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Assessing the Response of Different Soil Arthropod Communities to Fire: A Case Study from Northwestern Africa

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Abstract: In recent decades, forest fires in the Mediterranean basin have been increasing in frequency, intensity, and the area burnt. Simultaneously, insects, a group with extraordinary biodiversity that provides vital ecosystem services such as pollination and decomposition, are undergoing a precipitous decline. Unfortunately, the impact of fire on arthropod communities has been poorly addressed despite the high diversity of taxonomic and functional arthropod groups. Responses to fire can differ considerably, depending on the life history and functional traits of the species. In the present study, we investigate the short-term impact of fire (three years after a blaze) on the abundance and species composition of soil arthropods in a burnt pine forest located in Ceuta (Spain, northwestern Africa). Soil arthropods were collected from pitfall traps in burnt and unburnt pine forest sampling points. In terms of total abundance per taxonomic order, Blattodea and Diptera were the only orders seemingly affected by the fire, whereas other arthropod groups (e.g., Araneae, Coleoptera, and Isopoda) showed no differences. In terms of species composition, Coleoptera and Formicidae (Hymenoptera) communities differed between burnt and unburnt sampling points, having more species associated with burnt areas than with unburnt ones. In burnt areas, some species from open areas built nests, fed in/on the ground, and dispersed over longer distances. Within the unburnt plots, we found more species in vegetated habitats, particularly those with shorter dispersal distances. We conclude that arthropod communities differ between burnt and unburnt sites and that the response of each taxon appears to be related to particular functional traits such as habitat preference (from open to forested landscapes) and ecological specialization (from generalist to specialist species).

Keywords: soil arthropods; fire; pine plantations; Mediterranean basin



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1. Introduction

Fire, one of the most influential natural disturbances in fire-prone areas such as the Mediterranean region [1], can act as a major driver of animal community composition [2]. Over the last few decades, humans have been altering fire regimes through land-use shifts (land abandonment and forestry) as well as human contributions to climate change and its consequences, particularly drought [3]. Even though fire is commonly viewed as disastrous, it is considered a critical driver of biodiversity in fire-prone ecosystems [4,5], accelerating

nutrient cycling [6,7] and enabling an extraordinary amount of plant diversity [8]. In fact, there is considerable variety in how different plant and animal species respond to fire, leading to the notion that in fire-exposed landscapes, “pyrodiversity generates biodiversity” [9]. Therefore, knowing how plants and animal communities respond to fire is key to predicting how fire might influence biodiversity in forest ecosystems [10].

The strategies of plant species to respond to fire are known [11], whereas in animals, knowledge is uneven among groups, and little is known about fire’s effect on many arthropod taxonomic orders [12]. This knowledge gap contrasts with the fact that arthropods constitute the world’s most diverse animal group, dominating many terrestrial food webs and providing vital ecosystem functions [13,14], such as organic decomposition, seed dispersal, pollination, predation, and waste disposal [10]. Additionally, owing to their functional diversity (e.g., herbivores, predators, and pollinators), insects provided insights into changes in community function that reflect shifts in environmental and ecological conditions [15,16]. In recent decades, 41% of insect species have been found to be in decline, at an annually declining rate of roughly 2.5% of insect biomass around the world, and nearly a third of all insect species are threatened [17]. Given their significance in the functioning of the food web and environment, arthropod losses are ecological and conservational concerns.

In the short term, wildfires have a negative impact on soil biota, particularly arthropods [18,19], firstly due to the destruction of the vegetation structure and secondly by the elimination of the organic layer (humus) of the upper soil [20]. In a broad context, fire can affect the abundance and diversity of soil arthropods either positively or negatively [21,22], with impacts differing based on the life-history traits of particular taxa [23]. For instance, some insect groups significantly decline both immediately (hours during and after fire) and over the short term (0 to 1–2 months after fire), relative to pre-fire or unburnt control samples [24,25]. Conversely, other insects belonging to various families around the world demonstrate attractions to fire or smoke or lay eggs in freshly burnt wood [26,27]. After the fire, communities gradually reassemble through diverse regeneration processes, including deterministic environmental restrictions (e.g., changes in resource availability [28,29]). For example, insects with poor dispersal abilities tend to be more directly threatened by fire [21]. Conversely, certain soil arthropod communities are resilient after wildfires [30,31], owing to their life history, morphology, and behavior, which enable some species to be either opportunistic or to be specialists under post-fire conditions [32]. For instance, ants have a great ability to relocate to non-burnt areas, even underground, thereby lowering the mortality rate of their populations in the face of fire events [33]. Conversely, grasshoppers often, but not always, become more abundant in short-term burnt plots, as they are generalist/invasive species, with broad dispersal capabilities [34–36]. In summary, soil arthropod communities are appropriate for evaluating the effect of ecological disturbances such as fire because of their sensitivity to habitat change and their ability to disperse, enabling the early detectability of changes in the community diversity and structure [37].

Given the diversity of arthropod responses to fire, assessments on how different soil arthropod groups are impacted by fire becomes urgent in order to direct biodiversity conservation and to design landscape management guidelines in a period of declining biodiversity [10]. In this study, our objective is to evaluate the effect of fire on the abundance and species composition of soil arthropods in a burnt pine forest located in Ceuta (Spain, northwestern Africa). Specifically, we evaluate the responses to fire of three diverse arthropod groups (Formicidae (Hymenoptera), Coleoptera, and Orthoptera) by comparing species abundance between pitfalls in burnt and unburnt plots. Thus, we seek to answer the following questions: (1) Do the abundance and diversity of arthropods decline in the burnt area? (2) Does the composition of beetle, ant, and grasshopper communities differ between burnt and unburnt sampling points? (3) Given that burnt and unburnt habitats differ in terms of canopy and vegetation structure, can the species found at burnt and unburnt points be considered open and forest specialists, respectively? In short, are there different functional responses of arthropod species due to fire?

2. Materials and Methods

2.1. Study Area

The study area, in Ceuta (Spain), is located in the easternmost part of the Strait of Gibraltar (Tingitanian Peninsula, northwestern Africa), between 35.903° and 35.881° latitude and between −5.284° and −5.369° longitude (Figure 1). Due to its location, Ceuta constitutes a convergence area between the Atlantic Ocean and the Mediterranean Sea. The climate is subhumid, with an average annual rainfall of 625 mm and an average annual temperature of 16.4 °C [38,39]. The non-urbanized landscape (1100 ha in total) is a mixture of cork oak (*Quercus suber* L.) forest patches (related to *Myrto communis-Quercetum suberis* association) and diverse xeric scrub of the herguel type (related to the *Asparago aphylli-Calicotometum villosae* association) [38,40]. There are also patches of mixed stone pine (*Pinus pinea* L.), Aleppo pine (*Pinus halepensis* Mill.), and resin pine (*Pinus pinaster* Ait.), all from afforestation conducted in the 1950s and 1960s [38,39,41]. In the last decade, the forested area of Ceuta has undergone several fires (see historical fire polygons in Figure 1): the 2014 fire burned 36 hectares, the 2015 fire burned 30 hectares, the 2018 fire burned 63 h, and the 2019 fire burned 60 ha. The last fire occurred in 2022 and burned 125 hectares.

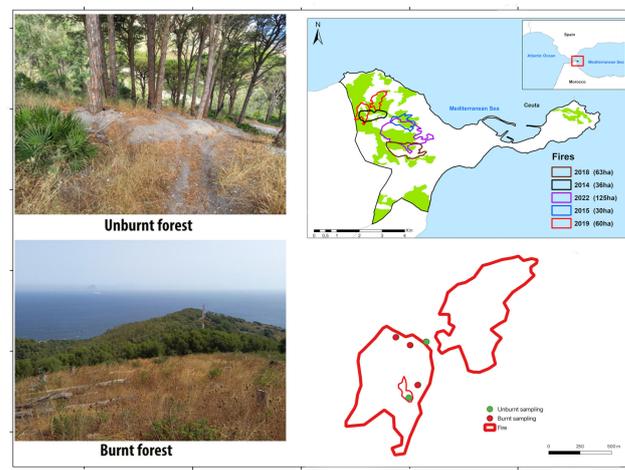


Figure 1. Location of the study areas city of Ceuta and pictures of unburnt and burnt plots where pitfalls were installed. The upper-right panel shows the forested area in Ceuta (green polygons) and the perimeter of the historical fires. The lower-right panel shows the 2019 fire perimeter and the location of the sampling points (red circles are burnt sampling, and green circles are unburnt sampling).

2.2. Arthropod Sampling

Soil arthropods were sampled in a pine plantation in which 60 ha burned during a summer fire in 2019. Gutter pitfall traps (6 cm in diameter) were used, partly filled with soapy water and salt. Five sampling points were established: three in the unburnt and two in the burnt area. In the latter, pitfalls were set in patches with similar pre-fire vegetation (i.e., pine forest) to that of the unburnt area. We acknowledge that the number of replicates is small; this was caused by the small size of the fire perimeter and the lack of many similar pre-fire vegetation patches (pine plantations) in areas surrounding the burnt area. Unburnt pine plots far from a burnt area could demonstrate that the differences between unburnt and burnt plots are caused by other factors (e.g., climate, slope and aspect, and lithology) than fire.

At each sampling point, 5 pitfalls were placed 10 m apart along 50 m linear transects. After pitfall installation, the soil was restored with similar litter from the surrounding area. The distance between burnt and unburnt sampling points averaged 104 ± 2.46 (standard error) meters. Pitfalls were collected after 6 consecutive days on two sampling occasions (July 2022 and October 2022). No pitfalls became completely dry after the 6-day period. Arthropods from pitfall traps were preserved in 70% ethanol until identification. In the lab, specimens were separated by class and identified to the order level. Formicidae

(Hymenoptera), Coleoptera, and Orthoptera specimens were classified to species level, thanks to the taxonomic and faunistic expertise of northwestern African fauna by the authors (P.B. for Orthoptera, J.L.R. for Coleoptera, and A.T. for Formicidae). Arthropod sampling was conducted under permit from the Ceuta authorities.

3. Data Analysis

Three types of analyses were performed:

- (1) Abundance values of the top 10 most-abundant arthropod orders were compared between pitfalls in burnt and unburnt areas, using Generalized Linear Mixed Models (GLMMs). This analysis was carried out using a Poisson distribution due to the discrete nature of the dependent variables (counting the number of individuals captured). The fire condition (burnt or unburnt) of the sampling points was used as an independent variable, whereas the sampling point and the sampling month (July and October) were treated as random effects. Statistical analyses were performed using the lme4 package [42], and figures were performed using the ggplot 2 package [43].
- (2) The composition and species abundance of ant, beetle, and orthopteran communities found in the burnt vs. unburnt pitfall traps were compared by permutational analysis of variance (PERMANOVA). For each arthropod group, the pairwise similarity in species abundance and presence among pitfall traps were assessed using the Bray–Curtis similarity distance for the relative abundance data and using the adonis2 function from the vegan package [44]. Similar to the GLMM design, the fire condition was used as a fixed factor, whereas the sampling point and season were used as random factors in the PERMANOVAs. All analyses were performed using R software (Core Team 2021).
- (3) Based on the abundance of beetle, ant, and grasshopper species per pitfall trap, we calculated the Shannon diversity index. Then, we used Generalized Linear Mixed Models (GLMMs) using the lme4 package [42], with a Gaussian distribution, to examine the effect of the fire condition (burnt and unburnt) on the Shannon diversity per trap. The sampling point and the sampling month (July and October) were treated as random effects.

4. Results

In total, 3131 arthropods were collected, with a mean of 67 arthropods per pitfall (± 7.57 SE) belonging to four classes, namely, Crustacea ($n = 233$ individuals), Arachnida ($n = 966$ individuals), Myriapoda ($n = 3$ individuals), and Insecta ($n = 1963$ individuals) (Table 1). Among insects, the most-abundant taxa collected were Formicidae (Hymenoptera). The GLMMs indicated that the total arthropod abundance values per pitfall did not differ significantly between burnt and unburnt samples (Table 2). The comparison for the top 10 most-abundant arthropod orders (Araneae, Coleoptera, Isopoda, Blattodea, Diptera, Collembola, Orthoptera, Formicidae (Hymenoptera), and non-Formicidae Hymenoptera) and the subclass Acari did not show differences in abundance per pitfall between burnt and unburnt samples for the majority of groups, except in the cases of Blattodea and Diptera (Table 2). For these two orders, the abundance was higher in pitfall traps from unburnt sampling points than from burnt sampling points (Table 2 and Figure 2a,b).

Table 1. Abundance of arthropod taxonomic groups collected in pitfall traps from Ceuta (Spain).

Class	Subclass/Order	Suborder/ Family	Fire Condition		Total	Proportion (%)
			Unburnt	Burnt		
Crustacea	Isopoda		97	136	233	7.4
Arachnida	Acari		442	390	832	26.6
	Araneida		47	64	111	3.5
	Pseudoescorpionida		6	9	15	0.5
	Opiliones		4	4	8	0.3

Table 1. Cont.

Class	Subclass/Order	Suborder/ Family	Fire Condition		Total	Proportion (%)
			Unburnt	Burnt		
Myriapoda Insecta			0	3	3	0.1
	Hymenoptera	Formicidae	314	623	937	29.9
		Others	18	74	92	2.9
	Diptera		179	119	298	9.5
	Collembola		118	123	241	7.7
	Coleoptera		78	107	185	5.9
	Blattodea		66	10	76	2.4
	Hemiptera	Heteroptera	8	29	37	1.2
		Others	7	5	12	0.4
	Orthoptera		3	8	11	0.4
	Archaeognatha		6	0	6	0.2
	Thysanoptera		2	1	3	0.1
	Neuroptera		0	1	1	0.0
Unknown nymph		12	18	30	1.0	
Total			1407	1724	3131	100

Table 2. Results of the generalized linear mixed models for the abundance of the most common arthropod taxa in pitfall traps between burnt and unburnt sites in Ceuta (Spain). For the orders with significant differences, there is the group (unburnt/burnt) with higher abundance shown in brackets.

Order	Fire Condition (Burnt and Unburnt)			
	Estimate	Std. Error	Z	P
All arthropods	0.222	0.174	1.272	ns
Araneae	0.168	0.192	0.876	ns
Coleoptera	0.131	0.219	0.595	ns
Formicidae	−0.249	0.518	−0.480	ns
Isopoda	0.479	0.841	0.570	ns
Blattodea (unburnt)	2.378	0.627	3.796	0.00015
Diptera (unburnt)	0.845	0.284	2.972	0.00296
Collembola	0.370	0.424	0.872	ns
Orthoptera	−0.501	0.696	−0.719	ns
Acari	0.253	0.633	0.400	ns
Hymenoptera	−0.873	0.782	−1.116	ns

We recorded a total of 937 ants (Formicidae) from 16 species, 185 individuals from 35 species of Coleoptera belonging to 19 families, and a total of 11 Orthoptera from 5 species (Supplementary Materials Table S1). The PERMANOVA analyses revealed that the beetle and ant communities differed between burnt and unburnt sampling points (Table 3). By contrast, the grasshopper species composition did not differ in this regard, probably due to the small sample size collected for this group. Overall (with beetle, ant, and grasshopper species pooled), no differences were observed in the Shannon diversity scores between burnt and unburnt sampling points ($t = 0.012$, $p = 0.990$; Figure 3).

Tenebrionidae (seven mainly saprophagous species), and Carabidae (six species of predatory and phytophagous species including a granivorous species, *Carterus rotundicollis*, present only at burnt sites) were the beetle families with the highest numbers of species collected. Among the 35 species of beetles recorded (Supplementary Materials Table S1), 16 were found exclusively in burnt areas, 10 only in unburnt areas, and 9 in both areas.

In terms of functional (trophic) groups, the most-abundant beetle groups in unburnt pitfalls were saprophagous (47.3%, nine species, including saproxylic and sapro-coprophygous), followed by predatory (26.3%, five species) and phytophagous beetles (15.7%, three species). At burnt sites, saprophagous beetles (52%, 13 species, including saproxylic and sapro-coprophygous) also comprised the most-abundant functional group,

followed by phytophagous (32%, 8 species, including anthophilous and granivorous) and predatory beetles (16%, 4 species).

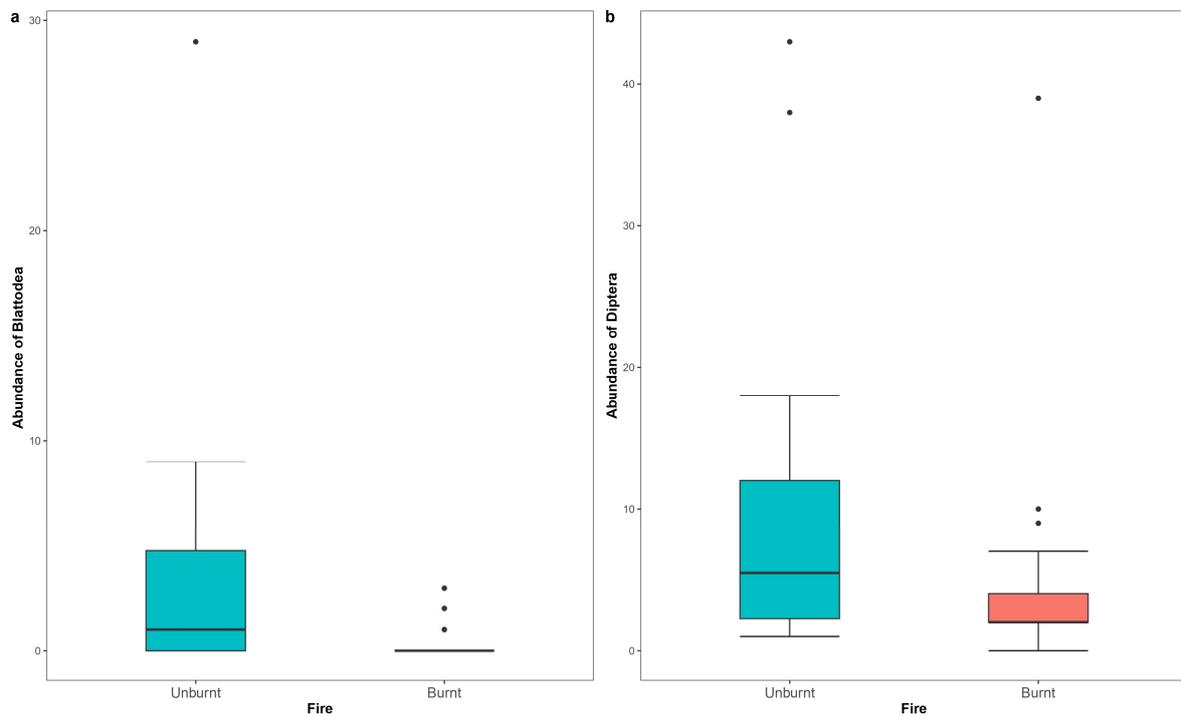


Figure 2. Box plots of the abundance of Blattodea (a) and Diptera (b) in samples collected from pitfall traps at burnt and unburnt points in Ceuta (Spain) after a fire that occurred in 2019. The line represents the median value; the 25th and 75th percentiles represent the box limits.

Table 3. Mean abundance and standard error (SE) of Coleoptera, Formicidae (Hymenoptera), and Orthoptera abundance values from pitfall traps at burnt and unburnt sites; results of the PERMANOVA analyses comparing the community composition between burnt and unburnt samples.

Order	Mean Abundance (SE)		PERMANOVA		
	Unburnt	Burnt	F	R ²	P
Coleoptera	5.2 (1.03)	3.8 (0.43)	2.6783	0.06132	0.005
Formicidae (Hymenoptera)	21 (6.5)	23 (5.23)	5.6046	0.1229	0.001
Orthoptera	0.4 (0.6)	1.8 (0.37)	1.1365	0.11212	0.429

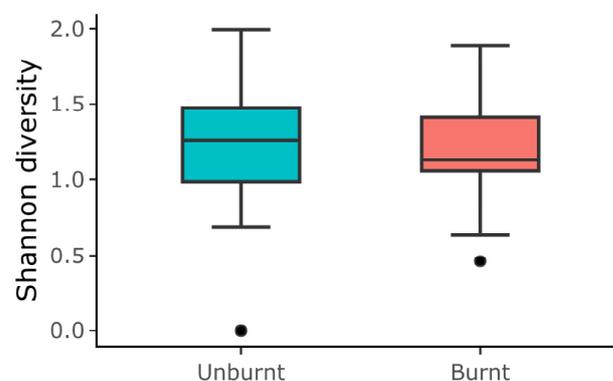


Figure 3. Average and standard error of the Shannon diversity scores of pitfall traps collected at burnt and unburnt points. The index was calculated based on the abundance of beetle, ant, and grasshopper species found in Ceuta (Spain).

Regarding specific abundance, the most-abundant epigeal species were, in descending order, *Stenosis hispanica* (Tenebrionidae: flightless, detritivorous, lapidicolous, and dwelling under tree bark), *Steropus (Sterocorax) globosus* (Carabidae: flightless, predatory, and lapidicolous), *Orthomus maroccanus* (Carabidae: flightless, predatory, and lapidicolous), *Thorectes laevigatus* (Geotrupidae: flightless, sapro-coprophagous, and acorn-eating), and *Pactolinus major* (Histeridae: flying, predatory, and copro-necrophilous). All of these were common to burnt and unburnt areas. These species are mostly generalist in terms of habitat preference, with a relatively wide distribution in the Maghreb, i.e., much of northern Africa, except Egypt [45–50]. The most-abundant species, *S. hispanica*, forms aggregations (sometimes of more than 15 individuals) under stones or pine and eucalyptus bark (personal observation), which could favor its abundance in pitfall traps, whereas *S. globosus* is an opportunistic species that colonizes burnt forests [51,52].

Among the species exclusively found at unburnt sites, at least four showed an affinity for moist substrates or were clearly hygrophilous (*Brachinus andalusicus*, *Dienerella separanda*, *Ocypus olens*, and *Sepedophilus* sp.), while another species, *Ripidius quadriceps*, which is very rare in North Africa, parasitizes species of Blattodea (mainly genera *Ectobius* and *Blattella* [53,54]), a taxonomic group showing a significantly higher abundance in unburnt areas.

At burnt sites, thermophilic, opportunistic, and generalist species proved predominant, being characteristic mainly of open habitats (e.g., *Acmaeoderella adspersula* and *Ophonus ardosiacus*: flying; *Morica planata*, *Pachychila salzmanni*, *Boromorphus tagenioides*, *Asida septemsis*, and *Andrion regensteinense*: flightless); some of these were markedly heliophilous, such as *A. adspersula*, *M. planata*, and *P. salzmanni*. Among these species, *Asida (Planasida) septemsis* (Tenebrionidae: flightless, detritivorous, and lapidicolous) is endemic to the northern tip of the Tingitanian Peninsula, showing a marked preference for open scrub areas and forest clearings [55].

For ants, two subfamilies were recorded: Myrmecinae, with 10 species and five genera, and Formicidae, with 6 species and three genera (Supplementary Materials Table S1). Of the 16 species captured (all native to Ceuta), 9 were forest species (mesoforest or euforest species), and 7 had a wide range of habitats, usually nesting in open and well-exposed places. Of these nine forest species, four species were common in burnt and unburnt areas, whereas three species were located only in burnt areas. These three species were *Camponotus spissinodis*, which is a strictly arboreal species that burrows into and nests in wood; *Camponotus ali*, which lives under stones; and *Plagiolepis barbara*, which lives under stones and in litter. The rest of the species found in the burnt areas (*Messor barbarus*, *M. sanctus*, and *Cataglyphis viatica*) were species of open and thermophilic areas.

The forest species *Temnothorax recedens*, *Crematogaster scutellaris*, and *Tetramorium exasperatum* were collected exclusively in unburnt areas (Supplementary Materials Table S1). *T. recedens*, a relatively thermophilic mesoforest species, was found mostly in subhumid, warm, and mild climate zones [56], *C. scutellaris* nests in dead branches, sometimes spreading to the ground at the base of a tree [57], while *T. exasperatum* not only nests in litter and under stones in cork oak forests [58,59] but also occurs in open places [60].

Tetramorium semilaeve proved to be the most-abundant ant species in burnt as well as unburnt areas. The species is known to use a wide range of open and well-exposed habitats such as grasslands and scrublands [60]. It was followed by two forest species, *Temnothorax curtulus* and *Tetramorium exasperatum*, in unburnt areas, and by two species of open and dry habitats, *Crematogaster auberti* and *Messor sanctus*, in burnt areas [60,61].

Orthoptera captures were scarce (Supplementary Materials Table S1) and mostly of immature specimens. In general, they were generalist species. *Pezotettix giornae* appeared in herbaceous environments, quite commonly at medium altitudes and coastal plains, reaching up to 2300 m a.s.l., though it was absent near the sea. It, reportedly, frequently occurs along with *Calliptamus barbarus* on fallow lands [62]. This latter species is also common in flat areas in wastelands and in open scrub surrounded by fallow areas. It is distributed from the coast to elevations above 2000 m. *C. barbarus* is the most-frequent and

abundant Orthoptera species in northern Morocco, with adults appearing from June to October [63]. Existing records of *Gryllomorpha uclensis* in North Africa should be reviewed, as several very morphologically similar species were identified to the species level by studying only the male genitalia [64,65]. Its presence was confirmed in Algeria [66]. In our case, no adult males were captured to allow for a study of this structure, so the identification is preliminary until there is confirmation with adult male specimens.

5. Discussion

This is the first study available that characterizes the species-level effects of fire on several soil arthropod groups in northwestern Africa. The present field study data show that the short-term arthropod-community responses to fire differed among arthropod groups. On the whole, arthropod abundance was indistinguishable between burnt and unburnt areas, with the exceptions of Blattodea and Diptera, which decreased in burnt areas. However, a finer analysis in terms of species composition revealed that beetle and ant communities varied between burnt and unburnt sampling points. Although the sampling design was limited to a single fire, several pieces of evidence indicated that arthropod communities differ between burnt and unburnt points and that species responses are linked in part to their functional traits [23].

5.1. Effects of Fire on the Abundance of Arthropod Taxa

Landscape openness is a major driver affecting the soil arthropod fauna over the short-term following a fire [67]. However, the response to fire can vary among arthropod taxa, as particular traits can boost the probability of surviving fire, the capacity for dealing with future environmental conditions, and the likelihood of colonizing burnt areas [68,69]. In terms of total abundance, the results show that Blattodea and Diptera were the only orders apparently affected by fire. These groups are known to be among those sensitive to fire [70]. A possible explanation for the negative effect of fire on these two orders is the short-term elimination of the existing layer of litter and decomposing vegetation on the ground. Thus, the decreases for Blattodea and Diptera could reflect an intolerance to soil dryness in recently burnt habitats [71]. Frouz [72] found that soil moisture and the input of organic matter are the main factors that influence Diptera abundance after fire. The decline of Blattodea in burnt areas might be caused by the post-fire alteration of the vegetation structure in pine plantations [73] and a short-term post-fire reduction in leaf-litter deposition, the primary food source for cockroaches [30]. While these two orders decreased after fire, other groups of arthropods (i.e., Araneae, Coleoptera, and Isopoda) showed significant resilience in terms of abundance. This is most probably attributable to the depth at which they live during their preimaginal stages, their burrowing capability, the availability of shelters such as logs and rock piles [31], and their high capacity for early colonization from nearby unburnt areas, especially in open habitats [74–76].

5.2. Effects of Fire on the Composition of Arthropod Communities

On a short-term basis, fire is an environmental filter that screens for species that are better-suited to the restricted environmental conditions following a blaze [77]. The early post-fire succession enhances open areas and promotes a change in dominant animal species, which frequently results in different assemblages in burnt and unburnt areas [78,79]. Within the burnt plots, species more characteristically from open areas were expected to be found, including those that construct nests, forage in/on the soil, and disperse over longer distances. For unburnt plots, species more typically found in vegetated habitats were expected, especially those with shorter dispersal distances [10]. The results support these expectations, as significant differences were found in the (functional) composition of ant and beetle communities between burnt and unburnt sites.

The most-abundant beetle species in both areas were flightless, generalists in terms of habitat preference, and opportunistic (except *Pactolinus major*, which also takes refuge under stones [50]), so their capacity for dispersal and the rapid recolonization of burnt areas

would presumably be lower than that for flying species. The abundance of these species at burnt and unburnt sites proved similar. This is because they all present hypogeous preimaginal stages, with larvae and pupae living buried in the ground at a certain depth (Tenebrionidae and Geotrupidae) and, in some cases (Carabidae), also under stones (which act as shelter), giving them a high resilience to fire, especially against more superficial burning [76,80].

At burnt points, generalist, thermophilic, and heliophilous beetle taxa predominated, preferring open habitats or those with little tree cover. The greater richness of the beetle species found in burnt areas was widely observed by other authors (e.g., [74,75,81–83]). In this case, the pattern would have two main causes (see [76]): the resistance and resilience to fire of generalist species and the relatively rapid exogenous colonization from nearby non-forested areas by thermophilic species, typical of open habitats with scrub. The pine plantations in the Ceuta area are generally homogeneous and have shady undergrowth with little diversity [38, authors' personal observation]. Three years post-fire (when the sampling was made), burnt pine patches still lacked tree cover and were, at that time, being colonized by diverse scrub and herbaceous plants; furthermore, these patches presented greater floristic diversity, structural complexity, and heterogeneity than the unburnt pine stands did. This structure offers greater availability of microhabitats and trophic resources for coleopterans, especially phytophagous species (including canthophilous), saprophagous species, and their predators [75,84,85]. In addition, the reduction or disappearance of tree cover would favor the colonization of heliophilous and floricolous beetles, typical of open habitats [74,79,85].

Most studies reported that ant composition is significantly altered by fire [86–88]. As such, fire is considered a main driver of functional diversity change in ants [68]. Our findings show that more ant species were associated with burnt areas. This could be explained by the fact that the majority of ant species nest in the soil and dig galleries that are sometimes very deep, with a slight temperature rise a few centimeters below ground, ensuring that the majority of ants would survive a fire [88–90]. The presence of forest species in burnt areas in our study is due to their resistance to fire in cryptic habitats, as in the cases of *Camponotus ali* and *Plagiolepis barbara*, which can dig deep galleries under stones, for example, or to the reoccupation of burnt areas from the neighboring forests.

The two harvester ant species (*M. barbarus* and *M. sanctus*) are strictly granivorous (the only herbivorous species collected in this study). These two species prefer to nest in open and warm environments rather than under tree canopies [91]. Thus, burnt areas offer them suitable environmental conditions: landscape openness with grass seeds and glumes for food [92]. These post-fire open and thermophilic environments could also encourage the colonization of other species captured only by pitfalls in burnt areas, such as *C. viatica*.

The presence of other common ant species in both burnt and unburnt pitfalls (e.g., *Tetramorium caespitum*) evidences their relatively high plasticity, with respect to their habitats and microhabitats (with the exception of *Camponotus ruber*, which is arboreal). These generalist species can all nest on the ground, under dead spindles, under bark, in lodges, and also in galleries under stones. We presume that this plasticity allows them to escape the direct effects of fire—heat, dryness, and smoke [93].

The three arboreal species collected in this study (*Camponotus spissinodis*, *Crematogaster scutellaris*, and *Temnothorax recedens*) are relatively indicative of the nature of the ecosystem prior to pine reforestation and before the fire. In fact, these species generally characterize oak forests in Morocco ([56,94], unpublished personal data).

Our findings suggest that the differences in the ant-species composition between burnt and unburnt areas may be due to changes in microclimatic conditions and food resources caused by fire [87]. Moreover, the majority of species found in unburnt areas have relatively large colony sizes (*Messor*, *Camponotus*, *Cataglyphis*, and *Solenopsis* genera, for example). It was demonstrated that the larger an ant colony is, the better it can buffer disturbances, offering the species more ecological advantages of resistance [68,95]. In addition, a greater abundance was observed in burnt areas for some species associated

with the highest values of body size and worker polymorphism traits (the genera *Messor*, *Cataglyphis*, and *Camponotus*). A positive relationship between heat tolerance and body size in ants was supported by several studies [96,97]. Large workers can remain active and move greater distances at higher temperatures than small workers can, as longer legs enable them to elevate themselves over the warm substrate and attain higher running speeds [98].

Several authors indicated that Orthoptera communities have positive responses to fire due to the increase in plant diversity after fire [22,35,99], although this diversity could decrease after several years with vegetal homogenization. Moreover, Orthoptera diversity may vary depending on the season when the fire occurs [35]. Additionally, the depth at which orthopteran egg pods are laid determines their survival after a fire [100]. This situation may also apply to buried crickets. However, the extremely scarce number of Orthoptera captures in our study precludes any conclusions concerning this group. Both caeliferan species, *P. giornae* and *C. barbarus*, are common, widely distributed, and also found in agricultural areas [101], whereas cricket species were found to live buried in soil or under large- to medium-sized stones. All these traits suggest that these species can survive brief fire events (the 2019 fire burned for approximately 14 h).

5.3. Concluding Remarks

Being by far the richest group of animals in the world in terms of biodiversity, insects need further study to address their conservation needs [10]. For example, scientists have limited knowledge of how insect communities respond to wildfire, as the pyroentomological literature presents a mixture of both positive and negative responses [102]. The ability to forecast ecological and community responses to wildfire necessitates an understanding of how fire and biota relate to each other [103]. In this light, the present research focuses on the species-level effects of fire on several soil arthropod groups. Despite the small scale of the fire event studied, compared to the current megafires in the Mediterranean basin [104,105], the arthropod communities in Ceuta are spatially structured according to fire occurrence. These differences are driven by species' functional traits [23], given that in burnt areas we found species more characteristic of open areas. By contrast, species more typically found in vegetated habitats, especially with shorter dispersal distances, were found in unburnt plots. According to our results, conservation managers should focus on individual taxa rather than total insect biodiversity [102], since our study's taxa demonstrated different overall responses to fire. Additionally, future research that examines the impact at multiple life stages when faced with different fire intensities, in different seasons, and over longer time scales will be essential to establish details pertaining to overall and specific arthropod responses to fire [22].

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/fire6050206/s1>, Table S1: List and total abundance of Hymenoptera Formicidae, Coleoptera and Orthoptera species collected in pitfall traps from Ceuta (Spain).

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