

**Turkish Journal of Zoology** 

http://journals.tubitak.gov.tr/zoology/

#### **Research Article**

# Habitat structure and host plant specialization drive taxonomic andfunctional composition of Heteroptera in postfire successional habitats

Eduardo MATEOS\*'\*\* (10), Marta GOULA (10), Teresa SAURAS (10), Xavier SANTOS\* (10)

Department of Evolutionary Biology, Ecology, and Environmental Sciences, University of Barcelona, Barcelona, Spain

Received: 26.10.2017	•	Accepted/Published Online: 28.03.2018	•	Final Version: 26.07.2018
----------------------	---	---------------------------------------	---	---------------------------

Abstract: Changes in habitat structure are the main driving forces for responses of animal assemblages to fire. According to the disturbance theory, generalist species are expected to outperform specialists in variable environments. Thus, we hypothesized that omnivorous and polyphagous species will become more abundant in unstable postfire successional vegetation, whereas monophagous (specialists), due to their strong dependence on host plants, are expected to respond according to the responses of plant hosts. We compared the responses of true bug (Heteroptera) assemblages in stable (unburnt) versus unstable (postfire successional) environments as this group shows a high diversity of feeding strategies. Redundancy analysis fitted our hypothesis as omnivorous and polyphagous bugs responded positively to fire whereas oligophagous bugs did not. Thus, the most generalized bugs in terms of diet were found in disturbed (burnt) habitats whereas specialized bugs were found in undisturbed (unburnt) habitats. Moreover, the most specialized bugs (monophagous species) responded to fire in accordance to the responses of their specific host plants. Although based on small bipartite networks, the lower modularity in burnt sites corresponded to a scenario of lower segregation of plant resources and fits the higher presence of generalist bugs in these sites. Our results suggest that plant–bug trophic interactions shape the response of Heteroptera to fire, and this response seems to be mediated by the degree of feeding specialization.

Key words: Bipartite network, multivariate ordination, disturbance theory, fire, species interaction, trophic specialization

#### 1. Introduction

Fire is a common disturbance in many regions and a key component to understanding ecosystem functioning (Bond et al., 2005). The number and extent of wildfires have increased in recent decades, and this pattern is expected to continue due to current warming (Moriondo et al., 2006) and land abandonment (Chergui et al., 2017). For this reason, it is of great interest to analyze the effects of fire on biodiversity and to determine which mechanisms explain the response of organisms to this disturbance. Several studies have argued that fire can be expected to have direct and indirect effects on animal communities (Warren et al., 1987) and to act as an evolutionary driver for animal diversity (Pausas and Parr, 2018). Although taxon-dependent, the response of animals to fire is strongly driven by vegetation structure and composition (Briani et al., 2004; Swan et al., 2015; Santos et al., 2016). Also, the effect of fire on flowering phenology could have a direct (by the absence of flowers) or indirect (by the scarcity of nectar in the early postfire years) effect on

pollinator populations (Neeman et al., 2000). Accordingly, animal communities change from unburnt forests to burnt open habitats in a wide number of taxa following habitat changes over postfire succession (e.g., Brotons et al., 2008 for birds; Driscoll and Henderson, 2008 for reptiles; Santos et al., 2009 for snails). Thus, species enter a community when their preferred habitat type has developed and then decline as the plant succession proceeds beyond their optimal habitat conditions (Fox, 1982; Letnic et al., 2004). In postfire scenarios, plants and animals show parallel trends in response to fire related to persistence (ability to survive), resilience (ability to recover), and mobility traits (Moretti and Leg, 2009). These results suggest that plantanimal interactions may promote postfire recolonization, being a key factor to track ecosystem functioning during postfire succession.

Examining the taxonomic and functional responses to fire is a useful approach to understand the underlying factors that cause the response (Moretti et al., 2006; Arnan et al., 2013). This method has illustrated, for example, that

<sup>\*</sup> These authors contributed equally to this work.

<sup>\*\*</sup> Correspondence: emateos@ub.edu

in dry temperate regions (e.g., the Mediterranean basin), functional stability in fire-prone ecosystems is achieved by the replacement of functionally similar species (Moretti et al., 2009). However, Arnan et al. (2013) reported that fire promotes higher functional diversity in ant communities, and Mateos et al. (2011) reported that Hymenoptera parasitoids may respond positively to fire according to the abundance of species to be parasitized. Despite these pioneering examples, very few studies have examined functional responses to fire by animal communities (Moretti et al., 2009; Arnan et al., 2013; Santos and Cheylan, 2013; Smith, 2018), and general predictive models need more empirical evidence.

Animal groups showing a high functional diversity are adequate model groups to examine functional responses to fire and the role of animal-plant interactions in driving these responses. To address this question, we have used Heteroptera (true bugs) since it represents the largest and most diverse group of hemimetabolous insects (Schuh and Slater, 1995). Heteroptera species occupy an enormous array of different habitats, performing a range of ecological functions and services (Henry, 2009). Heteroptera exploit a large range of food sources. Zoophagy is widespread among terrestrial true bugs, but the majority of species are phytophagous, feeding on any part of a plant (Schuh and Slater, 1995). Bugs show a wide range of host specificity towards their host plants, ranging from species feeding on a single plant (monophagous), a genus, or a family (oligophagous) to those that are highly polyphagous, feeding on multiple plant families (Carver et al., 1991). Omnivory (also named zoophytophagy), or the ability of feeding on plants and animals, is also found among Heteroptera. Floristic composition and vegetation structure are the environmental factors that best explain the biodiversity and distribution patterns of true bug assemblages (Bröring and Wiegleb, 2005; Frank and Künzle, 2006; Zurbrügg and Frank, 2006) and feeding group distributions (Torma and Császár, 2013; Torma et al., 2014, 2017). In the short term, fire reduces vegetation biomass, simplifies habitat structure (Keeley et al., 2012), and drives changes in faunal composition (Kelly and Brotons, 2017). In addition, the response of animal species to fire can be modeled by postfire management, i.e. the use of burnt vegetation (Bros et al., 2011). Thus, fire and postfire management are expected to induce taxonomic and functional responses of Heteroptera communities in accordance to species-specific bug feeding strategies and degree of specialization.

Our specific objectives were: i) to study variation in vegetation (plant composition and structure), bug species, and feeding group composition among fire and managed postfire areas; ii) to seek relationships between vegetation and Heteroptera composition among areas; and iii) to examine whether plant-bug interactions shape Heteroptera species and feeding group abundance in burnt and unburnt areas.

#### 2. Materials and methods

#### 2.1. Study area

The field work was conducted in Sant Llorenç del Munt i l'Obac Natural Park (Barcelona Province, NE Spain, Figure 1a). The climate is subhumid Mediterranean with mean annual temperature of 12.2 °C and annual rainfall around 600 mm. The natural park is prone to fast-spreading fires during hot, dry summers. Field sampling was done in an area burned on 10 August 2003 (Figure 1b). The burnt landscape was composed of a pine reforestation (46.4% Pinus halepensis Mill. and 25.3% P. nigra J.F.Arnold) with small patches of Holm oak forests (18%), scrublands (6.9%), and abandoned agricultural lands. Postfire timber removal began soon after the fire, and 2 years later, most of the area was completely logged. Woody debris remained on the ground. After logging, a subarea was also subsoiled (breaking up soil 30-46 cm deep) to plant mainly coniferous (Pinus sp.) stands. The area burnt in 2003 included an area that was previously burnt in 1970 (Figure 1b). Between both fires, this area was logged and grazed, being a scrubland habitat in 2003. The study area was a heterogeneous landscape mosaic both in terms of habitat structure and postfire management. Logging and subsoiling have different impacts on ecosystem function and structure, as well as on animal and plant diversity (Lindenmayer and Noss, 2006; Bros et al., 2011). Moreover, repeat burn regimes have also been reported to affect vegetation structure and composition and fauna (Fontaine et al., 2009). For these reasons, logging, subsoiling, and repeatedly burnt areas were separately considered in further analyses.

We defined four different sampling sites (Figure 1): 1) Repeat-burnt (R) was the scrubland site burnt in 1970, later logged and grazed, and burnt again in 2003. At this site, the most frequent plant species, among others, were Coris monspeliensis L., Helianthemum oelandicum (L.), Psoralea bituminosa L., and Cistus albidus L. 2) Logged (L) was the site only burnt in 2003 with subsequent logging; the most frequent plant species were Filago pyramidata L., Brachypodium phoenicoides (L.), Ononis minutissima L., and Sedum sediforme (Jacq.). 3) Subsoiled (S) was the site only burnt in 2003 with subsequent logging and subsoiling; the most frequent plant species were Daphne gnidium L., Cistus albidus, and young individuals of tree species Quercus ilex L. and Pinus sp. 4) Unburnt (U) was the control unburnt site in a pine forest with an understory dominated by Quercus ilex, Linum tenuifolium L., and Thymus vulgaris L. In each sampling site, five replicated plots of  $20 \times 5$  m were selected (Figure 1).



**Figure 1.** Geographic location of the study area in NE Spain (inner rectangle) and distribution of sampled sites. Squares: burnt, logged, and subsoiled site (site S); Circles: burnt and logged site (site L); Triangles: repeat-burnt site (site R); Stars: unburnt site (site U). The striped area was logged after the 2003 fire and the squared area was subsoiled. Light and dark gray areas represent surfaces affected by one (2003) and two (1970 and 2003) fires, respectively. The green line is the limit of the natural park. The black area is a village.

Site and plot selection was constrained by the location of the areas with different postfire practices (see Figure 1). Thus, site selection was spatially confounded as replicated plots within the same treatment were clustered. To reduce this spatial bias, replicated plots were selected to control for similar slope orientation and ground lithology and to find unburnt control plots with similar vegetation structure and dominant tree species as burnt plots. Moreover, we examined preburnt vegetation structure with an aerial photograph taken in 2001, two years before the fire. At each sampling plot, we counted the number of trees in a 50-m buffer and checked differences among sites. The average number of pines in a 50-m buffer circle around each sampling plot did not differ among the Logged, Subsoiled, and Unburnt sites (Logged site: mean = 94.6 pines; SE 16.4, range 62–151; Subsoiled site: mean = 66.6 pines; SE 20.7, range 19–132; Unburnt site: mean = 93.6 pines; SE 22.2, range 44–147; Kruskal–Wallis test, H =1.58, d.f. = 2, P = 0.45). Accordingly, the unburnt control site had similar vegetation structure to that at burnt sites prior to the 2003 fire in terms of the main element of the habitat structure, i.e. number of pines. In contrast, the Repeat-burnt site in the 2001 aerial picture did not have pines, probably due to the combined effects of the fire and further grazing.

### 2.2. Field sampling

Field sampling was conducted in July 2007 within the limits of the Sant Llorenç del Munt i l'Obac Natural Park, under permits of the Servei de Biodiversitat i Protecció dels Animals (Direcció General del Medi Natural i Biodiversitat, Catalan Government, Spain) and Sant Llorenç del Munt i l'Obac Natural Park (Diputació de Barcelona, Spain). Heteroptera were collected by net-sweeping five random samples from each plot. Each sample consisted of 20 sweeps while walking at a constant speed along a straight path. The five samples from each plot were merged, forming one sample per plot. The net had a light frame of 40 cm in diameter and was 50 cm deep. Specimens were preserved in 70% ethanol and classified to the species level, except nymphs (22% of individuals), which were removed from statistical analyses. Bug species were assigned to one of the three feeding groups: omnivorous, zoophagous, and phytophagous, the latter divided into monophagous, oligophagous, or polyphagous. Bug species identification and trophic levels were established from the literature (Appendix 1).

Vegetation (plant species presence and abundance) was sampled at the same plots as were Heteroptera, using three complementary techniques: i) presence was recorded by identifying all plant species in each plot; ii) abundance of grass, herbs, and shrub species was quantified for each plot by counting the species along a linear transect with 40 contact points spaced 0.5 m; iii) abundance of tree species was assessed counting all tree individuals within each plot.

#### 2.3. Statistical analyses

#### 2.3.1. Spatial autocorrelation among sampled sites

In the sampling design, the four sites (R, L, S, U) form a categorical variable in which each site is a factor (variable RLSU). To avoid the spatial autocorrelation effect of plots within each site, we elaborated the variable "position", reflecting the relative distance of each plot with respect to the others. For this we performed a principal coordinate analysis of a truncated matrix of distances among plots. From this analysis, principal coordinates of neighbor matrices (PCNMs) were obtained by eigenvalue decomposition, and the first (more explicative) PCNM axis was selected as the explanatory spatial variable "position" (Borcard et al., 1992). This statistical procedure was conducted by SpaceMaker2 software (Borcard et al., 2004; available at http://adn.biol.umontreal.ca/~numericalecology/old/ spacemaker.html). The variable "position" was included in further analyses.

#### 2.3.2. Plant and bug species richness and abundance

We quantified plant and bug species richness and abundance per sampling plot. Bugs were also separated into feeding groups, and the abundance of each feeding group was calculated for each plot. We tested the general effect of sites (variable RLSU) on species richness and abundance of plants, bugs, and bug feeding group datasets. We used generalized linear models (glm) with the assumption of Poisson errors and a logarithmic link function. In analyses where residual deviance was higher than residual degrees of freedom, quasi-Poisson errors distribution was used. These analyses were performed using the 'glm' function of the 'stats' package in R (R Development Core Team, 2008). With each dataset two glm analyses were done: A) with sites (RLSU) as factor variable and position as covariable, B) with sites (RLSU) as factor variable without covariable.

#### 2.3.3. Vegetation composition

From the overall matrix of presence/absence data of all plant species, we carried out a principal component analysis (PCA) to establish the similarity in plant species composition among plots. The raw data matrix was transformed in a similarity matrix of plots using the Hellinger distance index (Legendre and Gallagher, 2001). The Vegan package in R-language (http://cran.r-project. org/web/packages/vegan/) was used to compute Hellinger data transformation (decostand function, method = hell) and PCA analysis (rda function). The primary outcome of a PCA is a spatial configuration in which the 20 plots are represented as points, arranged in such a way that their distances correspond to their similarities in plant species composition. X and Y coordinates of each plot represent the best multivariate estimates of their plant species composition.

#### 2.3.4. Plant and bug species composition between sites

We tested the general effect of sites (variable RLSU) on plant species composition (using the plant species presence/ absence dataset), bug species composition (using the bug species abundance dataset), and bug feeding groups composition (using the percentage of each feeding group in each sampling plot dataset) by means of the Hellinger distance index and PERMANOVA analysis (Anderson, 2001). Previously, abundance data were square-root transformed to reduce asymmetry in the data distribution. The Vegan package in R-language was used to compute Hellinger indexes (decostand function, method = hell) and PERMANOVA analyses with 999 permutations (adonis function). With each dataset two glm analyses were done: A) with sites (RLSU) as factor variable and position as covariable, B) with sites (RLSU) as factor variable without covariable.

## 2.3.5. Contribution of vegetation structure and composition to bug community assemblage

The contribution of vegetation structure to bug species and feeding group composition in the area was examined by a set of redundancy analyses (RDAs). Two datasets were used as response variables: bug species abundance in each sampling plot, and percentage of feeding groups in each sampling plot. Nine environmental variables were introduced in the model: variable position (to analyze the effect of spatial autocorrelation) and eight vegetation variables (to assess the contribution of vegetation structure), two of them representing plant species composition (scores of the first and second axes of vegetation PCA; i.e. variables PCA1 and PCA2), and the other six representing plant strata: grass and herb (G), shrub (S), and tree (T) species richness (variables Grich, Srich, and Trich, respectively), and grass and herb, shrub, and tree abundance (variables Gab, Sab, and Tab, respectively). Position and vegetation variables were standardized in order to eliminate their physical dimension before being used together to produce an RDA ordination. For each variable, we performed an RDA analysis and a permutation test to assess its marginal effect on the bug species and feeding group composition. Automatic selection of environmental variables in the Vegan R package was used to performed the best RDA model, and a final RDA was performed with them. The Vegan R-language package was used for vegetation data standardization (decostand function, method = standardize), RDA analyses (rda function), and permutation tests (anova function with permutation options).

#### 2.3.6. Antagonistic plant-bug bipartite networks

We constructed bipartite networks taking into account potential feeding interactions between bug and plant species. A bipartite network is a network whose vertices or nodes can be divided into two disjoint sets, in our case bug species and plant species, such that every edge connects a node in the first set to one in the second set. In this study, each edge represents a plant-bug interaction. Feeding interactions were established from bug feeding preferences reviewed in the literature (Appendix 1). We constructed four local networks containing the potential interactions between bug species and the possible food plants found in the plots. For each network we calculated modularity, i.e. the extent, relative to a null model network, to which vertices cluster into community groups. Modularity was assessed with the Girvan and Newman algorithm (Girvan and Newman, 2002) using the software MODULAR (http://sourceforge.net/projects/programmodular/files/). This algorithm measures the number of clusters or subsets of nodes within which the node-node connections are dense. In bipartite networks this means that groups of species share resources and segregate from another group of species. Modularity values reached by this algorithm at each study site were then compared to 10,000 theoretical (null) networks following Bascompte et al. (2003). Null networks were based on a set of randomization of plantbug interactions, and MODULAR gives the proportion of theoretical networks with higher modularity values than the calculated value. Network plots and modularity structure were visualized using the bipartite R-language package (Dormann et al., 2008).

#### 3. Results

#### 3.1. Spatial autocorrelation among sampled sites

In the PCNM analysis performed with the data matrix of distances among plots (Appendix 2), coordinates of axis 1 (42.4% of total variance explained) and axis 2 (29.6% of total variance explained) summarized the between-plots relative position. Coordinate values of axis 1 (i.e. PCNM1) were used as variable "position" for further analyses.

#### 3.2. Plant and bug species richness and abundance

We recorded 135 species of grass, shrub and trees (Appendix 3). The glm analyses indicated that site effect (variable RLSU) was significant for all plant datasets except grass abundance and grass and shrub species richness (Gab, Grich, and Srich datasets, T2 tests, Table 1). Adding position effect as covariable (variable position), the effect of site was only significant for tree abundance and richness datasets (Tab and Trich, T1 tests, Table 1). Position effect (variable position) was significant for all plant datasets except grass and shrub species richness (Grich and Srich datasets, T1 tests, Table 1).

Overall, 736 bug specimens from 36 species and 10 families were found (Table 2). Of these, 22% of bugs were nymph specimens that could not be classified at species level and were therefore removed from further analyses. Of the 36 bug species found, 12 species were common (represented by 10 or more individuals). We found no common species exclusively from the Unburnt site (Table 2). At burnt sites, ca. 50% of the species (16 species out of 31) were recorded in only one of the treatments and were present in low numbers. The glm analyses indicated that site effect (variable RLSU) was significant for bug abundance and species richness (Hatab and Hatsp datasets, T2 tests, Table 3). Adding position effect as covariable (variable position), the effect of site was only significant for bug abundance (Hetab dataset, T1 tests, Table 3). Position effect (variable position) was significant for both bug abundance and richness (Hetab and Hetsp datasets, T1 tests, Table 3).

Phytophagous bugs were the commonest group in overall number of species (78%, 28 out of 36 species) and adult specimens (75%, 432 out of 574 specimens). Zoophagous and omnivorous groups were represented by 4 species each (11% each). At the unburnt site, phytophagous bug species were either polyphagous or oligophagous (50% each), whereas at burnt sites 72% of species were polyphagous, 16% oligophagous, and 12% monophagous (Table 2). The glm analyses indicated that site effect (variable RLSU) was significant for all bug feeding groups' abundance except zoophagous (zoo dataset, T2 tests, Table 3). Adding position effect as covariable, the effect of site was only significant for monophagous, omnivorous, and polyphagous feeding groups (mon, om, and pol datasets, T1 tests, Table 3). Position effect (variable position) was not significant only for oligophagous and zoophagous bugs (olig and zoo datasets, T1 tests, Table 3).

Table 1. Results of the glm analyses of plants. Test: T1, glm with variable RLSU as factor variable and variable position as covariable.
T2, glm with variable RLSU as factor variable, without covariable. Dataset (response variable): Gab, grass and herb abundance; Sab,
shrub abundance; Tab, tree abundance; Grich, grass and herb species number; Srich, shrub species number; Trich, tree species number.
Df, degrees of freedom; Dev, deviance; Res. df, residual degrees of freedom; Res. dev, residual deviance; P, probability level (ns, not
significant; * significance level $\leq 0.05$ ; ** significance level $\leq 0.01$ ; *** significance level $\leq 0.001$ ).

Test	Dataset	Variable	Df	Dev	Res. df	Res. dev	Р
T1	Gab	position	1	9.30	18	29.59	0.02252 *
T1	Gab	RLSU	3	0.69	15	28.90	0.94269 ns
T1	Sab	position	1	22.75	18	24.96	0.00012 ***
T1	Sab	RLSU	3	1.12	15	23.84	0.86676 ns
T1	Tab	position	1	105.45	18	121.06	<0.00001 ***
T1	Tab	RLSU	3	59.87	15	61.18	0.001182 **
T1	Grich	position	1	1.301	18	14.5	0.25400 ns
T1	Grich	RLSU	3	1.68	15	12.81	0.63980 ns
T1	Srich	position	1	0.003	18	2.29	0.95280 ns
T1	Srich	RLSU	3	0.07	15	2.22	0.99500 ns
T1	Trich	position	1	6.06	18	22.79	0.01375 *
T1	Trich	RLSU	3	13.10	15	9.68	0.00442 **
T2	Gab	RLSU	3	8.38	16	30.52	0.19310 ns
T2	Sab	RLSU	3	20.32	16	27.40	0.00752 **
T2	Tab	RLSU	3	164.17	16	62.35	<0.00001 ***
T2	Grich	RLSU	3	1.85	16	13.94	0.60320 ns
T2	Srich	RLSU	3	0.04	16	2.25	0.99730 ns
T2	Trich	RLSU	3	18.75	16	10.10	0.00030 ***

The PERMANOVA analyses detected that site (variable RLSU, T2 test, Table 4) was significant for the three datasets analyzed (plant species presence/absence, bug abundance, and bug feeding groups). Adding position effect as covariable, the effect of site was not significant for the bug feeding groups dataset (variable RLSU, T1 test, Table 4). Position effect (variable position) was significant for the three datasets (variable position) was significant for the three datasets (variable position, T1 tests, Table 4).

#### 3.3. Vegetation composition

In the PCA performed with plant species presence/ absence data (Appendix 4), axis 1 (14.3% of explained variance) discriminated between unburnt and burnt plots, whereas axis 2 (10.2% of explained variance) conformed to a gradient of burnt plots. Coordinate values of axis 1 and 2 (i.e. PCA1 and PCA2) summarized plant composition in plots and were used for further analyses.

## 3.4. Vegetation structure and its contribution to bug community assemblage

The Pearson correlation between variable position and the eight vegetation variables used in the RDA analyses was high for several vegetation abundance and richness variables (correlation values: 0.49 with Gab, -0.74 with Sab, -0.69 with Tab, 0.28 with Grich, -0.04 with Srich, -0.58 with Trich,) and for vegetation composition variables (correlation values: -0.80 with PCA1 and -0.49 with PCA2).

In the RDAs performed with the bug abundance dataset as response variable and each environmental variable individually (marginal analyses, Table 5), position and plant species composition variables (PCA1 and PCA2) had a significant contribution, as well as the three plant strata abundance variables, i.e. abundance of grass (Gab), shrubs (Sab), and trees (Tab). Shrub (Srich), grass (Grich), and tree (Trich) species richness did not have a significant effect on bug species composition. Although the position variable had a highly significant contribution to the total inertia, due to its high correlation with the other significant variables, it was not included for further RDA analysis. Automatic selection in the Vegan package selected environmental variables PCA1, PCA2, tree abundance (Tab), and shrub abundance (Sab) to be included in the best RDA model (Table 5). In the RDA biplot obtained with the best model (Figure 2), axis 1 was significant and correlated with all environmental variables, especially with shrub abundance (Sab) and vegetation composition

**Table 2.** Abundances of Heteroptera species per site. Each numeric column represents the sum of individuals detected in the five replicateplots of each site. Abbreviations of sites: R, Repeat-burnt; L, burnt logged; S, burnt logged and subsoiled; U, control unburnt. Abbreviationsof feeding groups (FG): Mon, Monophagous; Oli, Oligophagous; Om, Omnivorous; Ph, Phytophagous; Pol, Polyphagous; Zoo, Zoophagous.

Family	Code	Code	Species	R	L	S	U	FG
Alydidae	CAMLAT	1	Camptopus lateralis	0	1	0	0	Pol
Berytidae	GAMPUN	2	Gampsocoris punctipes	0	1	0	0	Pol
Coreidae	LOXDEN	3	Loxocnemis dentator	0	0	1	0	Pol
Lygaeidae	BEOMAR	5	Beosus maritimus	0	0	3	0	Pol
Lygaeidae	HETART	6	Heterogaster artemisiae	1	0	0	0	Olig
Lygaeidae	LYGSAR	7	Lygaeosoma sardeum	0	1	0	0	Pol
Lygaeidae	MACFAS	8	Macroplax fasciata	9	18	26	0	Pol
Lygaeidae	MELALB	9	Melanocoryphus albomaculatus	1	0	0	0	Pol
Lygaeidae	NYSCYM	10	Nysius cymoides	5	1	0	0	Pol
Miridae	ADELIN	11	Adelphocoris lineolatus	7	1	5	0	Pol
Miridae	CYRGEN	12	Cyrtopeltis geniculata	0	3	0	0	Om
Miridae	DERSER	13	Deraeocoris serenus	4	3	8	0	Zoo
Miridae	HALMAC	14	Halticus macrocephalus	0	0	1	0	Pol
Miridae	HETTIG	15	Heterocapillus tigripes	5	52	99	0	Pol
Miridae	LEPANC	16	Lepidargyrus ancorifer	7	25	0	0	Pol
Miridae	MACCOS	17	Macrolophus costalis	5	14	5	0	Om
Miridae	MACATR	18	Macrotylus atricapillus	0	1	1	0	Pol
Miridae	MACBIP	19	Macrotylus bipunctatus	10	0	0	0	Olig
Miridae	MAVPAY	20	Macrotylus paykulli	32	12	0	0	Pol
Miridae	MIMRUG	21	Mimocoris rugicollis	0	0	0	1	Pol
Miridae	MONFIL	22	Monalocoris filicis	0	1	2	0	Mon
Miridae	ORTSTY	23	Orthotylus stysi	5	3	0	18	Olig
Miridae	ORTVIR	24	Orthotylus virescens	0	10	0	0	Om
Miridae	PACYEL	25	Pachyxyphus yelamosi	0	1	0	0	Mon
Miridae	PHYVAR	26	Phytocoris varipes	50	28	1	7	Om
Pentatomidae	SCIHEL	29	Sciocoris helferi	0	0	0	1	Pol
Pentatomidae	SCIMAC	30	Sciocoris maculatus	0	1	1	0	Pol
Pentatomidae	STALUN	31	Staria lunata	0	1	0	0	Pol
Reduviidae	CORPER	32	Coranus pericarti	0	1	0	0	Zoo
Reduviidae	PHYCRA	33	Phymata crassipes	0	0	0	1	Zoo
Reduviidae	RHICUS	34	Rhinocoris cuspidatus	0	1	1	0	Zoo
Rhopalidae	CORHYO	35	Corizus hyoscyami	0	1	0	0	Pol
Rhopalidae	LIOHYA	36	Liorhyssus hyalinus	2	0	0	0	Pol
Rhopalidae	STIPUN	37	Stictopleurus punctatonervosus	0	1	0	0	Olig
Scutelleridae	EURTES	39	Eurygaster testudinaria	0	0	0	1	Olig
Tingidae	PHAPAR	40	Phaenotropis parvula	48	11	7	0	Mon
Nymphs	-		unidentified	27	98	12	25	-
			Total abundance	218	291	173	54	
			Zoophagous (Zoo)	4	5	9	1	
			Phytophagous (Ph)	132	133	146	21	
			Omnivorous (Om)	55	55	6	7	
			Total species richness (adults)	15	25	14	6	
			Zoophagous (Zoo)	1	3	2	1	
			Phytophagous (Ph)	12	18	10	4	
			Omnivorous (Om)	2	4	2	1	

**Table 3.** Results of the glm analyses of bugs. Test: T1, glm with variable RLSU as factor variable and variable position as covariable. T2, glm with variable RLSU as factor variable, without covariable. Dataset (response variable): Hetab, Heteroptera abundance; Hetsp, Heteroptera species number; mon, monophagous Heteroptera abundance; olig, oligophagous Heteroptera abundance; om, omnivorous Heteroptera abundance; pol, polyphagous Heteroptera abundance; zoo, zoophagous Heteroptera abundance. Df, degrees of freedom; Dev, deviance; Res. df, residual degrees of freedom; Res. dev, residual deviance; P, probability level (ns, not significant; \* significance level  $\leq 0.05$ ; \*\* significance level  $\leq 0.01$ ).

Test	Dataset	Variable	Df	Dev	Res. df	Res. dev	Р
T1	Hetab	position	1	110.05	18	336.79	0.00267 **
T1	Hetab	RLSU	3	136.23	15	200.56	0.01089 *
T1	Hetsp	position	1	19.33	18	24.90	0.00005 ***
T1	Hetsp	RLSU	3	7.22	15	17.68	0.10760 ns
T1	mon	position	1	41.95	18	84.08	0.00031 ***
T1	mon	RLSU	3	36.37	15	47.71	0.01053 *
T1	olig	position	1	8.43	18	82.75	0.17220 ns
T1	olig	RLSU	3	25.65	15	57.10	0.12900 ns
T1	om	position	1	34.16	18	89.45	0.00003 ***
T1	om	RLSU	3	58.88	15	30.57	<0.00001 ***
T1	pol	position	1	70.63	18	343.12	0.01108 *
T1	pol	RLSU	3	172.71	15	170.41	0.00125 **
T1	Z00	position	1	2.90	18	36.49	0.24390 ns
T1	Z00	RLSU	3	5.03	15	31.45	0.50260 ns
T2	Hetab	RLSU	3	186.98	16	259.87	0.00720 **
T2	Hetsp	RLSU	3	25.94	16	18.29	<0.00001 ***
T2	mon	RLSU	3	77.16	16	48.87	0.00001 ***
T2	olig	RLSU	3	34.07	16	57.11	0.04566 *
T2	om	RLSU	3	87.58	16	36.05	<0.00001 ***
T2	pol	RLSU	3	190.72	16	223.04	0.00399 **
T2	Z00	RLSU	3	7.52	16	31.88	0.29210 ns

**Table 4.** Global test values from the PERMANOVA analyses made with three datasets: Plants (vegetation presence/absence data), Bugs Ab (bug abundance data), and Bugs FG% (bug feeding-group percentages). Test: T1, analyses performed with sites (R, L, S, U) as factor variable and variable position as covariable; T2, analyses performed with sites (R, L, S, U) as factor variable, without covariable. df, degrees of freedom; F, pseudo-F value; p, permuted P-value (ns, not significant; \*\* significance level  $\leq 0.01$ ; \*\*\* significant level  $\leq 0.001$ ).

Variables	Test	46	Plants		Bugs Ab		Bugs FG%	
variables	Test		F	Р	F	Р	F	Р
Position	T1	1	2.6342	0.001***	6.1810	0.001***	14.9765	0.001***
RLSU	T1	3	1.3817	0.005**	2.0126	0.004**	1.6961	0.117 ns
RLSU	T2	3	1.9495	0.001***	3.9788	0.001***	7.0156	0.001***

**Table 5.** Results of the redundancy analyses and Monte Carlo permutation tests (with 999 permutations) analyzing the contribution of position and vegetation structure variables (environmental variables) on bug species composition with bug species abundance on each plot as response variable. Analysis: Marginal, RDA analyses performed with only one environmental variable at a time; Best model, RDA analysis automatically selected as the best model. Var/Axis: environmental variable or axis selected; <sup>a</sup> denotes environmental variables selected for the best model. Eigen, eigenvalues. %Var, percentage of variability explained by the corresponding eigenvalue. F, pseudo-F value in Monte Carlo permutation test. P, permuted P-value in Monte Carlo permutation test (+ significance level  $\leq 0.1$ ; \* significance level  $\leq 0.05$ ; \*\* significance level  $\leq 0.01$ ; \*\*\* significance level  $\leq 0.001$ ).

A se a lossi a	Var/Axis	Eigen	%Var	г	D
Analysis	Total inertia	0.6386	100.00	F	P
Marginal	Position	0.1450	22.70	5.288	0.002 **
Marginal	PCA2 <sup>a</sup>	0.1125	17.61	3.8479	0.005 **
Marginal	Sab <sup>a</sup>	0.0948	14.85	3.1401	0.005 **
Marginal	PCA1 <sup>a</sup>	0.0897	14.04	2.9401	0.015*
Marginal	Tab <sup>a</sup>	0.0807	12.63	2.6031	0.020*
Marginal	Gab	0.0654	10.24	2.0530	0.039*
Marginal	Trich	0.0551	8.63	1.6998	0.085
Marginal	Grich	0.0281	4.39	0.8270	0.560
Marginal	Srich	0.0244	3.82	0.7144	0.780
Best model	inertia	0.2771	43.40	2.8752	0.001 ***
Best model	Axis 1	0.1584	24.80	6.5757	0.001 ***
Best model	Axis 2	0.0593	9.28	2.4612	0.062+



**Figure 2.** Biplot of the best model redundancy analysis of the abundances of bug species in the 20 sampling plots (see best model in Table 5). Vegetation variables: PCA1, PCA2, Sab, Gab, Tab (see Section 2 for explanation of variables). For codes (numbers) of bug species, see Table 2. Bug species 1, 2, 3, 5, 6, 7, 9, 10, 12, 14, 18, 24, 25, 30, 31, 32, 34, 35, and 37 are located inside the circle situated in the center of the graph. Arrows pointing from origin to each bug species (numbers) have been omitted for clarity. Abbreviations of the sampling plots: R1 to R5, Repeat-burnt; L1 to L5, burnt logged; S1 to S5, burnt logged and subsoiled; U1 to U5 control unburnt. Axis 1 (horizontal) was significant (permutation test: 199 permutations, F ratio 6.5946, P = 0.005), representing 25.4% of the data variance. Axis 2 (vertical) was also significant (9.5% of explained variance; permutation test: 399 permutations, F ratio = 2.4677, P = 0.017).

(PCA2). This axis discriminated between unburnt sites (positive values) and burnt sites (negative values). Axis 2 was also significant and correlated with variables PCA1, tree abundance (Tab), shrub abundance (Sab) (positive correlation), and PCA2 (negative correlation). This axis discriminated among burnt sites. Bug species were projected onto Figure 2 in accordance with their relative abundance on plots.

In the RDAs performed with the bug feeding groups dataset as response variable and each environmental variable individually (marginal analyses, Table 6), position and plant species composition variables PCA1 and PCA2 were significant, as well as the four plant strata variables shrub abundance (Sab), tree abundance (Tab), grass abundance (Gab), and tree richness (Trich). As in previous analysis, although the position variable had a highly significant contribution to the total inertia, due to its high correlation with the other significant variables, it was not included for further RDA analysis. Automatic selection in the Vegan package selected environmental variables PCA1, PCA2, and shrub abundance (Sab) to be included in the best RDA model (Table 6). In the RDA biplot obtained with the best model (Figure 3), axis 1 was significant and discriminated between unburnt (positive values) and burnt sites (negative values). Bug feeding group structure differed in relation to fire and postfire management.

Using the bug functional groups, RDA demonstrated an association between burnt sites (R, L, and S) and the most generalist dietary species, i.e. polyphagous-phytophagous and omnivorous species. In contrast, oligophagous-phytophagous species were associated to the unburnt site. Finally, monophagous-phytophagous species were associated to burnt sites.

#### 3.5. Antagonistic bug-plant bipartite networks

In local networks from the three burnt sites, modularity did not differ from the null model values, whereas in the local network of the unburnt site modularity was higher than the theoretical null models (modularity 0.703, P = 0.033). The four modules detected in the unburnt site network are composed of only one or two bug species each (Figure 4), indicating a high segregation in resource consumption.

#### 4. Discussion

The four studied sites showed contrasting plant assemblages, with sharp differences in plant species composition and tree abundances and richness. Analysis of the 2001 aerial photograph confirmed that the prefire vegetation structure was similar between burnt and unburnt sites except for the plots affected by multiple fires. In parallel, we found specific and functional responses of the bug assemblage to this habitat transformation.

**Table 6.** Results of the redundancy analyses and Monte Carlo permutation tests (with 999 permutations) analyzing the contribution of position and vegetation structure variables (environmental variables) on bug species composition with bug feeding groups' abundance on each plot as response variable. Analysis: Marginal, RDA analyses performed with only one environmental variable at a time; Best model, RDA analysis automatically selected as the best model. Var/Axis: environmental variable or axis selected; <sup>a</sup> denotes environmental variables selected for the best model. Eigen, eigenvalues. %Var, percentage of variability explained by the corresponding eigenvalue. F, pseudo-F value in Monte Carlo permutation test. P, permuted P-value in Monte Carlo permutation test (\* significance level  $\leq 0.05$ ; \*\* significance level  $\leq 0.01$ ).

A	Var/Axis	Eigen	%Var	r.	D
Analysis	Total inertia	0.3255	100.00	F	P
Marginal	Position	0.1392	42.71	13.419	0.001 ***
Marginal	Sab <sup>a</sup>	0.1086	33.37	9.0156	0.005 **
Marginal	PCA1 <sup>a</sup>	0.0888	27.28	6.7532	0.005 **
Marginal	Tab	0.0739	22.72	5.2905	0.015 *
Marginal	PCA2 <sup>a</sup>	0.0569	17.49	3.8158	0.010 **
Marginal	Gab	0.0541	16.63	3.5904	0.010 **
Marginal	Trich	0.0439	13.48	2.8049	0.048 *
Marginal	Srich	0.0051	1.58	0.2883	0.860
Marginal	Grich	0.0027	0.84	0.1525	0.930
Best model	inertia	0.1662	51.06	5.5643	0.001 ***
Best model	Axis 1	0.1488	45.71	14.9482	0.001 ***
Best model	Axis 2	0.0106	3.26	1.0723	0.698



**Figure 3.** Biplot of the best model redundancy analysis of the percentage of bugs within each trophic group in the 20 sampling plots (see best model in Table 6). Environmental variables: PCA1, PCA2, Sab, Gab, Tab, Trich (see Section 2 for explanation of variables). Arrows pointing from origin to each bug feeding group have been omitted for clarity. Abbreviations of bug feeding groups: Om, omnivorous; Zoo, zoophagous; Pol, phytophagous-polyphagous; Oli, phytophagous-oligophagous; Mon, phytophagous-monophagous. Abbreviations of the sampling plots: R1 to R5, Repeat-burnt; L1 to L5, burnt logged; S1 to S5, burnt logged and subsoiled; U1 to U5 control unburnt. Axis 1 (horizontal) was significant (permutation test: 199 permutations, F-ratio = 15.2342, P = 0.005), representing 46. 7% of the data variance. Axis 2 (vertical) was not significant (6.3% of explained variance; permutation test: 399 permutations, F-ratio = 2.0471, P = 0.100).

Our results suggest that habitat changes in plant species composition and tree canopy can shape taxonomic and functional changes of the bug assemblage. These changes accounted for higher abundance of bugs at burnt than at unburnt sites, and also for species replacement. This taxonomic response has been similarly reported in a wide variety of animal taxa previously examined in the study area (snails [Santos et al., 2009], Hymenoptera [Mateos et al., 2011], and reptiles [Santos and Poquet, 2010]).

We acknowledge that our results could be partially biased by a spatial effect due to site selection limitations. The inclusion of a spatial variable in the glm models indicated a loss of significance of site effect only for the number of bug species and oligophagous bug abundance. Also, the inclusion of a spatial variable in the PERMANOVA models indicated a loss of significance of site effect only for bug community structure measured by percentage of feeding groups. The high correlation coefficients obtained between the spatial variable and all vegetation variables significantly affecting bug community structure allow its exclusion from multivariate RDA analyses. Also, the similarity of prefire vegetation structure in the area has made us convinced that the spatial effect, despite being statistically significant in some cases, has not had a real effect on our results. Thus, the final conclusions were made not taking into consideration the spatial effect.

Changes in habitat structure are major drivers of animal responses to fire, as occurs worldwide in regions where fire is a major and common disturbance (e.g., Briani et al., 2004; Parr et al., 2004; Lindenmayer et al., 2008; Izhaki, 2012; Deák et al., 2014). Our study indicated that bugs are also sensitive to fire and postfire conditions. This conclusion is similar to that reported by Ribes (2004) in another Mediterranean area (located close to our study area) as bug species richness and abundance were higher in burnt maquis plots than in unburnt *Pinus halepensis* forest plots.

In our study, polyphagous-phytophagous and omnivorous bugs were associated with burnt sites, this result suggesting that dietary generalist bug species (i.e. polyphagous and omnivorous) responded positively to perturbations such as fire. In contrast, the most specialized oligophagous-phytophagous bugs were associated with unburnt sites. This gradient of bug feeding specialization in burnt and unburnt sites fits the ecological theory as generalist and specialist species are distributed, respectively, in variable and stable environments according to some energetic costs (Richmond et al., 2005). In stable environments, generalists cannot outperform specialists due to the inherent extra physiological and behavioral costs associated with a generalist strategy, which accommodate multiple prey types or are adapted



**Figure 4.** Local networks indicating interactions between bug species and their potential food sources. For abbreviations of plant species (left side of the graph), see Appendix 3. For abbreviations of bug species (right side of the graph), see Table 2. Abbreviations of sites: R, repeat-burnt sites; L, burnt logged; S, burnt logged and subsoiled; U, control unburnt. Lines in network U define the four modules detected in the unburnt site network.

to variable environments (Levins, 1968). In variable or unpredictable environments, however, these costs may be small in comparison to benefits of the increased plasticity, and generalists may gain an advantage (Bergman, 1988). Hence, ecosystems characterized by abrupt environmental changes triggered by disturbances would promote generalist species (Futuyma and Moreno, 1988). The same conclusion was obtained in a study of plant-bee networks related to fire disturbance in a xeric biome in Argentina (Peralta et al., 2017). Similar effects have also been reported on plants by Valkó et al. (2018), i.e. generalist species can better tolerate fire.

Although our results apparently support the general trend of generalist species being favored in disturbed plots, the association of monophagous-phytophagous bug species to burnt plots is contradictory to previous statements. These monophagous-phytophagous bug species were Monalocoris filicis feeding on fern spores of Dryopteris filix-mas and Eupteris aquilina (Goula, 1986), Pachyxyphus yelamosi associated to Cistus clusii and C. monspeliensis (Ribes and Ribes, 2000), and Phaenotropis parvula associated to Dorycnium suffruticosum (Péricart, 1984). Although these plants were not found in the studied replicates, they are common in burnt sites: e.g., Cistus spp. have active postfire germination from the seed bank (Paula and Pausas, 2008), D. suffruticosum resprouts after fire (Rego et al., 1993), and many ferns survive as rhizomes are protected underground (Paula et al., 2009). Fire may create early successional habitats that attract species that specialize in that kind of habitat (Valentine et al., 2012). In our study site, monophagous-phytophagous bugs seem to respond to fire according to the response of their hosts. This conclusion highlights that the response of organisms to a disturbance may be mediated by a complex of species interactions and stresses the interest of further investigating the role of antagonistic interactions as a key element of community responses to disturbances such as fire.

Differences in network modularity among unburnt and burnt sites also support the importance of the specialization gradient to understand the response of bug species to fire. Lower modularity in burnt sites, i.e. lower segregation of bugs in the use of plant resources, fits the association of generalist bugs to burnt sites observed in the RDAs. Two factors suggest that conclusions based on the comparison of modularity between sites should be accepted with caution: 1) our networks are small, especially in the unburnt site due to the low number of species found in unburnt plots,

#### References

- Anderson MJ (2001). A new method for non-parametric multivariate analysis of variance. Austral Ecol 26: 32-46.
- Arnan X, Cerdá X, Rodrigo A, Retana J (2013). Response of ant functional composition to fire. Ecography 36: 1182-1192.
- Bascompte J, Jordano P (2006). The structure of plant-animal mutualistic networks. In: Pascual M, Dunne JA, editors. Food Webs as Complex Adaptive Networks: Linking Structure to Dynamics. Oxford, UK: Oxford University Press, pp. 143-159.
- Bascompte J, Jordano P, Melián CJ, Olesen JM (2003). The nested assembly of plant-animal mutualistic networks. P Natl Acad Sci USA 100: 9383-9387.

some of them represented by just one specimen; 2) we do not know what might be the role of monophagousphytophagous bugs in the network modularity. However, results between network modularity and RDA ordination were consistent. Thus, the changes detected in network modularity values between the unburnt and burnt sites could be due to a functional replacement of bug species (see also Mateos et al., 2011 and Santos et al., 2014 for similar conclusions in other groups examined in the same study area). This conclusion opens future research to examine the role of plant-bug interactions in postfire ecological trajectories. Plant-herbivore feeding interactions are key phenomena for understanding processes that maintain biodiversity (Novotny et al., 2010). These interactions make up antagonistic networks characterized by cohesive groups of interacting species (Bascompte and Jordano, 2006) and promote compartmentalization through coevolution of specific defenses and counter-defenses that generate greater specificity (Thompson, 2005). Recent studies have emphasized that interaction networks show complex responses to disturbance (Piazzon et al., 2011; Villa-Galaviz et al., 2012). This complexity evidences the need for further empirical studies to uncover the role of plant-animal interactions as a driver of postfire animal responses.

#### Acknowledgments

We are very grateful to managers of the Sant Llorenç del Munt i l'Obac Natural Park for their logistic support. We are grateful to Luís Mata for bug classification; Flávia Marquitti, Paulo R Guimarães, and Márcio S Araujo for introducing us to software to examine network modularity; and Cristina García for her valuable suggestions on an early draft of the manuscript. Xavier Santos was supported by a postdoctoral grant (SFRH/BPD/73176/2010) by Fundação para a Ciência e a Tecnologia, Portugal. Two anonymous reviewers provided helpful comments that improved the manuscript.

- Bergman E (1988). Foraging abilities and niche breadths of two percids, *Perca fluviatilis* and *Gymnocephalus cernua*, under different environmental conditions. J Anim Ecol 57: 443-453.
- Bond WJ, Woodward FI, Midgley GF (2005). The global distribution of ecosystems in a world without fire. New Phytol 165: 525-538.
- Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H (2004). Dissecting the spatial structure of ecological data at multiple scales. Ecology 85: 1826-1832.
- Borcard D, Legendre P, Drapeau P (1992). Partialling out the spatial component of ecological variation. Ecology 73: 1045-1055.

- Briani DC, Palma ART, Vieira EM, Henriques RPB (2004). Post-fire succession of small mammals in the Cerrado of central Brazil. Biodiv Conserv 13: 1023-1037.
- Bröring U, Wiegleb G (2005). Soil zoology II: Colonization, distribution, and abundance of terrestrial Heteroptera in open landscapes of former brown coal mining areas. Ecol Eng 24:135-147.
- Bros V, Moreno-Rueda G, Santos X (2011). Does postfire management affect the recovery of Mediterranean communities? The case study of terrestrial gastropods. For Ecol Manag 261: 611-619.
- Brotons L, Herrando S, Pons, P (2008). Wildfires and the expansion of threatened farmland birds: the ortolan bunting *Emberiza hortulana* in Mediterranean landscapes. J Appl Ecol 45: 1059-1066.
- Carver M, Gross GF, Woodward, TT (1991). Hemiptera. In: Naumann ID, Carne PB, Lawrence JF, Nielsen ES, Spradbery JP, Taylor RW, Whitten MJ, Littlejohn MJ, editors. The Insects of Australia. 2nd ed. Carlton, Australia: Melbourne University Press, pp 429-509.
- Chergui B, Fahd S, Santos X, Pausas JG (2017). Socioeconomic factors drive fire-regime variability in the Mediterranean Basin. Ecosystems (in press).
- Clarke KR (1993). Non-parametric multivariate analysis of changes in community structure. Austr J Ecol 18: 117-143.
- Deák B, Valkó O, Török P, Végvári Z, Hartel T, Schmotzer A, Kapocsi I, Tóthmérész B (2014). Grassland fires in Hungary? A problem or a potential alternative management tool? Appl Ecol Env Res 12: 267-283.
- Dormann CF, Gruber B, Fründ J (2008). Introducing the bipartite package: analysing ecological networks. R News 8: 8-11.
- Driscoll DA, Henderson MK (2008). How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. Biol Conserv 141: 460-471.
- Fontaine JB, Donato DC, Robinson WD, Law BE, Kauffman JB (2009). Bird communities following high-severity fire: Response to single and repeat fires in a mixed-evergreen forest, Oregon, USA. For Ecol Manag 257: 1496-1504.
- Fox BJ (1982). Fire and mammalian secondary succession in an Australian coastal heath. Ecology 63: 1332-1341.
- Frank T, Künzle U (2006). Effect of early succession in wildflower areas on bug assemblages (Insecta: Heteroptera). Eur J Entomol 103: 61-70.
- Futuyma DJ, Moreno G (1988). The evolution of ecological specialization. Ann Rev Ecol Syst 19: 207-233.
- Girvan M, Newman MEJ (2002). Community structure in social and biological networks. P Natl Acad Sci USA 99: 7821-7826.
- Goula M (1986). Contribución al estudio de los Hemípteros (Insecta, Heteroptera, Familia Miridae). PhD, Universitat de Barcelona, Barcelona, Spain (in Spanish).
- Henry TJ (2009). Biodiversity of Heteroptera. In: Foottit RG, Adler PH, editors. Insect Biodiversity: Science and Society. Oxford, UK: Blackwell Publishing, pp. 223-263.

- Izhaki I (2012). The impact of fire on vertebrates in the Mediterranean Basin: an overview. Israel J Ecol Evol 58: 221-233.
- Keeley JE, Bond WJ, Bradstock RA, Pausas JG, Rundel PW (2012). Fire in Mediterranean Ecosystems: Ecology, Evolution and Management. Cambridge, UK: Cambridge University Press.
- Kelly LT, Brotons L, (2017). Using fire to promote biodiversity. Science 355: 1264-1265.
- Legendre P, Gallagher ED (2001). Ecologically meaningful transformations for ordination of species data. Oecologia 129: 271-280.
- Letnic M, Dickman CR, Tischler MK, Tamayo B, Beh CL (2004). The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. J Arid Environ 59: 85-114.
- Levins R (1968). Evolution in Changing Environments. Princeton, NY, USA: Princeton University Press.
- Lindenmayer DB, Noss RF (2006). Salvage logging, ecosystem processes, and biodiversity conservation. Conserv Biol 20: 949-958.
- Lindenmayer DB, Wood JT, MacGregor C, Michael DR, Cunningham RB, Crane M, Montague-Drake R, Brown D, Muntz R, Driscoll DA (2008). How predictable are reptile responses to wildfire? Oikos 117: 1086-1097.
- Mateos E, Santos X, Pujade-Villar J (2011). Taxonomic and functional responses to fire and post-fire management of a Mediterranean Hymenoptera community. Environ Manag 48: 1000-1012.
- Moretti M, de Bello F, Roberts SPM, Potts SG (2009). Taxonomical vs functional responses of bee communities to fire in two contrasting climatic regions. J Anim Ecol 78: 98-108.
- Moretti M, Duelli P, Obrist MK (2006). Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. Oecologia 149: 312-327.
- Moretti M, Legg C (2009). Combining plant and animal traits to assess community functional responses to disturbance. Ecography 32: 299-309.
- Moriondo M, Good P, Durao R, Bindi M, Gianakopoulos C, Corte-Real J (2006). Potential impact of climate change on fire risk in the Mediterranean area. Clim Res 31: 85-95.
- Ne'eman G, Dafni A, Potss SG (2000). The effect of fire on flower visitation rate and fruit set in four core-species in east Mediterranean scrubland. Plant Ecology 146: 87-104.
- Novotny V, Miller SE, Baje L, Balagawi S, Basset Y, Cizek L, Craft KJ, Dem F, Drew RAI, Hulcr J et al. (2010). Guild-specific patterns of species richness and host specialization in plant-herbivore food webs from a tropical forest. J Anim Ecol 79: 1193-1203.
- Parr CL, Robertson HG, Biggs HC, Chown SL (2004). Response of African savanna ants to long-term fire regimes. J Appl Ecol 41: 630-642.
- Paula S, Arianoutsou M, Kazanis D, Tavsanoglu Ç, Lloret F, Buhk C, Ojeda F, Luna B, Moreno JM, Rodrigo A, et al. (2009). Firerelated traits for plant species of the Mediterranean Basin. Ecology 90: 1420.

- Paula S, Pausas JG (2008). Burning seeds: germinative response to heat treatments in relation to resprouting ability. J Ecol 96: 543-552.
- Pausas JG, Parr CL (2018). Towards an understanding of the evolutionary role of fire in animals. Evol Ecol (in press).
- Peralta G, Stevani EL, Chacoff, NP, Dorado J, Vázquez DP (2017). Fire influences the structure of plant-bee networks. J Anim Ecol (in press).
- Péricart J (1984). Hémiptères Berytidae euro-méditerranéens. Faune de France. France et regions limitrophes, 70. Paris, France: Féderation française des Sociétés de Sciences Naturelles (in French).
- Piazzon M, Larrinaga AR, Santamaría L (2011). Are nested networks more robust to disturbance? A test using epiphyte-tree, comensalistic networks. PLoS One 6: e19637.
- Rego F, Pereira J, Trabaud L (1993). Modelling community dynamics of a *Quercus coccifera* L. garrigue in relation to fire using Markov chains. Ecol Model 66: 251-260.
- Ribes E (2004). Els Heteròpters del Parc de Collserola: Faunística, bioecología i gestió. PhD, Universitat de Barcelona, Barcelona, Spain (in Catalan).
- Ribes E, Ribes J (2000). Noves dades d'Hemípters per a Catalunya i Territoris limítrofs (Heteroptera). Ses Entom ICHN-SCL 10: 5-29 (in Catalan).
- Richmond CE, Breitburg DL, Rose KA (2005). The role of environmental generalist species in ecosystem function. Ecol Model 188: 279-295.
- Santos X, Badiane A, Matos C (2016). Contrasts in short- and longterm responses of Mediterranean reptile species to fire and habitat structure. Oecologia 180: 205-2016.
- Santos X, Bros V, Miño A (2009). Recolonization of a burnt Mediterranean area by terrestrial gastropods. Biodiv Conserv 18: 3153-3165.
- Santos X, Cheylan M (2013). Taxonomic and functional response of a Mediterranean reptile assemblage to a repeated fire regime. Biol Conserv 168: 90-98.
- Santos X, Mateos E, Bros V, Brotons V, de Mas E, Herraiz JA, Herrando S, Miño A, Olmo-Vidal JM, Quesada J et al. (2014). Is response to fire influenced by dietary specialization and mobility? A comparative study with multiple animal assemblages. PLoS One 9: e88224.

- Santos X, Poquet JM (2010). Ecological succession and habitat attributes affect the post-fire response of a Mediterranean reptile community. Eu J Wildl Res 56: 895-905.
- Schuh RT, Slater JA (1995). True Bugs of the World (Hemiptera, Heteroptera): Classification and Natural History. Ithaca, NY, USA: Cornell University Press.
- Smith AL (2018). Successional changes in trophic interactions support a mechanistic model of post-fire population dynamics. Oecologia 186: 129-139.
- Swan M, Christie F, Sitters H, York A, Di Stef J (2015). Predicting faunal fire responses in heterogeneous landscapes: the role of habitat structure. Ecol Appl 25: 2293-2305.
- Thompson JN (2005). The Geographic Mosaic of Coevolution. Chicago, IL, USA: University of Chicago Press.
- Torma A, Bozsó M, Tölgyesi C, Gallé R (2017). Relationship of different feeding groups of true bugs (Hemiptera: Heteroptera) with habitat and landscape features in Pannonic salt grasslands. J Insect Conserv 21: 645-656.
- Torma A, Császár P (2013). Species richness and composition patterns across trophic levels of true bugs (Heteroptera) in the agricultural landscape of the lower reach of the Tisza River Basin. J Insect Conserv 17: 35-51.
- Torma A, Gallé R, Bozsó M (2014). Effects of habitat and landscape characteristics on the arthropod assemblages (Araneae, Orthoptera, Heteroptera) of sand grassland remnants in Southern Hungary. Agr Ecosyst Environ 196: 42-50.
- Valkó O, Kelemen A, Miglécz T, Török P, Deák B, Tóth K, Tóth JP, Tóthmérész B (2018). Litter removal does not compensate detrimental fire effects on biodiversity in regularly burned semi-natural grasslands. Sci Total Environ 622-623: 783-789.
- Valentine LE, Reaveley A, Johnson B, Fisher R, Wilson BA (2012). Burning in Banksia Woodlands: how does the fire-free period influence reptile communities? PLoS One 7: e34448.
- Villa-Galaviz E, Boege K, del-Val E (2012). Resilience in plantherbivore networks during secondary succession. PLoS One 7: e53009.
- Warren SD, Scifres CJ, Teel PD (1987). Response of grassland arthropods to burning: a review. Agr Ecosyst Environ 19: 105-130.
- Zurbrügg C, Frank T (2006). Factors influencing bug diversity (Insecta: Heteroptera) in semi-natural habitats. Biodiv Conserv 15: 275-294.

**Appendix 1.** Identification of bug specimens and plant–bug interactions were established from the following literature.

#### **Family Tingidae**

Péricart J (1983). Hémiptères Tingidae euroméditerranéens. Faune de France. France et régions limitrophes 69: 1-618 (in French).

#### Family Miridae

Goula M (1986). Contribución al estudio de los Hemípteros (Insecta, Heteroptera, Familia Miridae). PhD, Universitat de Barcelona, Barcelona, Spain (in Spanish).

Wagner E (1974). Die Miridae Hahn, 1931, des Mittelmeerraumes und der Makaronesischen Inseln (Hemiptera, Heteroptera). Teil. Entomologische Abhandlungen herausgegeben vom Staatlichen Museum für Tierkunde Dresden [Dresden] 39: 1-421 (in German).

Wagner E (1975). Die Miridae Hahn, 1831 des Mittelmeeraumes und der Makaronesischen Inseln (Hem.,Het.). Teil 3. Entomologische Abhandlungen herausgegeben vom Staatlichen Museum für Tierkunde Dresden [Dresden] 40: 1-483 (in German).

Wheeler AG Jr (2001). Biology of the Plant Bugs (Hemiptera: Miridae). Pests, Predators, Opportunists. Ithaca, NY, USA: Cornell University Press.

#### Family Reduviidae

Putshkov PV, Moulet P (2009). Hémiptères Reduviidae d'Europe Occidentale. Faune de France.

France et régions limitrophes 92: 1-668 (in French).

### Family Berytidae

Péricart J (1984). Hémiptères Berytidae euroméditerranéens. Faune de France. France et régions limitrophes 70: 1-165 (in French).

#### Family Lygaeidae

Péricart J (1999a). Hémiptères Lygaeidae Euro-Méditerranéens, 1. Faune de France. France et régions limitrophes 84A: 1-468 (in French). Péricart J (1999b). Hémiptères Lygaeidae Euro-Méditerranéens, 2. Faune de France. France et régions limitrophes 84B: 1-453 (in French).

Péricart J (1999c). Hémiptères Lygaeidae Euro-Méditerranéens, 3. Faune de France. France et régions limitrophes 84C: 1-487 (in French).

#### Family Alydidae

Moulet P (1995). Hémiptères Coreoidea (Coreidae, Rhopalidae, Alydidae) Pyrrhocoridae, Stenocephalidae Euro-Méditerranéens. Faune de France. France et régions limitrophes

81: 1-336 (in French).

#### **Family Coreidae**

Moulet P (1995). Hémiptères Coreoidea (Coreidae, Rhopalidae, Alydidae) Pyrrhocoridae, Stenocephalidae Euro-Méditerranéens. Faune de France. France et régions limitrophes

81: 1-336 (in French).

#### Family Rhopalidae

Moulet P (1995). Hémiptères Coreoidea (Coreidae, Rhopalidae, Alydidae) Pyrrhocoridae, Stenocephalidae Euro-Méditerranéens. Faune de France. France et régions limitrophes

81: 1-336 (in French).

#### **Family Pentatomidae**

Derjanschi VV, Péricart J (2005). Hémiptères Pentatomoidea euro-méditerranéens 1. Généralités.

Systématique: Première partie. Faune de France 90: 1-494 (in French).

#### Family Scutelleridae

Ruiz D, Goula M, Infiest, E, Monleón T, Pujol M, Gordún E (2003). Guía de identificación de los chinches de los cereals (Insecta, Heteroptera) encontrados en los trigos españoles. Boletín Sanidad Vegetal Plagas 29: 535-552 (in Spanish). **Appendix 2.** Principal coordinates of neighbor matrices analysis (PCNM) obtained with matrix of distances among plots. Abbreviations of the sampling plots: R1 to R5, Repeat-burnt; L1 to L5, burnt logged; S1 to S5, burnt logged and subsoiled; U1 to U5 control unburnt.



**Appendix 3.** Vegetation results. List of plant species (and abbreviations) found at each sampling site and replicate. Each numeric column includes plant species presence (1) or absence (0) in replicates. Biotype codes (bt code) for each plant species: G, grass; S, shrub; T, tree. Abbreviations of sites: R, Repeat-burnt; L, burnt logged; S, burnt logged and subsoiled; U, control unburnt.

		bt	Repeat burnt I			Logged					Subsoiled						Unburnt					
		code	R1	R2	R3	R4	R5	L1	L2	L3	L4	L5	S1	S2	S3	S4	S5	U1	U2	U3	U4	U5
Ajuga chamaepitys L.	ajucha	G	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Allium asphaerocephalon L.	allasp	G	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anacamptis pyramidalis (L.) L.C.M.Richard	anapyr	G	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anagallis arvensis L.	anaarv	G	1	0	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	0	0	0
Andryala integrifolia L.	andint	G	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Antirrhinum sp.	antspc	G	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Aphillanthes monspeliensis L.	aphmon	G	0	0	0	0	0	1	1	0	0	1	1	1	0	1	0	1	1	0	1	0
Arbutus unedo L.	abrune	Т	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0
Argyrolobium zanonii (Turra) P.W.Ball	argzan	G	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0
Asparagus acutifolius L.	aspacu	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Asperula cynanchica L.	aspcyn	G	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Asphodelus cf.	aspspc	G	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asteriscus spinosus (L.) Sch.Bip.	astspi	G	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Asterolinon linum-stellatum (L.) Duby	astlin	G	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Astragalus monspessulanus L.	astmon	G	0	0	0	0	0	1	1	0	0	1	1	0	1	1	1	1	1	1	0	0
Astragalus sesameus L.	astses	G	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Avenula bromoides (Gouan) H.Scholz	avebro	G	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0
Blakstonia perfoliata (L.) Hudson	blaper	G	0	1	0	1	1	1	1	1	0	1	0	1	0	1	0	1	1	0	0	0
Brachypodium distachyon (L.) Beauv.	bradis	G	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
Brachypodium phoenicoides (L.) Roem. & Schultes	brapho	G	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Brachypodium retusun (Pers.) Beauv.	braret	G	1	1	1	1	0	1	0	0	1	1	0	0	0	1	1	0	1	1	0	1
Bupleurum fruticescens Loefl. ex L.	bupfru	G	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Bupleurum fruticosum L.	bupfri	s	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Campanula erinus L.	cameri	G	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Carex flacca Schreber	carfla	G	0	0	0	0	0	1	0	0	1	1	1	1	0	1	0	1	0	0	1	0
Carex sp.	carspc	G	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Catapodium rigidum (L.) C.E.Hubb.	catrig	G	0	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0
Centaurea aspera L.	cenasp	G	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0
Centaurea sp.	censpc	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Centaurium pulchellum (Swartz) Druce	cenpul	G	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Cistus albidus L.	cisalb	s	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	0
Cistus salviifolius L.	cissal	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Clematis flammula L.	clefla	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Conopodium majus (Gouan) Loret in Loret & Barrandon	conmaj	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Convolvulus arvensis L.	conarv	G	1	0	0	1	0	1	1	0	1	0	1	1	0	1	0	0	0	1	0	0
Convolvulus lineatus L.	conlin	G	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coriaria myrtifolia L.	cormyr	S	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	0	1
Coris monspeliensis L. subsp. monspeliensis	cormon	G	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	1
Crupina cf.	cruspc	G	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Crupina vulgaris Cass.	cruvul	G	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dactylis glomerata L.	dacglo	G	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0
Daphne gnidium L.	dapgni	s	1	1	1	0	1	0	1	0	0	0	1	1	1	1	1	1	0	1	0	1
Dorycnium hirsutum (L.) Ser.	dorhir	G	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Dorycnium pentaphyllum Scop.	dorpen	G	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Echium vulgare L.	echvul	G	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Epipactis cf. atrorubens	epiatr	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Erica multiflora L.	erimul	s	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	1	1	1
Erucastrum cf.	eruspc	G	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Erucastrum nasturtiifolium (Poir.) O.E.Schulz	erunas	G	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Eryngium campestre L.	erycam	G	0	1	1	0	0	0	1	1	1	0	0	1	0	0	0	1	1	1	1	0
Euphorbia cf. exigua	eupexi	G	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Euphorbia nicaeensis All.	eupnic	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Euphorbia serrata L.	eupser	G	1	0	1	0	1	0	1	0	1	1	1	1	1	0	0	0	0	1	1	1
Euphorbia sp.	eupspc	G	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Festuca gr. ovina	fesovi	G	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0

Filago pyramidata L.	filpyr	G	1	0	1	0	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0	0
Fumana ericoides (Cav.) Gandg.	fumeri	G	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Galactites tomentosa Moench	galtom	G	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0
Galium lucidum All.	galluc	G	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium pumilum Murray non Lam.	galpum	G	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Genista scorpius (L.) DC. in Lam. & DC.	gensco	S	0	0	1	0	0	0	1	1	1	1	1	1	1	0	1	0	0	0	1	0
Globularia alypum L.	gloaly	s	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Helianthemum oelandicum (L.) Dum. Cours.	heloel	G	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	0	0	0	1	0
Helichrysum stoechas (L.) Moench	helsto	G	0	0	1	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	1
Hieracium sp.	hiespc	G	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0
Hippocrepis comosa L.	hipcom	G	0	0	0	0	0	1	1	0	0	1	1	1	1	1	0	0	0	0	1	0
Hypericum perforatum L.	hypper	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hypochoeris radicata L.	hyprad	G	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Juniperus oxycedrus L.	junoxy	S	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0	1	1	1	1	1
Koeleria vallesiana (Honckeny) Gaud.	koeval	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Lactuca serriola L.	lacser	G	0	1	1	0	0	1	0	1	1	0	0	1	1	1	0	0	0	0	0	0
Lavandula latifolia Medic.	lavlat	G	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Leontodon taraxacoides (Vill.) Mérat	leotar	G	1	1	1	0	0	1	1	1	1	0	1	0	1	1	1	1	1	0	0	0
Leuzea conifera (L.) DC	leucon	G	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ligustrum vulgare L.	ligvul	Т	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Linum narbonense L.	linnar	G	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Linum strictum L.	linstr	G	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Linum tenuifolium L.	linten	G	0	1	0	0	0	0	1	0	0	1	1	1	1	0	1	1	1	1	1	1
Lonicera implexa Ait.	lonimp	s	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0
Medicago lupulina L.	medlup	G	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Medicago minima (l.) L.	medmin	G	0	1	1	1	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0
Medicago sp.	medspc	G	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0
Melilotus sp.	melspc	G	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0
Minuartia cf.	minspc	G	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Olea europaea L.	oleeur	Т	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Onobrychis saxatilis (L.) Lam.	onosax	G	0	1	0	0	0	1	1	1	0	1	0	0	1	0	0	0	1	0	0	1

	1			<u> </u>	1	<u> </u>	1		<u> </u>	1	1	<u> </u>		<u> </u>	r	r	T		1		1	T
Ononis minutissima L.	onomin	S	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1
Ononis natrix L.	onomat	S	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Orobanche sp.	orospc	G	0	0	1	0	0	1	1	0	1	1	1	0	0	1	0	1	1	0	0	1
Oryzopsis miliacea (L.) Asch. & Graebn.	orymil	G	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Phagnalon rupestre (L.) D.C.	pharup	G	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Phleum phleoides (L.) Karsten	phlphl	G	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Pinus sp.	pinspc	Т	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
Pistacia lentiscus L.	pislen	s	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0
Plantago lanceolata L.	plalan	G	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1
Polygala rupestris Pourr.	polrup	G	0	1	1	1	1	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0
Populus alba L.	popalb	Т	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Populus nigra L.	popnig	Т	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Psoralea bituminosa L.	psobit	G	1	1	1	1	1	0	1	0	1	0	0	0	1	1	0	1	0	0	1	1
Quercus cerrioides Willk. & Costa	quecer	Т	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	1
Quercus coccifera L.	quecoc	s	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Quercus ilex L. subsp. ilex	queile	Т	0	1	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
Reseda phyteuma L.	resphy	G	1	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Rhamnus alaternus L.	rhaala	s	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Rosa sp.	rosspac	s	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Rosmarinus officinalis L.	rosoff	S	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Rubia peregrina L. subsp. peregrina	rubper	G	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1
Rubus ulmifolius Schott	rubulm	S	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	1	1
Sanguisorba minor Scop.	sanmin	G	0	0	1	0	1	0	1	1	1	1	1	1	0	0	1	0	1	0	1	1
Santolina chamaecyparissus L.	sancha	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Satureja calamintha (L.) Scheele	satcal	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Satureja montana L.	satmon	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Scorzonera angustifolia L.	scoang	G	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Sedum sediforme (Jacq.) Pau	sedsed	G	0	1	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0	0	0	0
Sideritis hirsuta L. subsp. hirsuta	sidhir	G	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0
Smilax aspera L.	smiasp	s	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Sonchus asper (L.) Hill	sonasp	G	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Sonchus sp.	sonspc	G	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Sonchus tenerrimus L.	sonten	G	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0
Spartium junceum L.	spajun	S	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Staehelina dubia L.	stadub	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
Stipa offneri Breistr.	stioff	G	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0
Silybum marianum (L.) Gaertn.	sylmar	G	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Teucrium botrys L.	teubot	G	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Teucrium chamaedrys L.	teucha	G	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0
Teucrium polium L. subsp. capitatum (L.) Arcang.	teupol	G	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1
Thymus vulgaris L.	thyvul	G	0	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1
Trigonella monspeliaca L.	trimon	G	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ulex parviflorus Pourr.	ulepar	s	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Urospermum picroides (L.) Scop. ex F.W.Schmidt	uropic	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Verbascum sp.	verspc	G	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Verbena officinalis L.	veroff	G	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Vinca difformis Pourr.	vinspc	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Viola sp.	viospc	G	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Vitis sp.	vitspc	S	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1

**Appendix 4.** Principal component analysis (PCA) obtained with the overall matrix of presence/absence data of all plant species. Abbreviations of the sampling plots: R1 to R5, Repeat-burnt; L1 to L5, burnt logged; S1 to S5, burnt logged and subsoiled; U1 to U5 control unburnt.

