301. Ecosystem Research Report no. 5. Commission European Communities, Brussels.

Haim, A. & Izhaki, I. (2000) The effect of different treatments on the community composition of small mammals in a post-fire pine forest. *Journal of Mediterranean Ecology*, **1**, 249–257.

Haim, A., Izhaki, I. & Golan, A. (1996) Rodent diversity in pine forests recovering from fire. *Israel Journal of Zoology*, **42**, 353–359.

Haim, A., Rozenfeld, A. & Izhaki, I. (1997) Post-fire response of shrews (*Crocidura suaveolens*) on Mount Carmel, Israel. *Mammalia*, **61**, 527–536.

Hinsley, S.A., Bellamy, P.E., Newton, I. & Sparks, T.H. (1995) Habitat and landscape factors influencing the presence of individual breeding bird species in woodland fragments. *Journal of Avian Biology*, **26**, 94–104.

Huston, M.A. (1994) *Biological diversity*. Cambridge University Press, Cambridge.

Izhaki, I. (1993) The resilience to fire of passerine birds in an east-Mediterranean pine forest on mount Carmel, Israel: the effect of different managements. *Fire in Mediterranean ecosystems* (ed. by L. Trabaud and R. Prodon), pp. 303–314. Ecosystem Research Report no. 5. Commission European Communities, Brussels.

Izhaki, I. (2000) Passerine bird communities in Mediterranean pine forests. *Ecology, biogeography and management of Pinus halepensis* and *P. brutia*. Forest ecosystems in the Mediterranean basin (ed. by G. Ne'eman and L. Trabaud), pp. 237–250. Buckhuys Publishers, Leiden.

Izhaki, I. & Adar, M. (1997) The effects of post-fire management on bird community succession. *International Journal of Wildland Fire*, **7**, 335–342.

Liacos, L.G. (1973) Present studies and history of burning in Greece. *Proceedings of the Annual Tall Timber Fire Ecology Conference*, **14**, 65–95.

Lo Valvo, F. & Longo, A.M. (2001) *Anfibi e rettili di Sicilia*. L'Epos editrice, Palermo.

Lo Valvo, M., Massa, B. & Sarà, M. (1993) Uccelli e paesaggio in Sicilia alle soglie del terzo millennio. *Naturalista siciliano*, **17**, 1–373.

Meffe, G.K. & Carrol, C.R. (1997) *Principles of conservation biology*. Sinauer, Sunderland, MA.

Milazzo, A., Falletta, W. & Sarà, M. (2003) Habitat selection of fat dormouse (*Glis glis italicus*) in deciduous woodlands of Sicily. *Acta Zoologica Academiae Scientiarum Hungaricae*, **49**, 117–124.

Morrison, M.L., Block, W.M., Dale Strickland, M. & Kendall, W. (2001) *Wildlife study design*. Springer-Verlag, New York.

Naveh, Z. (1990) Fire in the Mediterranean, a landscape ecological perspective. *Fire ecosystem dynamics* (ed. by J.G. Goldammer and M.J. Jenkins), pp. 1–20. Academic Publishing, Den Haag.

Ovaskainen, O. (2002) Long-term persistence of species and the SLOSS problem. *Journal of Theoretical Biology*, **218**, 419–433.

Pickett, S.T. & White, P.S. (1985) *The ecology of natural disturbance and patch dynamics*. Academic Press, New York.

Pignatti, S. (1997) *Ecologia del Paesaggio*. UTET, Torino.

Preston, F.W. (1960) Time and space and the variations of species. *Ecology*, **41**, 611–627.

Prodon, R. (1987) Fire, bird conservation and land management in the north-Mediterranean area. *Ecologia Mediterranea*, **13**, 127–133.

Prodon, R. & Lebreton, J.D. (1981) Breeding avifauna of a Mediterranean succession: the holm oak and cork oak series in the eastern Pyrenees, 1. Analysis and modelling of the structure gradient. *Oikos*, **37**, 21–38.

Prodon, R. & Pons, P. (1993) Post-fire bird studies: methods, questions, and perspective. *Fire in Mediterranean ecosystems* (ed. by L. Trabaud and R. Prodon), pp. 332–343. Ecosystem Research Report no. 5. Commission European Communities, Brussels.

Prodon, R., Fons, R. & Peter, A.M. (1984) L'impact du feu sur la végétation, les oiseaux et les micromammifères dans diverses formations des Pyrénées-orientales: premiers résultats. *Revue Ecologie, Terre et Vie*, **39**, 129–158.

Prodon, R., Fons, R. & Athias-Binche, F. (1987) The impact of fire on animal communities in the Mediterranean area. *The role of fire on ecological systems* (ed. by L. Trabaud), pp. 121–157. SPB Academic Publishing, The Hague.

Quinn, J.F. & Hastings, A. (1987) Extinction in subdivided habitats. *Conservation Biology*, **1**, 198–208.

Raimondo, F.M. (1998) Carta del Paesaggio e della Biodiversità vegetale della Provincia di Palermo. *Quaderni di Botanica Ambientale e Applicata*, **9**, 3–160.

Reed, D.H. (2004) Extinction risk in fragmented habitats. *Animal Conservation*, **7**, 181–191.

Sarà, M. (2000) *Ghiri in Sicilia*. DoraMarkus, Palermo.

Sarà, M. & Casamento, G. (1993) Analisi del popolamento di topo selvatico (*Apodemus sylvaticus*) in un querceto mediterraneo. *Hystrix*, **4**, 17–27.

Sarà, M. & Casamento, G. (1995) Distribution and ecology of dormice (Myoxidae) in Sicily: a preliminary account. *Hystrix*, **6**, 161–168.

Sarà, M. & Vitturi, R. (1996) *Crocidura* populations (Mammalia, Soricidae) from the Sicilian–Maltese insular area. *Hystrix*, **8**, 121–132.

Sarà, M., Spinnato, A., Casamento, G. & Romano, S. (2000) Conservazione del moscardino *Muscardinus avellanarius* (L. 1958) (Mammalia, Myoxidae) nel Parco delle Madonie. *Naturalista Siciliano*, **24**, 69–95.

Sarà, M., Casamento, G. & Spinnato, A. (2001) Density and breeding of *Muscardinus avellanarius* in woodlands of Sicily. *Trakia University Journal of Scientific Research*, **2**, 85–94.

Sarà, M., Milazzo, A., Falletta, W. & Bellia, E. (2005) Exploitation competition between hole-nesters (*Muscardinus avellanarius*, Mammalia and *Parus caeruleus*, Aves) in Mediterranean woodlands. *Journal of Zoology, London*, **265**, 347–357.

Sousa, W.P. (1984) The role of disturbance in natural communities. *Annual Review Ecology and Systematics*, **15**, 353–391.

Trabaud, L. & Prodon, R. (1993) *Fire in Mediterranean ecosystems*. Ecosystem Research Report no. 5. Commission European Communities, Brussels.

USSAB (2003) *Carta delle aree a rischio d'incendio*. Ufficio Speciale Servizio Antincendio Boschivo Regione Sicilia, Palermo.

Wiens, J.A. (1989) *The ecology of bird communities*, Vol. I. Cambridge University Press, Cambridge.

BIOSKETCHES

Maurizio Sarà teaches biogeography in the Faculty of Science at the University of Palermo. His research field is the ecology, distribution and conservation of vertebrates in the Mediterranean area.

Andrea Milazzo is a PhD student and his thesis project concerns the ecological response of vertebrate communities to fire.

Enrico Bellia is a graduate student and his thesis deals with the relationship between birds and fire.

Editor: Jon Sadler