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RESEARCH ARTICLE

On the relative importance of resource availability and habitat connectivity as drivers of soil biodiversity in Mediterranean ecosystems

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Abstract

1. Soil biota influences nutrient cycling and climate regulation and represents an important fraction of global biodiversity, yet we know very little about how this soil biota responds to habitat fragmentation and degradation of habitat quality.
2. We studied the response of different soil trophic groups (microbes and soil fauna), and their trophic structure, to changes in their habitat derived from forest long-term management and extensive tree die-off in a Mediterranean ecosystem. Specifically, we evaluated changes in (i) habitat size, (ii) habitat resource availability and heterogeneity and (iii) habitat connectivity. To do this, we sampled the soil biota of 43 holm oak trees (and five open interspaces) differing in size, quality, heterogeneity, connectivity and the effect of die-off (healthy or affected). We sorted soil biota by trophic group and related their richness to habitat characteristics.
3. Seven of the 12 trophic groups evaluated increased their species richness with soil organic carbon content, which was the most frequently selected driver of soil biota (both microbial and faunal richness). Habitat connectivity positively affected the richness of larger organisms (fauna) and plant attributes (richness, productivity and specific leaf area) also showed significant but contrasting effects depending on the group evaluated.
4. Due to the idiosyncratic responses of different groups, the entire trophic structure (microbes and fauna) was affected by a more complex set of factors than most trophic groups in isolation, including interactions between habitat size and resource availability or connectivity. A major factor influencing habitat resource

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availability was the die-off of the dominant tree species (drastically altering tree productivity). We found weaker and more negative relationships between trophic groups under trees suffering from die-off than beneath healthy trees, particularly between microbial rather than faunal groups.

5. *Synthesis.* We provide a comprehensive assessment of the response of key members of the soil food web to habitat fragmentation and tree die-off (landscape-level plant–soil interactions), illustrating the major role of soil carbon, habitat connectivity and tree die-off in driving soil biodiversity and trophic structure.

KEYWORDS

connectivity, die-off, habitat size, plant–soil interactions, *Quercus rotundifolia*, soil macro- and meso-fauna, soil microbes, soil organic C

1 | INTRODUCTION

Soil biota is essential for ecosystem functioning and represents a key component of biodiversity in terrestrial ecosystems (Delgado-Baquerizo et al., 2020; Rillig et al., 2019; Thakur, 2020). For instance, soil organisms are a major driver of the carbon cycle, nutrient availability, water infiltration, plant growth and community structure (Blankinship et al., 2011; Crowther et al., 2019; Hättenschwiler et al., 2005). As other organisms, soil biota faces anthropogenic pressures, through changes in land use or habitat loss and fragmentation, which are fundamental drivers of plant and animal biodiversity change (Haddad et al., 2015). However, the effect of these global change drivers is still not well understood for soil biota (Cameron et al., 2018; Jiménez-Chacón et al., 2018; Rillig et al., 2019). This knowledge is critical to ensure the conservation of soil biota and the sustainability of soil environments and may help us to understand the implications of plant–soil interactions at the landscape scale.

Habitat loss and fragmentation are considered two of the biggest threats to biodiversity, as they alter the size, quality, spatial configuration and connectivity of habitats (Haddad et al., 2015; Newbold et al., 2015; Sala et al., 2000). First, habitat loss increases the risk of non-random loss of species as a result of declining population sizes (Rantalainen et al., 2004, 2006; Santos & Tellería, 2006; Vanbergen et al., 2007). Second, smaller habitats may host fewer niches, therefore increasing competition between species and directly reducing species richness (Bascompte & Sole, 1996). Third, degraded habitats may provide less resources (or of lower quality) and a limited ability to host viable populations (Bregman et al., 2015). The latter is of particular importance in many forests worldwide, as they may suffer from widespread tree die-off events due to climate change, pest outbreaks and wildfires, drastically affecting their productivity and habitat quality (Allen et al., 2010; Hammond et al., 2022). Tree die-off can directly affect the composition of the plant community underneath and the availability of soil nutrients, with potential effects on soil biota (Ávila et al., 2021; Gómez-Aparicio et al., 2022). Fourth, habitat fragmentation increases the distance between habitat patches and diminishes connectivity between populations (Staddon et al., 2010; Tewksbury et al., 2002), which can increase

population sensitivity to environmental change. Soil biota is particularly sensitive to changes in light and soil moisture (e.g. Blankinship et al., 2011; Maestre et al., 2015). Therefore, habitat fragmentation could reduce the mobility of soil biota between habitats if they are far from each other, and the matrix between habitats has contrasting conditions of light or soil moisture (Meloni et al., 2020). Despite our knowledge regarding the response of soil biota to habitat loss and fragmentation is increasing (e.g. Moreno et al., 2013, 2020; Rantalainen et al., 2004, 2006), the relative contribution of the multiple factors associated with habitat quality, size and connectivity, or resource availability and heterogeneity, in explaining the distribution of soil biodiversity still remains poorly understood.

As with many other organisms and drivers of biodiversity loss, the response to habitat fragmentation may not be consistent across trophic levels, and therefore, habitat fragmentation may impair their relative proportion and alter the trophic structure within the soil food web (Wilson et al., 2016). For example, diverse plant litter (an indicator of resource heterogeneity for soil biota) enhances fungal diversity but decreases that of bacteria (Santonja et al., 2017). In addition, light availability and tree defoliation, common consequences of tree die-off, reduce the abundance of detritivores and subsequently that of their predators and pathogens (Homet et al., 2021; Jiménez-Chacón et al., 2018). These contrasting responses of different trophic groups to the multiplicity of environmental changes affecting soil biota can cause trophic mismatches in soil food webs (Domínguez-Begines et al., 2019; Thakur, 2020). The changes in trophic structure reported for climate and habitat quality changes could well extend to habitat fragmentation and may have significant consequences on the functioning of these communities and their ability to resist disturbances (Tyllianakis et al., 2008). For example, habitat degradation, edge effects and isolation negatively affect key mutualisms above-ground, such as pollination and seed dispersal (Liu et al., 2018) and also other biotic interactions, including predation and parasitism (Bascompte et al., 2006). These effects could extend to important functions related to soil biota, such as nutrient cycling, CO₂ storage in the soil or water infiltration (Delgado-Baquerizo et al., 2015, 2020). Studies on the response of soil biota to environmental changes normally focus on global change drivers

other than habitat fragmentation and on a subset of these organisms (e.g. microbes [Delgado-Baquerizo et al., 2016], acari and collembola [George et al., 2017] or arthropods [Jiménez-Chacón et al., 2018; Moreno et al., 2020]). Therefore, we lack a comprehensive understanding on how habitat loss and fragmentation simultaneously affect the multiple trophic groups living below-ground or their trophic structure, which could modulate the impact of soil biodiversity declines on ecosystem functioning.

Here, we quantify species richness of eight trophic groups within soil biota (detritivores, predators, omnivores, parasites, fungivores and herbivores for both fauna and microbes, and mixotrophs and mutualists for microbes) and their trophic structure. We measured the diversity of those groups in 43 habitats (oak trees) with contrasting sizes (from 15 to 280 m²), habitat resource availability, heterogeneity and connectivity in Mediterranean ecosystems from eastern Spain. We aimed to answer the following questions: (1) which are the most important habitat characteristics driving soil biodiversity?; (2) how do different soil trophic groups respond to environmental changes related to habitat loss and fragmentation? and (3) how do changes in habitat quality and resource availability (such as those induced by major tree die-off events) affects soil biota and its trophic relationships?

2 | MATERIALS AND METHODS

2.1 | Study area

We carried out our study in a 10-ha area in southeastern Spain (Parque Natural del Carrascal de la Font Roja, Alicante, 38°39'25"N, 0°33'12"W, Figure S1). This area is characterized by a dry Mesomediterranean climate, with an average annual temperature of 11°C and mean precipitation of 400 mm per year (Pérez Cueva, 1994). Soils are shallow, dominated by limestones, and with numerous rock outcrops. Vegetation is an open woodland, with scattered patches of holm oak *Quercus rotundifolia* within a matrix of open vegetation dominated by dwarf shrubs and tussock grasses, such as *Cistus albidus*, *Salvia rosmarinus* and *Macrochloa tenacissima*. Open and oak microhabitats show very contrasting characteristics (light availability, vertical structure, plant productivity and composition underneath or soil fertility). These contrasting characteristics can be regarded as a small-scale equivalent to those differences found between forest patches and more open land uses at the landscape scale (Bascompte & Rodríguez, 2001; Maestre & Cortina, 2005; Moreno et al., 2020), which allowed us to perform a detailed sampling of their soil biota and habitat characteristics. Abandoned croplands in the Mediterranean Basin are being encroached by forests (mostly *Pinus* spp.; Otero et al., 2015). However, our study area is not an abandoned cropland, but rather a long-managed *Q. rotundifolia* open woodland. In this area and over the last decades, many trees have been lost, either cut down for charcoal production (Martínez-Fernández et al., 2015) or due to extensive tree die-off episodes caused by extreme drought events (de Luis et al., 2010; Gazol et al., 2022), such

as the one in 2014 (García de la Serrana et al., 2015). In addition, new recruitments are limited both by overgrazing of feral ungulates in the area (*Ammotragus lervia*, *Ovis orientalis*; Font Roja NP staff, pers. comm.) and the drier climate experienced over the last decades (de Luis et al., 2010). The legacy of all these events has generated the patchy open woodland present in our study area today (Figure S1), and therefore, it may well represent the effects of habitat loss in Mediterranean oak open woodlands.

2.2 | Habitat size, resource availability, heterogeneity and connectivity

In June 2018, we selected 43 *Q. rotundifolia* trees with the aim of maximizing variation in their size, resource availability, heterogeneity and degree of isolation. We sampled five additional inter-spaces to compare their soil community with those found in vegetated areas.

At each tree, we characterized 12 habitat properties related to its size (canopy area), connectivity, and resource availability and heterogeneity (full details in Table S2). We estimated habitat size as the canopy area of targeted *Q. rotundifolia* trees, using aerial images (see below).

We measured resource quality and availability in situ within each tree and complemented these measures with information obtained from aerial images (see below). In situ measurements were depth of litter layer, soil carbon content, total number of understorey plant species and their community-weighted mean of the specific leaf area (SLA; a proxy of litter quality as it is related to plant resource strategy, leaf N and litter decomposability; García-Palacios et al., 2013). These in situ measurements are related not only to the amount, diversity and quality of organic inputs into the soil but also to the environmental conditions and habitat available for soil organisms (Asner et al., 2003; Delgado-Baquerizo et al., 2018; García-Palacios et al., 2013; Santonja et al., 2017; Tedersoo et al., 2014; Van den Hoogen et al., 2019).

To estimate plant richness and litter depth, in each of the 43 oak trees, we sampled four 0.5 m × 0.5 m quadrats. At each quadrat, we noted the presence and abundance of each plant species. We also measured litter depth qualitatively, using the soil surface analysis (Tongway & Hindley, 2004), which estimates litter cover, its depth and degree of incorporation into the soil.

We obtained SLA values for our species from TRY (Kattge et al., 2011), estimating its community-weighted mean by using the species by abundance matrix of each 0.5 m × 0.5 m quadrat. At each of these quadrats, we sampled a soil core (5 cm × 5 cm × 10 cm deep). One composite subsample of this soil was immediately frozen for DNA analysis (see below), and another part was air-dried and sieved at 2 mm to estimate soil organic carbon content by wet digestion (Walkley & Black, 1934) and pH (1:5 soil: water dissolution). To obtain a tree-level metric of each of the variables measured in the field and the laboratory, we calculated the mean across the four subsamples taken per tree.

We also considered tree status (affected by a widespread die-off in 2014 [20 trees sampled] or healthy [23 trees]) as a measure of habitat quality. Holm oak's die-off is caused by the oomycete *Phytophthora cinnamomi* or other plant pathogens (e.g. *Pythium* spp.), acting in tandem with temperature and soil moisture changes (Gómez-Aparicio et al., 2012; Hardham & Blackman, 2018; Jiménez-Chacón et al., 2018; Romero et al., 2007). Oak's die-off involves the loss of most of the leaves in the canopy, resulting in a short-term large contribution of carbon inputs into the soil and strong differences in the micro-environment underneath (changes in light availability and soil moisture). These changes affect soil organisms' diversity, abundance and trophic structure (nematodes; Domínguez-Begines et al., 2019; mesofauna: Homet et al., 2019; microbes: Gómez-Aparicio et al., 2022). Whether or not a given oak tree had been affected by a die-off event was evident in the field, due to the smaller and thicker leaves, brownier colour and the lower productivity characterizing these oaks. It was also related with significant lower productivity and a (non-significant) trend towards lower soil organic carbon and SLA (Table S1).

We used low-altitude flights (4–5 m) with an RPA (Remotely Piloted Aircraft) multirotor (drone) equipped with 1" sensors to perform a high-resolution digital elevation model. From this digital elevation model, we extracted three measures related to *habitat size*: (i) canopy area of each tree (in m²), *habitat connectivity*, (ii) the size of the area potentially contributing run-off water to the tree sampled (maximum and mean flow length, a measurement of hydraulic connectivity), (iii) distance to the six nearest *Quercus* trees and (iv) proportion of the area surrounding [10-m diameter] occupied by other oak trees (the latter two related to spatial connectivity). The drone was also equipped with 16MP (Megapixel) red and infra-red sensors to measure tree productivity (NDVI, one of the measures of resource availability we used), and its heterogeneity (standard deviation in NDVI).

2.3 | Sampling of soil biota

2.3.1 | Soil fauna

To sample soil fauna, we collected two 25 × 25 cm samples per tree (and the five inter-spaces), including all the litter and the first two centimetres of soil (adapted to ISO 23611-5 (ISO 2011)). Both samples were mixed into a single composite sample per tree. We used the Berlese-Tullgren funnel method (Berlese, 1905; Tullgren, 1918) to extract the macro- (body size >2 mm) and meso-fauna (body size between 2 and 0.5 mm) during 3 days (hereafter we refer to all these organisms as 'fauna', for simplicity). Since soil fauna of Mediterranean dry soils proved very resistant to light and soil dryness, after 3 days in the funnel, we placed the samples in trays to collect the remaining fauna, mainly macrofauna, with forceps. We identified specimens collected to the finest taxonomic level possible and classified them in six trophic groups: herbivores, detritivores,

parasites, fungivores, predators and omnivores. We classified faunal and microbial (see below) trophic groups using available databases and manuals (e.g. fungi [Nguyen et al., 2016], archaea and bacteria [Whitman, 2015], protists [Archibald et al., 2017]; further details in <https://figshare.com/s/6db815fe76fd50ce08f3>). It must be noted, however, that available information for some of these organisms (especially for bacteria or protists) is limited and did not allow us to finely classify each organism within a trophic group. If we could not find the trophic group for the taxonomic level considered we went up in the taxonomical order (genus, family, or even order, in some cases), so there are generalized assumptions of some organisms that should be considered.

2.3.2 | Soil microbes

We estimated soil microbes using DNA analyses. We extracted soil DNA from 0.25 g of defrosted soil samples using the DNeasy PowerSoil Kit (QIAGEN) and sequenced it using the Illumina MiSeq platform to characterize the soil bacterial (16S rRNA gene), eukaryotic (18S rRNA gene) and fungal (ITS2) regions (see full methods in [Supporting Information S1](#)). Our dataset included a total of 2857, 3386 and 7112 OTUs for the 16S rRNA gene, 18S rRNA gene and ITS amplicons, respectively. We classified microbes into seven trophic groups: detritivores, parasites, mutualists, herbivores, predators, fungivores, mixotrophs and omnivores (see further details at <https://figshare.com/s/6db815fe76fd50ce08f3>). We established these trophic groups to be similar as those used for fauna. For example, we grouped pathogens of animals or plants into parasites and saprotroph organisms into detritivores. We could assign a trophic group for 5839 of the microbial OTUs identified (44%), which were the ones considered in our analyses.

2.3.3 | Community assessment

We estimated species richness for every trophic group for each tree, which we used for further analysis. We also calculated overall community response, using the Multidiversity Index, combining changes across all trophic groups (fauna and microbes) for each tree (average of standardized scores of richness across the 12 trophic groups considered; Allan et al., 2014). High values of the multidiversity index mean high diversity across trophic groups (Table 1). In addition, to obtain a metric of how equitable the distribution of species between trophic groups was, we calculated the Shannon evenness index, but using richness per trophic group as 'abundance' and each trophic group as a 'species' (see Crotty et al., 2018 for a similar approach). High values of the evenness index mean that the community is balanced regarding the distribution of species across trophic groups. Due to the contrasting methodologies and large differences in our richness estimates, we decided to analyse the faunal and microbial data separately to calculate evenness indices.

TABLE 1 Spearman's correlations of the richness of each trophic group with Multidiversity Index (average of standardized scores of richness of the trophic groups). Richness range of each trophic group, including maximum and minimum of species across all vegetated patches (plant soil) and bare soil samples.

Trophic groups	Spearman's correlations with multidiversity	Richness range					
		Fauna			Microbes		
		Total richness	Max. richness	Min. richness	Total richness	Max. richness	Min. richness
Detritivores	0.81	39	18	0	2269	614	393
Fungivores	0.32	5	2	0	3	2	0
Herbivores	0.58	26	5	0	8	2	0
Mixotrophs	0.43	—	—	—	185	55	22
Mutualists	0.70	—	—	—	1027	221	109
Omnivores	0.63	19	5	0	81	19	4
Parasites	0.77	8	7	0	638	136	93
Predators	0.84	46	15	0	991	231	87
Plant soil (n=43)		143	52	0	5202	1173	740
Bare soil (n=5) (including all trophic groups)		26	7	0	3806	1280	836

2.4 | Statistical analysis

To find the main drivers of soil microbial and faunal diversity, we used generalized linear models taking as response variables the richness (number of species for fauna and microbes) of each of the trophic groups considered. We also applied the same analyses to find the main drivers of trophic structure (measured as evenness across groups for fauna and microbes) and overall community diversity (measured with the Multidiversity index including fauna and microbes) (totaling 15 response variables).

To perform our analyses, we classified our predictors into three groups: (1) habitat size (tree area, in m²), (2) habitat resource availability and heterogeneity: soil organic carbon content, SLA, litter depth (LFA infiltration), NDVI (mean and standard deviation) and understorey plant richness and (3) habitat connectivity: hydraulic connectivity, distance to the nearest six trees and similar habitat surrounding (surrounding area occupied by oak trees; Table S2). To ease the interpretation of our connectivity metrics, the distance to the six nearest trees was multiplied by -1, so higher values of this predictor indicate greater connectivity. Additionally, we log-transformed all measures representing distances or surface (habitat size, similar habitat surrounding and hydraulic connectivity) to approximate normality in their distributions. We also included soil pH as an additional predictor in our models, due to its importance as a driver of soil biodiversity in global studies (Delgado-Baquerizo et al., 2018; Tedersoo et al., 2014; Van den Hoogen et al., 2019). We used richness instead of abundance with fauna because both are highly correlated ($\rho=0.88$), and results were more comparable with microbes when using richness. The tree status (die-off affected vs. healthy) was not included as an additional predictor in these analyses, as it was highly related to some of the other predictors considered (see next paragraph and Table S1), and the latter were continuous rather than categorical.

To select which predictors to use, we first calculated Spearman correlations between predictors to dismiss those providing redundant information (Figure S2). Considering that richness data usually exhibits zero-bounded distributions, we then evaluated the type of linear model that best fitted the distribution of each of our response variables (using either Gaussian, negative binomial or Poisson distributions). To do that, we used the function 'fitdist' from 'fitdistrplus' package selecting the best distribution between Gaussian, negative binomial or Poisson in each case, based on the lowest value of AIC. Due to our relatively small sample size, we did not evaluate potential interactions between all our predictors, but rather focus on their individual effects and habitat size \times resource availability and habitat size \times connectivity interactions. Thus, we build a model which considered eight interactions between habitat size and the rest of variables:

$$\text{Richness}_i \times \text{size} \times (6\text{NT} + \text{HC} + \text{HS}) + \text{size} \\ \times (\text{OC} + \text{PLR} + \text{NDVI} + \text{SLA} + \text{LFA}) + \text{pH},$$

where Richness_{*i*} is the richness of each trophic group/trophic structure or Multidiversity index analysed, size is the tree canopy area (in m²), 6NT is the inverse of the average distance to the six nearest trees (in m), HC is the hydraulic connectivity (in m), HS is the proportion of similar habitat surrounding (in %), OC is the soil organic carbon content (in %), PLR is understorey plant richness, NDVI is tree productivity, SLA is the specific leaf area and LFA is our qualitative measurement of litter depth. From this initial model, we performed model simplification using the function 'dredge' from MuMIn package to obtain those with the lowest AIC. The standardized effects of this single more parsimonious model selected for each response variable are the ones provided as results in Figure 1. Data on microbial herbivores and fungivores could not be analysed due to the generally low richness found for these groups.

In addition to these analyses, we also evaluated the effect of tree die-off on trophic structure, comparing such structure in trees

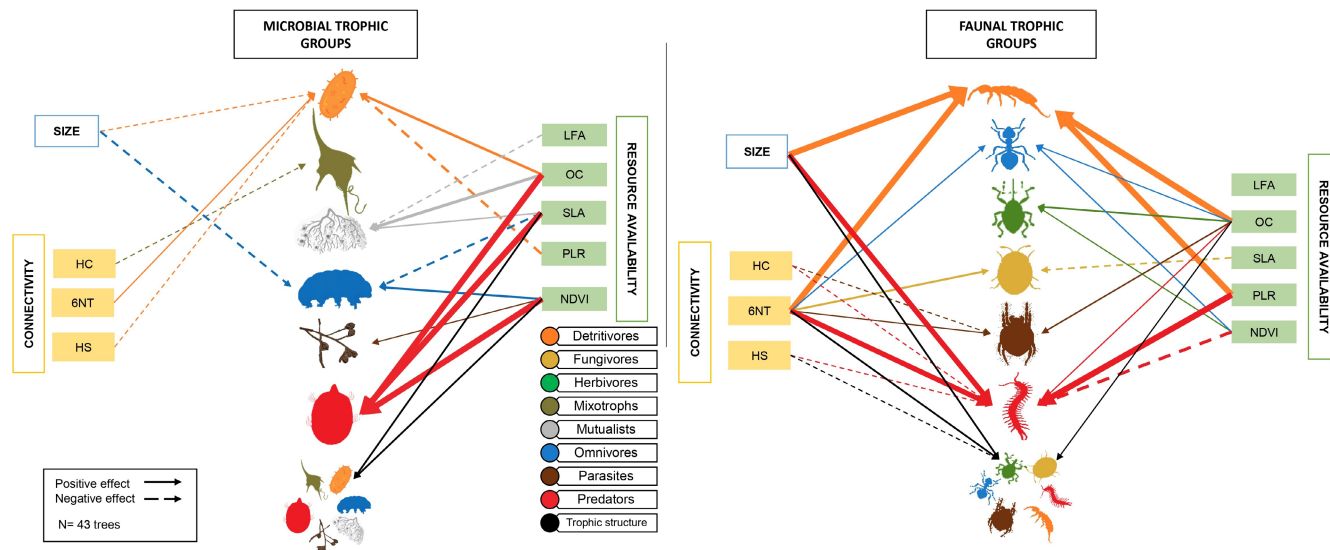


FIGURE 1 Summary of the linear models evaluating changes in the richness of microbial (microbes) and faunal (fauna) trophic groups in the 43 trees studied. Continuous and dashed lines indicate positive and negative effects, respectively. The model for each trophic group included holm oak's *Quercus rotundifolia* canopy area (in m²) [SIZE], resource availability (soil organic carbon [OC], tree productivity [NDVI], understorey plant richness [PLR], specific leaf area [SLA], litter depth and decomposition [LFA]) and connectivity (hydraulic connectivity [HC], distance to the nearest oak trees [6NT] and proportion of landscape covered by oaks [HS]). The size of the arrow is proportional to the effect of each predictor (full results in Table S3). Trophic structure = evenness index using species richness per trophic group as 'abundance' and each trophic group as 'species'.

that had suffered die-off versus those that were healthy. Die-off was associated to lower tree productivity, and a (non-significant) trend towards lower soil carbon contents and more recalcitrant litter (Table S1) and has been previously shown to affect soil fauna (Jiménez-Chacón et al., 2018) and trophic structure in nematodes (Domínguez-Begines et al., 2019). Hence, separation of our database into healthy ($N=23$) and die-off ($N=20$) affected trees allowed us a simple but comprehensive comparison of the effect of habitat changes on soil biota's trophic structure, complementing the information provided by the multidiversity and evenness indices and the richness of the trophic groups separately. To evaluate changes in trophic structure with die-off, we built correlational networks using Spearman's correlations between each pair of trophic groups in die-off affected versus healthy trees. To evaluate whether die-off caused significant changes in overall network connectance and on the strength of each pairwise relationship, we bootstrapped the data with replacement, building 100 networks, and estimated from each of them the differences in each pairwise relationship, as well as the overall connectance between healthy versus die-off affected trees, using Mann–Whitney tests. Overall connectance was calculated (following Felipe-Lucia et al., 2020) including both positive and negative relationships. Connectance was estimated as the weighted average of the strength from all possible links in the network, following this formula ($\text{Connectance} = \frac{\sum \text{pcc}}{n \times (n-1) / 2}$; where pcc are the absolute correlation coefficients and n is the number of nodes of the network [6 for both fauna and microbes]). We used R version 4.2.1 (R Core Team, 2022) and RStudio 2022.12.0.353 (Posit Team, 2022) to perform all the analyses. Fieldwork was performed in a protected area (Font Roja Natura Park) with permission granted to do so from

the Conselleria d'agricultura, desenvolupament rural, emergència climàtica i transició ecològica (Generalitat Valenciana, Spain).

3 | RESULTS

In our study, detritivores were the most species-rich groups; mites and springtails for fauna (e.g. *Tectocephus* spp., *Oribatulidae* spp., *Onychiuridae* spp. or *Entomobryidae*) and bacteria for microbes (*Solibacteres* [*Acidobacteria*], *Actinobacteria* and *Thermoleophilia* [*Actinobacteria*], *Gemmatimonadales*, *Tepidisphaerales* [*Planctomycetes*] or *Burkholderiaceae* [*Proteobacteria*]). Detritivore (*Cladophialophora* and *Penicillium*) and parasitic (*Phialemonium*) fungi, together with predator protists (*Litostomatea* and *Variosea*) were also very diverse. Indeed, predators were the second most species-rich trophic group in both the faunal and microbial communities (Table 1). We found a wide range of microbial richness in detritivores and predators, almost 200 species difference between the richest and the poorest trees (Table 1). Mutualists also represented an important part of the microbial richness, with fungivores being the most species-poor group.

In general, our predictors explained between 57% (faunal predators) and 8% (microbial parasites) of the variation in species richness of the soil organisms studied, which shows a large variation in their response to the environmental changes related to habitat loss and fragmentation (Figure 1; Table S3). Microbial and faunal detritivores were among the most responsive to our predictors ($R^2=0.53$ and 0.45 , respectively), together with microbial mutualists and faunal predators ($R^2=0.57$ in both cases; Table S3).

Seven of the 12 microbial and faunal groups evaluated responded generally positively to organic carbon, which was the predictor most frequently selected in the most parsimonious models overall (Figure 1; Table S3; Figure S3). Other predictors related to resource availability (particularly NDVI but also plant richness and SLA) also had strong and positive effects on many of the trophic groups evaluated. In addition to resource availability, habitat connectivity also had a remarkable importance for faunal groups, with contrasting positive and negative effects depending on the trophic groups. Generally, the inverse of the distance of the six nearest trees increased the richness of different trophic groups, whereas the amount of similar habitat (oak trees) in the area nearby reduced it (Table S3).

Overall trophic structure (evenness index) for both microbes and fauna also responded to habitat characteristics ($R^2=0.20$ and 0.38 , respectively). More specifically, microbial trophic structure responded to resources availability whereas faunal trophic structure responded to a more complex set of variables including size, connectivity and resource availability (Table S3). We found significant interactions between habitat size and connectivity in determining microbial trophic structure and multidiversity, with bigger habitats less dependent on connectivity to maintain balanced soil faunal trophic structures (Figures 1 and 2; Table S3). Overall soil biodiversity (multidiversity index including fauna and microbes) reflected the idiosyncratic responses of the different trophic groups and was the response variable affected by the largest set of predictors. Multidiversity increased with resource availability and heterogeneity (soil organic carbon, tree productivity [NDVI] and understorey plant richness) and was also influenced by habitat size, connectivity and interactions between these predictors (Figure 2; Table S3). Larger habitats were generally less dependent on connectivity (negative habitat size \times distance to six nearest trees interactions) or resource availability (negative habitat size \times plant richness interactions) to keep diverse soil communities.

For both microbes and fauna, links between trophic groups shifted to weaker and less positive (or even negative) in trees affected by die-off regarding healthy ones. These changes were more pronounced in microbes than in faunal groups (Figure 3). We found significant differences between the correlation among pairs of trophic groups based on tree status. Most (14 of the 15) links between trophic groups studied for either fauna or microbes significantly weakened under die-off affected trees (regarding those observed in healthy ones; Figure S4). Overall network connectance reflected those changes in pairwise relationships, as it decreased in both cases when trees were affected by die-off (Table S4).

4 | DISCUSSION

4.1 | Habitat resource availability importantly determines soil biodiversity, followed by habitat connectivity

We comprehensively evaluated the response of soil biodiversity to habitat loss and fragmentation, including most trophic groups in the

soil, and many of the environmental changes driven by habitat loss (changes in habitat size, resource availability and heterogeneity or habitat connectivity). Consistent with studies in other organisms (e.g. birds or mammals in forest fragments [Berg, 1997; Gardiner et al., 2018] or fauna in urban greenspaces [Garden et al., 2006]), habitat resource availability was generally the strongest predictor (strongest and most frequently found effects [Table S3]) of soil biodiversity. In particular, soil C was the predictor most consistently selected in our models, enhancing biodiversity across soil trophic groups and trophic structure, followed by tree productivity (NDVI; see also Ren et al., 2021). The pervasive role of soil C enhancing soil biodiversity is consistent with previous global studies on mycorrhiza (Tedersoo et al., 2014), bacteria (Delgado-Baquerizo et al., 2018) or nematodes (Van den Hoogen et al., 2019) and show that macro-scale drivers of soil biodiversity are matched by those driving biodiversity changes at smaller scales.

In addition to soil C, we found many significant effects of other predictors related to resource availability and heterogeneity (SLA, plant richness, litter depth), although these effects were generally weaker and less consistent than those found for soil C (Figure S3). Consistently with previous studies (Rantalainen et al., 2004; Ren et al., 2021), the diversity of many of the trophic groups studied increased with tree productivity (as measured with the NDVI) or leaf quality (SLA), which emphasizes the importance of plant-mediated processes in determining soil biodiversity (Meloni et al., 2020; Wardle et al., 2004). Despite idiosyncratic and inconsistent results across the different trophic groups studied, understorey plant richness was a strong and positive driver of soil multidiversity overall, which agrees with experimental studies showing positive bottom-up plant diversity effects on a wide range of different groups of organisms including primary producers, first- and second-order consumers (Scherber et al., 2010).

Next to habitat resource availability, changes in connectivity were the second most important driver of changes in soil organism diversity, particularly for faunal groups but also for the overall microbial and faunal trophic structure (Figure 2a; Table S3). Habitat fragmentation impacts important trophic relationships, such as predation and parasitism, which can lead to biodiversity loss above-ground (Bascompte et al., 2006). Focusing on a much smaller scale and on below-ground diversity, our results show that faunal predators preferred to forage on more isolated trees, perhaps because this lower connectivity also benefit their prey (particularly in resource-rich habitats; see interactions for detritivores in Table S3) or prevent them from escaping (Hawn et al., 2018). These results are at odds with previous findings showing positive effects of corridors or more connectivity on detritivores (Rantalainen et al., 2006) and calls for more studies evaluating the response of soil biota to habitat loss and fragmentation. Our study shows that it is particularly important to consider changes in connectivity together with associated changes in resource availability, quality and habitat size, as these may interact with each other in determining soil biodiversity (Table S3; see also Rantalainen et al., 2004).

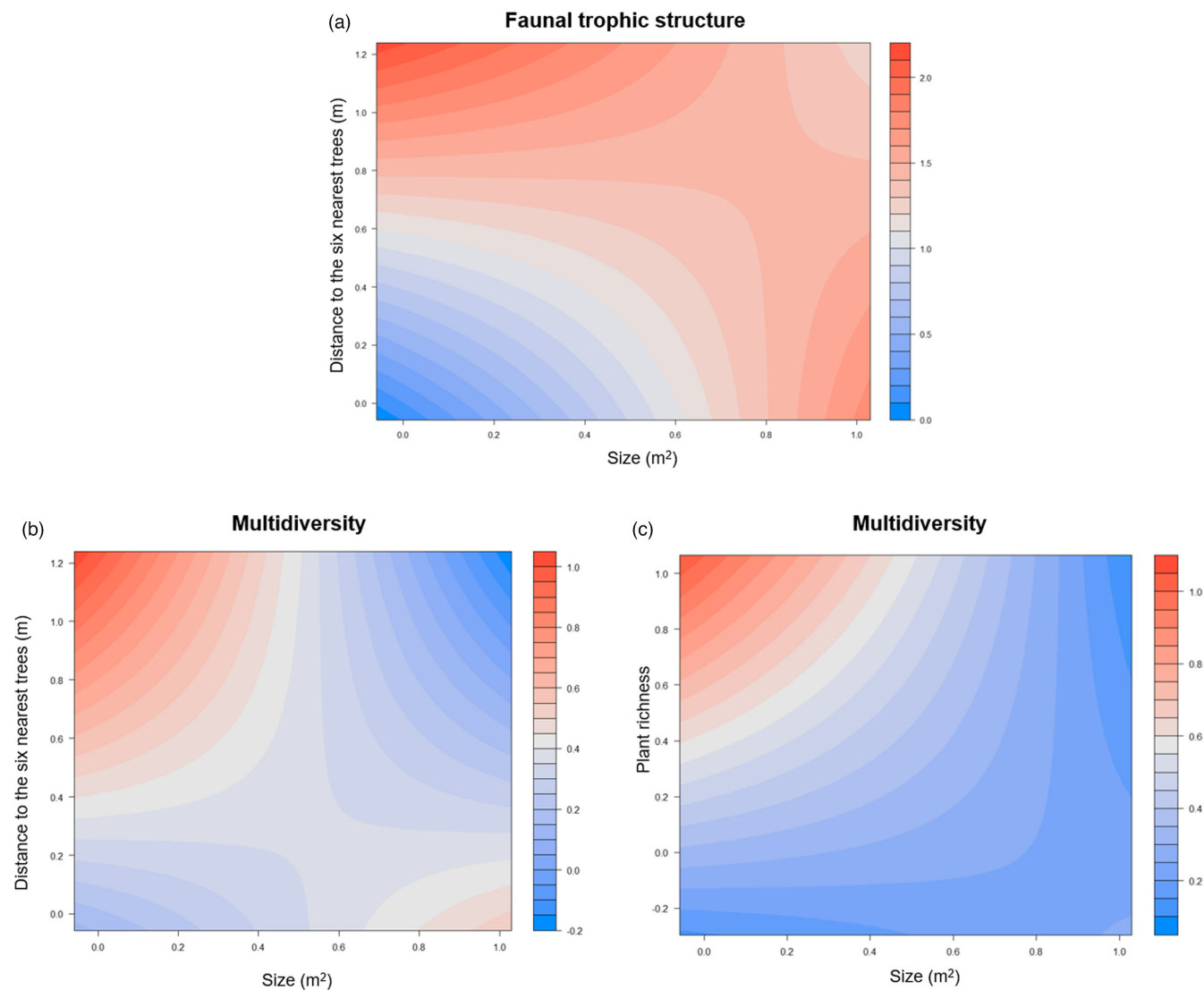
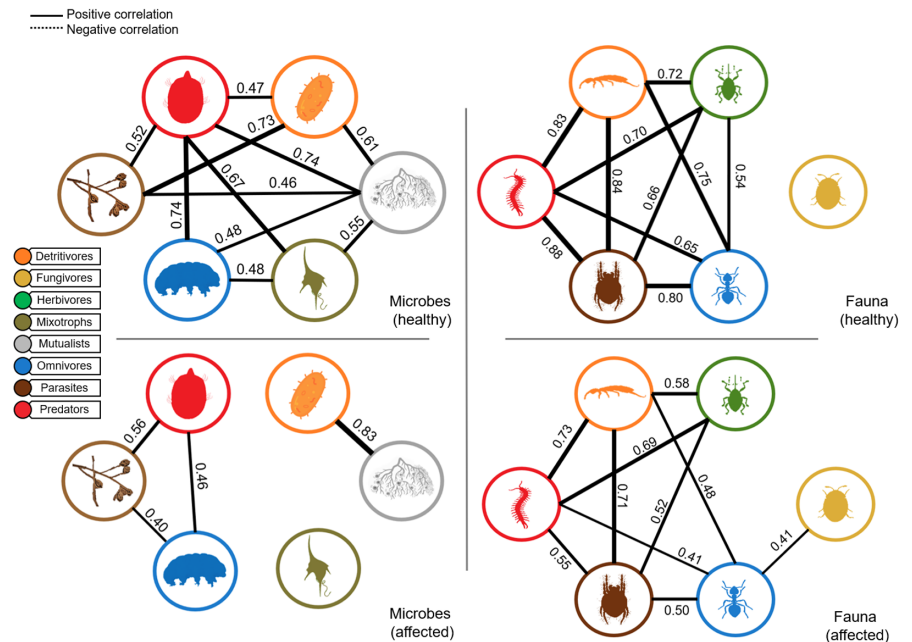


FIGURE 2 Contour plots illustrating the significant interactions between different predictors related to habitat characteristics on faunal trophic structure (a) and soil multidiversity (b AND c; full details in Table S3). All variables are standardized between 0 and 1 (values can be higher if extrapolated outside our data range). Habitat size: *Quercus rotundifolia* canopy area (in m²), Plant richness: understorey plant richness beneath each oak tree, Distance to the six nearest trees: mean distance to the six nearest oak trees, in m. The red/blue scale shows high/low values of faunal trophic structure (a) and soil multidiversity (b and c; all unitless).

The overall response of trophic structure (the evenness indices) and multidiversity reflected the influence of those habitat characteristics affecting the diversities of individual trophic groups. Indeed, soil multitrophic evenness and diversity responded to a more complex set of predictors than most trophic groups in isolation, including habitat size, connectivity and resource availability. The latter suggest that changes in trophic structure can be more difficult to predict than changes in the diversity of individual groups, as the former integrates all the idiosyncratic responses of the latter. As other summarizing metrics (e.g. those used for multiple ecosystem functions; Manning et al., 2018), our metric of trophic structure seems to reflect well the multiplicity of environmental drivers affecting different organisms in complex communities (see also Domínguez-Begines et al., 2019). Soil organic carbon increased the diversity of some

individual groups (e.g. detritivores) more than others (herbivores or omnivores), as found elsewhere in the response of contrasting faunal groups to environmental changes (Domínguez-Begines et al., 2019; Thakur et al., 2015). Despite these group-specific responses, soil organic carbon generally increased faunal multitrophic evenness, similar to results found for individual groups. Nevertheless, in some cases, such group-specific responses can lead to disruptions in trophic structure, as found for tree defoliation on nematode trophic structure, unpaired due to the increase in the abundance of lower trophic levels but the decrease of higher levels (Domínguez-Begines et al., 2019). Our results and those of previous literature clearly illustrate the importance of studying the response of multiple trophic levels to better understand how soil biota is influenced by environmental changes. Depending on the degree of coupling between trophic

FIGURE 3 Trophic networks in holm oak's *Quercus rotundifolia* trees that were healthy or affected by die-off (affected). Networks are separated by soil microbes (left) and fauna (right). Links between trophic groups represent Spearman's correlations between the richness of any given pair of trophic groups, the size of the arrow is proportional to the correlation between groups. All potential pairwise correlations were tested, but we only show those that were significant for clarity.



group-specific responses, environmental changes can disrupt soil food webs if these go in opposite directions or reinforce them if such responses are more aligned.

4.2 | Habitat size modulates the effects of plant-mediated and connectivity attributes on soil biodiversity

The relatively weak and inconsistent effects we found for connectivity and plant-mediated mechanisms on soil biodiversity could, at least partly, be justified by the strong interactions between those predictors and habitat size. Large habitats commonly host larger and more diverse communities (Haddad et al., 2015), similar to what we found for soil organisms. Hence, in large trees, soil biodiversity might be less dependent on the heterogeneity or amount of plant inputs into the soil, or the connectivity with neighbouring trees. The latter is supported by the significant interactions between habitat size and other predictors that we found for many groups (faunal detritivores, predators and microbial detritivores and omnivores) and their overall trophic structure and multidiversity (Figure 2; Table S3). These results warn about the sensitivity of small habitats to further disturbances, which could render substantial biodiversity loss, extending the 'extinction debt' frequently associated to habitat fragmentation (Bascompte & Sole, 1996) to below-ground organisms. In general, all the disturbances associated to changes in both the amount and configuration of habitat, like decreased habitat size, increased habitat isolation and increased edge area, are reported to cause generalizable responses at the population and community levels (Moreno et al., 2020; Wilson et al., 2016). In our case, we found that these effects are not independent and that declines in habitat quality and heterogeneity can have more negative effects on soil biodiversity in habitats of small size than in larger habitats.

4.3 | Weakened correlations and unbalanced trophic structures in response to tree die-off

Correlation networks reflected well the trophic mismatches caused by the contrasting response of each individual trophic group to environmental changes. These trophic networks became less connected with tree die-off, with weaker and less positive relationships between trophic groups (Figure 3). The latter supports previous findings reporting simplified nematode trophic networks underneath *Quercus* spp. suffering die-off (Domínguez-Begines et al., 2019). Previous reports on decreasing complexity, connectivity and modularity in networks associated to declining forests associate these declines to the dampening of cooperative and trophic interactions as response to the increase in resource availability following tree die-off (Gómez-Aparicio et al., 2022). However, we found a greater resource availability in healthy trees than in those affected by die-off (Table S1). This conflicting result suggests that the enhanced nutrient availability (and their associated soil network changes) that Gómez-Aparicio et al. (2022) found during tree die-off may be only temporary, shifting after some years towards less productive habitats, as we found, but still maintaining less connected soil networks.

An additional explanation to the lower connectance found in trees suffering die-off lays in the idiosyncratic responses of different trophic groups to environmental changes. The latter generates winners and losers in response to any given change, including tree die-off (Holden & Treseder, 2013; Lloret et al., 2015), and could explain the trophic mismatches we found if some groups increased their diversity whereas others declined in response to the habitat changes generated by die-off. In our case, declines in network connectivity were stronger for fungivores (faunal ones; Figure 3); whereas those involving parasites and predators, and mutualists and detritivores, were far more stable. Perhaps, fungivores are more sensitive to environmental changes due to their low richness

levels in our study area (Table 1), which could render more sensitive and less stable communities (Hagen et al., 2012). Another possibility could be that fungivores are deterred by fungal secondary metabolites (Rangel et al., 2021), and these could be more abundantly synthesized by those species increasing their presence in oaks suffering die-off. Regardless of the particular mechanism involved, our study adds to the piling evidence of altered network structures following habitat degradation, including the weakened and re-organized relationships of the diversity of multiple organisms and the functions they provide following land-use intensification (Felipe-Lucia et al., 2020) or less connected and stable networks in soil bacterial communities or above-ground parasitoids following habitat degradation (Ren et al., 2021; Tylianakis et al., 2007). These changes could produce soil communities more sensitive to further disturbances and the loss of specialized interactions and the functions they provide.

5 | CONCLUSIONS

Our comprehensive study on the effects of habitat loss and fragmentation on soil biodiversity and trophic structure revealed that habitat resource availability (championed by soil organic C and tree productivity) are the strongest predictors of soil biodiversity, although their positive effects dampen under larger or more connected landscapes. The idiosyncratic responses of individual trophic levels to environmental changes led to more weakly connected trophic structures following habitat degradation after tree die-off. Our results illustrate the importance of analysing the responses of different soil organisms simultaneously, together with the multiple environmental changes associated to habitat fragmentation, to better understand the consequences of widespread habitat degradation and tree die-off.

AUTHOR CONTRIBUTIONS

Santiago Soliveres conceived the idea with input from Andreu Bonet. Estrella Pastor and Santiago Soliveres conducted fieldwork and soil physical–chemical analyses. Jimmy Morales-Márquez identified soil fauna, and Paula Lopezosa, Juntao Wang, Brajesh K. Singh and Manuel Delgado-Baquerizo extracted and sequenced soil DNA. Paula Lopezosa curated and analysed the data, with assistance of Miguel Berdugo and Santiago Soliveres. Paula Lopezosa wrote the first draft of the manuscript, and all authors contributed revisions.

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CONFLICT OF INTEREST STATEMENT

The author(s) declare no conflict of interest. Manuel Delgado-Baquerizo is an Associate Editor of *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper.

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DATA AVAILABILITY STATEMENT

Data are available on Figshare: <https://doi.org/10.6084/m9.figshare.20750209> (Lopezosa, 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Aerial image from the study site.

Supplementary Material 1: Methodological details regarding soil DNA analyses.

Table S1: Results of ANOVA testing the effect of tree status (affected or healthy) on parameters associated to habitat quality.

Table S2: Summary and methodological details of all measured variables.

Figure S2: Spearman's correlation matrix of all measured variables.

Table S3: Results of the simplified linear models for our 15 response variables.

Figure S3: Importance relative of each predictor for trophic groups.

Figure S4: Boxplots showing the distribution of correlation coefficients between every pair of trophic groups of fauna and microbes.

Table S4: Overall network metrics.

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