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RESEARCH ARTICLE

Cascading spatial and trophic impacts of oak decline on the soil food web

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Abstract

1. Tree defoliation and mortality have considerably increased world-wide during the last decades due to global change drivers such as increasing drought or invasive pests and pathogens. However, the effects of this tree decline on soil food webs are poorly understood.
2. In this study, we evaluated the impacts of *Quercus suber* decline on soil food webs of Mediterranean mixed forests invaded by the exotic oomycete pathogen *Phytophthora cinnamomi*, using soil nematodes as bioindicator taxa. We used a spatially explicit neighbourhood approach to predict the characteristics of the nematode community (diversity, trophic structure, and several indices indicative of soil food web conditions) as a function of the characteristics of the tree and shrub community (species composition, size, and health status).
3. Our results indicate that the process of defoliation and mortality of *Q. suber* caused significant alterations in the nematode trophic structure increasing the abundance of lower trophic levels (bacterivores, fungivores, and herbivores) and decreasing the abundance of higher levels (predators and omnivores). Furthermore, *Q. suber* decline altered the functional composition of soil communities, producing a setback of the ecological succession in the soil food web to an earlier stage (decrease in the maturity index and increase in the plant parasitic index), simplified soil food webs (decrease in the structure index), and shifts in the predominant decomposition channel (increase in the fungivores/bacterivores ratio).
4. We also detected contrasting characteristics of the nematode community in neighbourhoods dominated by coexisting woody species, which suggests potential for long-term indirect effects on soil food webs due to the substitution of *Q. suber* by non-declining species.
5. **Synthesis.** Our study provides novel results that show the major impacts that ongoing health deterioration of dominant tree species can have on the structure and composition of soil food webs in forest systems invaded by exotic pathogens, with cascading consequences for soil biogeochemical processes in both the short- and long term.

KEYWORDS

bioindicators, neighbourhood models, *Phytophthora cinnamomi*, plant–soil interactions, *Quercus suber*, soil food web, soil nematodes, soil-borne pathogens, spatial patterns, tree mortality

1 | INTRODUCTION

Tree defoliation and mortality have considerably increased worldwide during the last decades due to global-scale environmental changes, such as more intense and frequent droughts, higher temperatures, and their interaction with invasive pests and pathogens (Allen, Breshears, & McDowell, 2015; Anderegg et al., 2015; Kautz, Meddens, Hall, & Arneth, 2017). Trees are fundamental components of forest communities that provide habitat and resources for many other species both above- and below-ground (Baldrian, 2016; Mitchell et al., 2007). More specifically, tree species strongly influence the soil community by modifying soil environmental conditions (i.e., temperature, water content) and generating root exudates and litter inputs (Prescott & Grayston, 2013; Urbanová, Šnajdr, & Baldrian, 2015). Therefore, changes in the abundance of a particular tree species could lead to significant modifications of soil food webs with cascading effects on the functioning of the whole ecosystem (Van der Heijden, Bardgett, & van Straalen, 2008; Wagg, Bender, Widmer, & van der Heijden, 2014). Despite its relevance, only a few recent studies have explored the effects of tree dieback on the diversity and composition of soil communities, mainly focussing on bacteria (Curiel Yuste et al., 2012; Ferrenberg et al., 2014; Mikkelsen, Lozupone, & Sharp, 2016) and fungi (Beule, Grüning, Karlovsky, & I-M-Arnold, 2017; Lancellotti & Franceschini, 2013; Štursová et al., 2014). Further research is still needed to better understand the role of increasing tree mortality rates as structuring forces of soil food webs.

The impacts of tree dieback on soil diversity and function can have complex spatiotemporal patterns when defoliation and mortality are species specific and affect a subset of the coexisting woody species in the forest community. For example, it has been shown that species-specific tree decline in mixed forests alters the spatial pattern of soil organisms directly associated to tree roots, such as soil-borne pathogens (Gómez-Aparicio et al., 2012) or ectomycorrhizal fungi (Ibáñez et al., 2015a), likely due to changes in host root availability and the abiotic environment. From a temporal perspective, species-specific tree decline can cause short-term direct impacts on soil biodiversity and function derived from the alteration of resource inputs (e.g., litterfall, root exudates) and outputs (e.g., nutrient leaching) associated to the mortality of individual trees, as well as long-term indirect impacts derived from subsequent species replacement (Ávila, Gallardo, Ibáñez, & Gómez-Aparicio, 2016; Curiel Yuste et al., 2012). Therefore, understanding the magnitude and extent of the implications of tree dieback for soil food webs will strongly benefit from the use of comprehensive spatiotemporal approaches.

Soil food webs are considerably complex, but their structural analysis can be inferred from indicator organisms, such as nematodes. Soil nematodes are the most abundant animals in the soil, ubiquitous in almost every environment (Wilson & Kakouli-Duarte, 2009), comprise most trophic groups (Yeates, Bongers, de Goede, Freckman, & Georgieva, 1993) and vary in life-history strategies that result in different sensitivities to disturbances (Ferris, Bongers, & de Goede, 2001). Their feeding activity on a diversity of organisms (e.g.,

plants, bacteria, fungi) affects primary production, soil organic matter decomposition, energy flow, and nutrient cycling (Neher, Weicht, & Barbercheck, 2012; Ruess & Ferris, 2004; Yeates, 2003). These characteristics make them powerful bioindicators for monitoring environmental changes, and several nematode-based indices have been developed to infer the degree of maturity of an ecosystem (maturity index), the complexity of the soil food web (structure index), or the availability of resources (enrichment index) (Bongers & Ferris, 1999; Ferris et al., 2001; Neher, 2001). However, besides few exceptions in conifer forests (Háněl, 2004; Ruess & Funke, 1995; Xiong, D'Atri, Fu, Xia, & Seastedt, 2011), soil nematodes have rarely been used to evaluate the impacts of forest dieback on below-ground communities and, to our knowledge, never with a spatially explicit approach.

In this study, we aim to analyse the impact of the decline of an important Mediterranean tree species, *Quercus suber* (cork oak), on soil food webs of mixed forests of southern Spain using nematodes as bioindicators. *Quercus suber* forests have a large ecological and economic value due to their high biodiversity and use for the industrial production of cork (Aronson, Pereira, & Pausas, 2009). However, in the last decades, a severe decline of this species has been reported in southern Europe and related to the attack by the aggressive exotic pathogen *Phytophthora cinnamomi*, very likely in combination with other stress sources such as climate change-related drought (Brasier, 1996; Camilo-Alves, da Clara, & de Almeida Ribeiro, 2013; Sánchez, Caetano, Romero, Navarro, & Trapero, 2006). As a result, *Q. suber* is currently included in the IUCN Red List of Threatened Species (Barstow & Harvey-Brown, 2017). Here, we used a spatially explicit approach to study the nematode community in declining *Q. suber* forests as a function of the characteristics of the neighbouring woody species. To gain in generality, we replicated the same study in two forest types representative of the main mixed *Q. suber* forests of the region: *Q. suber*–*Olea europaea* open woodlands and *Q. suber*–*Quercus canariensis* closed forests. We developed neighbourhood models (Canham & Uriarte, 2006) that predicted the variation in the characteristics of the nematode community (total abundance, diversity, abundance of the different trophic groups, and various indices representative of soil food web characteristics) as a function of the abundance, size, identity, health status, and distribution of woody species in the immediate neighbourhood. A main strength of the neighbourhood approach is that it allowed us to compare and predict the per-capita effects of individual *Q. suber* trees with different health status (i.e., healthy, defoliated or dead), and of different tree species growing intermingled in the canopy of these mixed forests (*Q. suber*, *Q. canariensis*, and *O. europaea*). In this way, we took into account the impacts of short-term changes in the soil food web directly related to the decline and mortality of individual *Q. suber* trees, as well as the potential indirect long-term impacts due to *Q. suber* replacement during secondary succession by coexisting species not affected by dieback. This approach has already been successfully used to characterize the impacts of *Q. suber* decline on soil processes and micro-organisms such as soil respiration (Ávila et al., 2016) and mycorrhizal fungi (Ibáñez et al., 2015a). The use of

a neighbourhood approach also implies that we did not explicitly explore potential direct effects of *P. cinnamomi* on soil nematodes, but focused on the indirect effects of the pathogen as a main driver of tree defoliation and death in the study forests. We considered unlikely the occurrence of *Q. suber* mortality totally independent of the presence of *P. cinnamomi* in the study forests, since the pathogen is widely distributed at a local scale and its abundance in the soil is strongly linked to the health status of *Q. suber* trees (Gómez-Aparicio et al., 2012).

We tested the following four specific hypotheses: firstly, we predicted that *Q. suber* decline would change the soil nematode community structure by modifying the total abundance, diversity, and abundance of the different trophic groups. More specifically, we expected an increase in the abundance of the trophic groups related to organic matter decomposition (i.e., bacterivores and fungivores) under defoliated and dead *Q. suber* trees as a result of higher carbon inputs from litter and dead roots. We also expected a decrease in the abundance of herbivores under defoliated and dead *Q. suber* trees due to the root rot caused by *P. cinnamomi*. Secondly, we predicted these changes in the soil nematode community to translate into a step back in the ecological succession of the soil food web (decrease in the maturity index and increase in the plant parasitic index), generating more unstable and unstructured soil food webs (decrease in the structure index) dominated by opportunistic species typical of high-nutrient levels (increase in the enrichment index). Thirdly, we hypothesized that the changes in the soil nematode community would also indicate a shift in the predominant decomposition channel to bacterial-dominated food webs (decrease in the fungivores/bacterivores ratio), which is typical for disturbed ecosystems (Van der Heijden et al., 2008). Finally, we predicted different “footprints” of coexisting woody species on soil nematodes given their differences in leaf and root traits (e.g., Aponte, García, & Marañón, 2013; Aponte, García, Pérez-Ramos, Gutiérrez, & Marañón, 2011), which would lead to long-term impacts on the ecosystem. Overall, we believe that the results of this study will provide novel understanding of the magnitude of the impacts in space and time of tree decline on soil food webs, as well as of their cascading implications for ecosystem functioning in mixed Mediterranean forests.

2 | MATERIALS AND METHODS

2.1 | Study site and species

The study was conducted in Los Alcornocales Natural Park (southern Spain). This natural park is part of the Baetic-Riffian region, identified as a hotspot of plant diversity within the Mediterranean Basin (Médail & Quézel, 1997), and contains the largest and best conserved *Q. suber* forests of Europe (Junta de Andalucía, 2005). The climate is subhumid Mediterranean, with warm, dry summers and mild, humid winters. Annual mean temperature ranges from 15.4°C to 17.3°C, and annual mean rainfall varies from 720 to 1100 mm (period 1951–1999, Ninyerola, Pons, & Roure, 2005). Soils are generally sandy, acidic, and nutrient poor, derived from a bedrock dominated

by Oligo–Miocene sandstones, but appear interspersed with soils richer in clay derived from layers of marl sediments. In the drier lowlands of the park, *Q. suber* forms mixed open woodlands with the evergreen and shade-intolerant *O. europaea* var. *sylvestris*. The understorey in these woodlands is usually very dense and dominated by shrub species such as *Pistacia lentiscus* L. (Supporting Information Table S1). In wetter areas, *Q. suber* coexists with the deciduous shade-tolerant *Q. canariensis* forming closed forests. These closed forests are characterized by a diverse understorey dominated by tall shrub species such as *Arbutus unedo* L., *Phillyrea latifolia* L., *Erica arborea* L., and *Erica scoparia* L. (Supporting Information Table S1).

Quercus suber forests within the natural park suffer severe problems of dieback driven by the exotic soil-borne oomycete *P. cinnamomi* Rands (Brasier, 1996; Gómez-Aparicio et al., 2012), with proportion of defoliated and dead trees as high as 64% and 38% (respectively) in local populations (Ávila, Linares, García-Nogales, Sánchez, & Gómez-Aparicio, 2017). This aggressive pathogen has a proposed origin in the New Guinea–Celebes region (Shepherd, 1975). It destroys the tree root systems, killing fine roots, and occasionally producing necrotic bark lesions in large roots (Weste & Marks, 1987). The effect of *P. cinnamomi* in root systems can interact with drought stress and lead to a severe decrease in tree survival (Corcobado, Cubera, Juárez, Moreno, & Solla, 2014; Camilo Alves, da Clara, & de Almeida Ribeiro, 2013). Trees may die suddenly within 1–2 years, depending on the severity of other stressors, but death often takes several years (Weste & Marks, 1987). No other tree or shrub species in the study area showed any symptoms of dieback.

2.2 | study design

This field study was conducted in two sites per type of forest (i.e., open woodland and closed forest) located in the north and south of Los Alcornocales Natural Park (Supporting Information Table S1). A plot was established at each site (Supporting Information Figure S1) and subdivided into thirty 10 × 10 m subplots with a sampling point in the centre (2 types of forest × 2 sites × 30 subplots = 120 sampling points). To characterize local neighbourhoods, we mapped and identified all live and dead trees with a DBH (diameter at breast height) ≥ 2 cm and shrubs around each sampling point using a total station Leica TC 407 (Leica Geosystems, Heerbrugg, Switzerland). We considered a tree neighbourhood as a 15-m radius circle around each sampling point (Gómez-Aparicio et al., 2012; Ibáñez et al., 2015b). For shrubs, we considered a neighbourhood size of 5 m to be large enough based on the small size of most shrubs in these forests (height usually <3 m; Gómez-Aparicio et al., 2012). We measured the DBH of each of the trees mapped ($n = 264$ in open woodlands, $n = 510$ in closed forests). Due to its multi-stem growth form, shrub size was characterized measuring the two diameters of the elliptical projection of its crown ($n = 913$ in open woodlands, $n = 1,283$ in closed forests). In addition, we classified *Q. suber* trees into three different health categories: healthy, defoliated, and dead (Ávila, Gallardo, Ibáñez, & Gómez-Aparicio, 2016; Gómez-Aparicio et al., 2012). Trees included in the dead category died within the last

10 years prior to the beginning of the study, most of them still showing a standing trunk and a variable accumulation of stem wood on the ground.

2.3 | Nematode sampling, identification, and indices

In spring 2014, soil samples were collected in all the sampling points (three replicates per point, Ø 3 × 20 cm depth, previous removal of the litter layer) and stored in plastic bags at 4°C until processing. The three replicates were combined and mixed by hand, and soil aggregates were broken. Nematodes were extracted from a subsample of 100–120 ml by the sugar centrifugation method (Jenkins, 1964), heat killed, and fixed in 4% formalin. They were counted at 100× magnification, and 100 individuals per sample were identified in temporary slides to the family and genus level (Andrássy, 2005, 2007, 2009; Bongers, 1994) at 400× and 1000× magnification. The estimated nematode abundance was expressed as number of individuals per gram of soil dry wt (ind/g). Richness and the Shannon index (H' , Shannon & Weaver, 1949) of genera were calculated as measures of nematode diversity.

Each nematode was assigned to a trophic group (bacterivore, fungivore, herbivore, omnivore, and predator, according to Yeates et al., 1993) and a c-p group (colonizer-persister scale with five levels) indicative of their life-history strategy (similar to r-K strategies, Bongers & Ferris, 1999). Trophic and c-p groups can be combined forming functional guilds (Bongers & Bongers, 1998). Feeding types and c-p groups were assigned using the NINJA online program (Sieriebriennikov, Ferris, & de Goede, 2014). Five indices indicative of food web characteristics were also calculated using NINJA: the maturity index for free-living taxa (MI), the plant parasitic index (PPI), the structure index (SI), the enrichment index (EI), and the fungivores/bacterivores ratio (F/B). The maturity index is an indicator of the ecological successional status of a soil community, and it considers the relative abundance of nematodes with differing life-history strategy: those in the higher c-p scale (longer life cycles and K-strategists) vs. those in the lower c-p scale (opportunistic, fast-growing, and r-strategists) (Bongers, 1990; Bongers & Ferris, 1999). The organisms in the higher c-p levels are considered to have a regulating role in the soil food web and to control soil-borne plant pathogens (Wilson & Kakouli-Duarte, 2009). The maturity index is calculated as the weighted mean of the % of free-living nematodes in each c-p group: $MI = \sum v_i f_i$, where v_i is the c-p value in the i_{th} taxon and f_i is the frequency of the i_{th} taxon in a sample (Bongers, 1990). The equivalent of the maturity index for plant-feeding nematodes is the plant parasitic index. The interpretation of plant parasitic index is the inverse to the maturity index, with undisturbed systems showing a high maturity index but a low plant parasitic index (Bongers, van der Meulen, & Korthals, 1997). The structure index measures the complexity of the soil food web, and it is calculated as $100 \times [s/(s + b)]$, where s is the structure component (calculated as the weighted frequencies of the functional guilds Ba3–Ba5, Fu3–Fu5, Pr3–Pr5, and Om3–Om5), and b is the basal component (calculated as the weighted frequencies of

Ba2 and Fu2 nematodes, Ferris et al., 2001). The enrichment index is a measure of nutrient enrichment, generally associated with nutrient addition or with the mortality of other organisms reflecting a nutrient flush, and therefore describes the resource availability in the soil (Ferris & Bongers, 2006). The enrichment index is calculated as $100 \times [e/(e + b)]$, where e is the enrichment component (calculated as the weighted frequencies of Ba1 and Fu2 nematodes) and b is the basal component (Ferris et al., 2001). The fungivores/bacterivores ratio (F/B) was calculated as an indicator of energy use efficiency in the soil decomposition process, where B is the abundance of bacterivore nematodes and F is the abundance of fungivore nematodes in a sample. This index was analysed to estimate the dominant decomposition channel in the soil. The channel index ($CI = 100 \times [0.8 \text{ Fu2}/3.2 \text{ Ba1} + 0.8 \text{ Fu2}]$) provided by NINJA program was not considered due to the extremely low abundance of bacterivores cp1, which were only present in 41.7% of the samples and representing <1% of the total of individuals per sample.

2.4 | Data analysis

We used a spatially explicit neighbourhood approach (Canham & Uriarte, 2006) and model selection (Johnson & Omland, 2004) to study the nematode community as a function of the characteristics of the neighbouring woody species. For each of the two forest types (open woodlands vs. closed forests), we fit linear models that predicted the total abundance and diversity (richness and H') of nematodes, the abundance of the different trophic groups, and the five indices of soil food web structure and functioning (MI, PPI, SI, EI, and F/B) as a function of (a) the site (north vs. south), (b) a tree neighbourhood index (NI_{Tree}), and (c) a shrub neighbourhood index (NI_{Shrub}). The NI_{Tree} quantifies the net effect of $j = 1, \dots, n$ neighbouring trees of $i = 1, \dots, s$ species on each nematode community variable, and was assumed to vary as a direct function of the size (DBH) and an inverse function of the distance to neighbouring trees following the equation:

$$NI_{Tree} = \sum_{i=1}^s \sum_{j=1}^n \frac{DBH_{ij}^{\alpha}}{distance_{ij}^{\beta}} \quad (1)$$

where α and β are the estimated parameters that determine the shape of the effect of the DBH (α) and the distance to neighbours (β) on nematodes. The α and β parameters were constrained to take the same value for the different groups of neighbouring trees included in the models. This is a standard procedure in neighbourhood models that avoids the inflation of the number of parameters and facilitates model convergence (e.g., Canham & Uriarte, 2006; Gómez-Aparicio & Canham, 2008).

The NI_{Shrub} is a simplified version of the tree neighbourhood index, and quantifies the net effect of $j = 1, \dots, n$ neighbouring shrubs of $i = 1, \dots, s$ species on nematodes following the equation:

$$NI_{Shrub} = \sum_{i=1}^s \sum_{j=1}^n area_{ij} \quad (2)$$

TABLE 1 Summary of models used to evaluate the effect of woody neighbours on nematode communities in Mediterranean mixed forests

No.	Model	Function	Par	Interpretation
1	Null	$Y \sim a_{\text{Site}}$	2	It ignores the effects of woody neighbours but considers differences between sites
2	All trees	$Y \sim a_{\text{Site}} + b \times \text{NI}_{\text{Trees}}$	5	It adds the effect of trees to the previous model. All tree species are considered to be equivalent
3	Tree species	$Y \sim a_{\text{Site}} + b \times \text{NI}_{Q_{\text{suber}}} + c \times \text{NI}_{O_{\text{europaea}}/Q_{\text{canariensis}}}$	6	It considers different effects of <i>Q. suber</i> and coexisting tree species (i.e., <i>Olea europaea</i> in open woodlands, <i>Quercus canariensis</i> in closed forests)
4	Health + Tree species	$Y \sim a_{\text{Site}} + b \times \text{NI}_{\text{Healthy}} + c \times \text{NI}_{\text{Def}} + d \times \text{NI}_{\text{Dead}} + e \times \text{NI}_{O_{\text{europaea}}/Q_{\text{canariensis}}}$	8	It considers not only differences among tree species, but also different effects of <i>Q. suber</i> trees varying in health status (healthy, defoliated, and dead).
5	Best tree model (2, 3, or 4) + Shrubs	$Y \sim a_{\text{Site}} + b \times \text{NI}_{\text{Trees}} + c \times \text{NI}_{\text{Shrubs}}$ $Y \sim a_{\text{Site}} + b \times \text{NI}_{Q_{\text{suber}}} + c \times \text{NI}_{O_{\text{europaea}}/Q_{\text{canariensis}}} + d \times \text{NI}_{\text{Shrubs}}$ $Y \sim a_{\text{Site}} + b \times \text{NI}_{\text{Healthy}} + c \times \text{NI}_{\text{Def}} + d \times \text{NI}_{\text{Dead}} + e \times \text{NI}_{O_{\text{europaea}}/Q_{\text{canariensis}}} + f \times \text{NI}_{\text{Shrubs}}$	7, 8, or 9	It considers not only tree effects, but also shrubs effects

Note. Par: number of parameters in the model; NI: neighbourhood index; Healthy: healthy *Q. suber* trees; Def: defoliated *Q. suber* trees; Dead: dead *Q. suber* trees.

The NI_{Shrub} was assumed to vary just as a direct function of the size (crown area) of neighbouring shrubs in a 5-m radius neighbourhood. We decided not to include distance in the calculation of the index given the already restricted area over which shrubs were mapped and to keep the number of parameters in the models manageable (Gómez-Aparicio et al., 2012).

We were particularly interested in exploring whether tree effects varied between individuals of different species or health status. For this purpose, we tested five models with different groupings of neighbouring trees with increasing complexity (Table 1): (a) a null model that ignored neighbour effects and calculated the nematode community just as a function of the site (*Null* model); (b) a model in which all trees were considered equivalent (*All trees* model); (c) a species-specific model that considered different effects of *Q. suber* and the coexisting tree species—either *O. europaea* or *Q. canariensis*—on the nematode community by including two separate NIs (*Tree species* model); (d) a model that also took into account the health status of *Q. suber* trees and therefore calculated four separate NIs (healthy *Q. suber*, defoliated *Q. suber*, dead *Q. suber*, and the coexisting tree species) (*Health + Tree species* model); and (e) a model that not only considered the effects of trees on nematode communities, but also of shrubs. This model added the shrub neighbourhood index (NI_{Shrub}) to the best tree model (either model 2, 3, or 4).

We used simulated annealing (a global optimization technique) to determine the most likely parameters (i.e., the parameters that maximize the log-likelihood) in our models (Goffe, Ferrier, & Rogers, 1994). The Akaike information criterion corrected for small sample sizes (AIC_c) was used to select the best model, that is, lower AIC_c (Burnham & Anderson, 2002). When there was more than one best model (the difference in AIC_c among them was lower than two units), the simplest model (i.e., with fewer parameters) was chosen. The slope of the regression (with a zero intercept) of observed on predicted values was used to measure bias (with an unbiased model having a slope of 1), and the R^2 of the regression of observed vs. predicted values was used as a measure of goodness-of-fit. Abundance and richness data were modelled using a Poisson error distribution, the Shannon index using a normal distribution, and the maturity index, plant parasitic index, structure index, and enrichment index using a binomial error distribution. Spatial autocorrelation in the model residuals was analysed with Mantel tests (Legendre & Fortin, 1989). Correlations among predicted neighbourhood indices for each trophic group and the nematode index were explored using Spearman correlations. Analyses were performed using the packages “LIKELIHOOD” (Murphy, 2012) and “ADE4” (Dray & Dufour, 2007) in R statistical software version 3.3.2 (R Core Team, 2016).

3 | RESULTS

The identified nematode community of the experimental sites included a total of 81 genera and 43 families in the open woodlands, and of 72 genera and 39 families in the closed forests (Supporting Information Tables S2 and S3). All best models (i.e., lowest AIC_c)

TABLE 2 Best models analysing the effect of woody neighbours on the nematode community in open woodlands. ΔAIC_c represents the differences between the AIC_c (Akaike information criterion corrected for small sample sizes) of the best and null models. The total number of parameters in the best model ("Par"), the slope of observed vs. predicted values, and the goodness-of-fit (R^2) are also given

Variable	Best model	Par	ΔAIC_c	Slope	R^2
Abundance	All trees + Shrubs	6	45	1.01	0.20
Richness	Null	2	0	1.00	0.19
Shannon index (H')	Null	2	0	1.00	0.19
Bacterivores	Health + Tree species + Shrubs	9	1344	1.01	0.30
Fungivores	Health + Tree species + Shrubs	9	4,467	1.02	0.35
Herbivores	Health + Tree species + Shrubs	9	2,381	1.00	0.11
Predators	Health + Tree species + Shrubs	9	349	0.99	0.11
Omnivores	Health + Tree species + Shrubs	9	449	1.00	0.15
Maturity index (MI)	Health + Tree species	8	19	1.00	0.45
Plant parasitic index (PPI)	Tree species + Shrubs	7	32	1.00	0.17
Structure index (SI)	Health + Tree species + Shrubs	9	15,002	1.00	0.53
Enrichment index (EI)	Health + Tree species + Shrubs	9	1,662	1.00	0.32
Fungivores/Bacterivores (F/B)	Health + Tree species + Shrubs	9	1,153	1.00	0.16

produced unbiased estimates of the analysed variables (i.e., slopes of predicted vs. observed were close to 1.0) and explained a percentage of the variation in the data that ranged from 0 to 53% (Tables 2 and 3). Although MI and SI were strongly correlated (Supporting Information Table S4), we decided to keep both indices since they were best explained by different sets of predictors (Tables 2 and 3), hence suggesting that some variability between them was captured by the neighbourhood analyses. The Mantel tests did not reveal any spatial autocorrelation in the model residuals ($P > 0.05$) (Supporting Information Table S5) and Spearman correlation analyses did not show any strong correlation among predicted neighbourhood indices (Supporting Information Table S6). Models that included the effects of tree neighbours on the nematode community had a better fit to the data than models that ignored them for 11 out of the 13 tested variables, both in open woodlands and closed forests (Tables 2 and 3). Moreover, most of these best models including tree effects (9/11 in the open woodland and 7/11 closed forests) were those that considered differences among individual trees varying in both health and species (*Health + Tree species* model). The best models also included the effect of shrub neighbours for most descriptor variables of the nematode community in both open woodlands (10/13) and closed forests (11/13).

3.1 | Impacts of *Q. suber* decline on the nematode community

The results of the models indicate that the total abundance, richness, and diversity of the nematode community in the soil were almost unaffected by the composition of the tree neighbourhood (Tables 2 and 3). However, the abundance of the different trophic groups, as well as most indices, varied strongly among *Q. suber* trees of different health in both open woodlands and closed forests. In open woodlands, we detected higher abundance of bacterivores,

fungivores, and herbivores in the neighbourhood of defoliated and dead *Q. suber* trees compared to healthy *Q. suber* (Figure 1a–c), whereas the opposite pattern was found for omnivores (Figure 1e). Predators were also more abundant in soils under healthy *Q. suber* trees than under defoliated *Q. suber*, but less abundant than under dead *Q. suber* (Figure 1d). In closed forests, the best models did not show any effect of *Q. suber* decline on the abundance of bacterivore and herbivore nematodes (Table 3), but showed a higher abundance of fungivores near dead *Q. suber* than near healthy *Q. suber* trees (Figure 2b). As generally found in open woodlands, the abundance of predators and omnivores in closed forests was lower in the neighbourhood of defoliated and dead *Q. suber* than of healthy *Q. suber* trees (Figure 2d and e).

The decline of *Q. suber* caused a reduction in the maturity index in open woodlands (Figure 3a) and an increase in the plant parasitic index (the equivalent of the maturity index for plant-parasite nematodes, but with inverse interpretation) in closed forests (Figure 4b). In the two types of forests, the structure index, the enrichment index, and the fungivores/bacterivores ratio were strongly affected by *Q. suber* decline. The structure index was lower under defoliated and/or dead than under healthy *Q. suber* trees (Figures 3c and 4c), whereas the opposite pattern was found for the enrichment index (Figures 3d and 4d). The fungivores/bacterivores ratio was higher under dead than under healthy *Q. suber* trees, whereas defoliated *Q. suber* trees showed the lowest values (Figures 3e and 4e).

3.2 | Differential impacts among woody species on the nematode community

All best models of abundance of the different trophic groups and indices showed contrasting impacts among the coexisting tree and shrub species on the characteristics of their associated nematode community. Individual trees of species coexisting with *Q. suber* (i.e.,

TABLE 3 Best models analysing the effect of woody neighbours on the nematode community in closed forests. ΔAIC_c represents the differences between the AIC_c (Akaike information criterion corrected for small sample sizes) of the best and null models. The total number of parameters in the best model ("Par"), the slope of observed vs. predicted values, and the goodness-of-fit (R^2) are also given

Variable	Best model	Par	ΔAIC_c	Slope	R^2
Abundance	Tree species + Shrubs	7	71	1.01	0.32
Richness	Null	2	0	1.00	0.00
Shannon index (H')	Null	2	0	1.00	0.01
Bacterivores	Tree species + Shrubs	7	2,005	1.00	0.28
Fungivores	Health + Tree species + Shrubs	9	4,338	1.01	0.28
Herbivores	Tree species + Shrubs	7	3,842	1.02	0.30
Predators	Health + Tree species + Shrubs	9	496	1.02	0.16
Omnivores	Health + Tree species + Shrubs	9	344	1.00	0.09
Maturity index (MI)	Tree species + Shrubs	7	22	1.00	0.21
Plant parasitic index (PPI)	Health + Tree species + Shrubs	9	141	1.00	0.39
Structure index (SI)	Health + Tree species + Shrubs	9	3,885	1.00	0.19
Enrichment index (EI)	Health + Tree species + Shrubs	9	3,114	1.00	0.24
Fungivores/Bacterivores (F/B)	Health + Tree species + Shrubs	9	349	1.00	0.11

O. europaea in the open woodland and *Q. canariensis* in the closed forest) showed in general a much higher abundance of all trophic groups (except omnivores) than (healthy) *Q. suber* trees (Figures 1 and 2). Neighbourhoods dominated by *O. europaea* in open woodlands also showed much higher values of the enrichment index and lower values of the maturity index, structure index, and fungivores/bacterivores ratio than neighbourhoods dominated by healthy *Q. suber* trees (Figure 3). In closed forests, neighbourhoods of *Q. canariensis* had similar values of the enrichment index than *Q. suber* neighbourhoods, but showed much higher values of the maturity index, plant parasitic index, and structure index, as well as a lower fungivores/bacterivores ratio (Figure 4). Shrub neighbourhoods were also characterized by nematode communities very different to healthy *Q. suber* trees. Yet, these communities showed similar characteristics as nematode communities under *O. europaea* and dead *Q. suber* trees in open woodlands (maturity index, structure index, enrichment index, and fungivores/bacterivores ratio, Figure 3), and as those of defoliated and particularly dead *Q. suber* trees in closed forests (plant parasitic index, structure index, enrichment index, and fungivores/bacterivores ratio; Figure 4).

3.3 | Variation of tree neighbour effects with size (α) and distance (β)

The α parameter in Equation 1 controlled the scaling of the effect of tree size on the characteristics of the nematode community. In open woodlands, for most variables, the effect of trees scaled with DBH (i.e., $\alpha = 1$), although for some variables (bacterivores, herbivores, predators, maturity index, structure index), it was disproportionately large relative to their biomass (i.e., $\alpha > 2$). Only for omnivores the values of α was close to zero, indicating that tree effects scaled with neighbour density, regardless of the size of individual trees (Figure 5, Supporting Information Tables S7 and S8). In closed forests, the

parameter α showed an increase from values closed to zero (fungivores, enrichment index) to much greater than 2 (total abundance, bacterivores, predators, omnivores, maturity index, structure index) (Figure 5, Supporting Information Tables S7 and S8).

The β parameter (Equation 1) controlled the magnitude of the decline in the effect of a neighbour with increasing distance from the soil sampling point. For most variables in open woodlands (9/11), the decline in distance of tree effects was virtually zero ($\beta = 0$), which implies that nematode communities were mainly affected by tree density and not by their spatial location within the 15-m neighbourhood (Figure 5, Supporting Information Table S7). In closed forests, on the contrary, the decline in distance varied from very steep ($\beta > 3$) for total abundance, bacterivores, maturity index, and structure index, to virtually zero ($\beta = 0$) for the rest of the trophic groups (fungivores, herbivores, predators, and omnivores) (Figure 5, Supporting Information Table S8).

4 | DISCUSSION

In this study, we used a spatially explicit approach to assess the impacts of tree decline on soil food webs as indicated by soil nematodes. Our results support strong alterations in the composition of nematode communities (i.e., abundance of different trophic groups) associated to the process of defoliation and mortality of a dominant Mediterranean oak, *Q. suber*. Moreover, these changes in nematode community composition indicated strong alterations in the functionality of the soil food web as shown by the significant changes in all compositional/functional indices (maturity index, plant parasitic index, structure index, enrichment index, and fungivores/bacterivores ratio). To our knowledge, this is the first study that analyses the spatial variability of soil nematodes considering complex neighbourhoods (i.e., composed by trees and shrubs of different species, size,

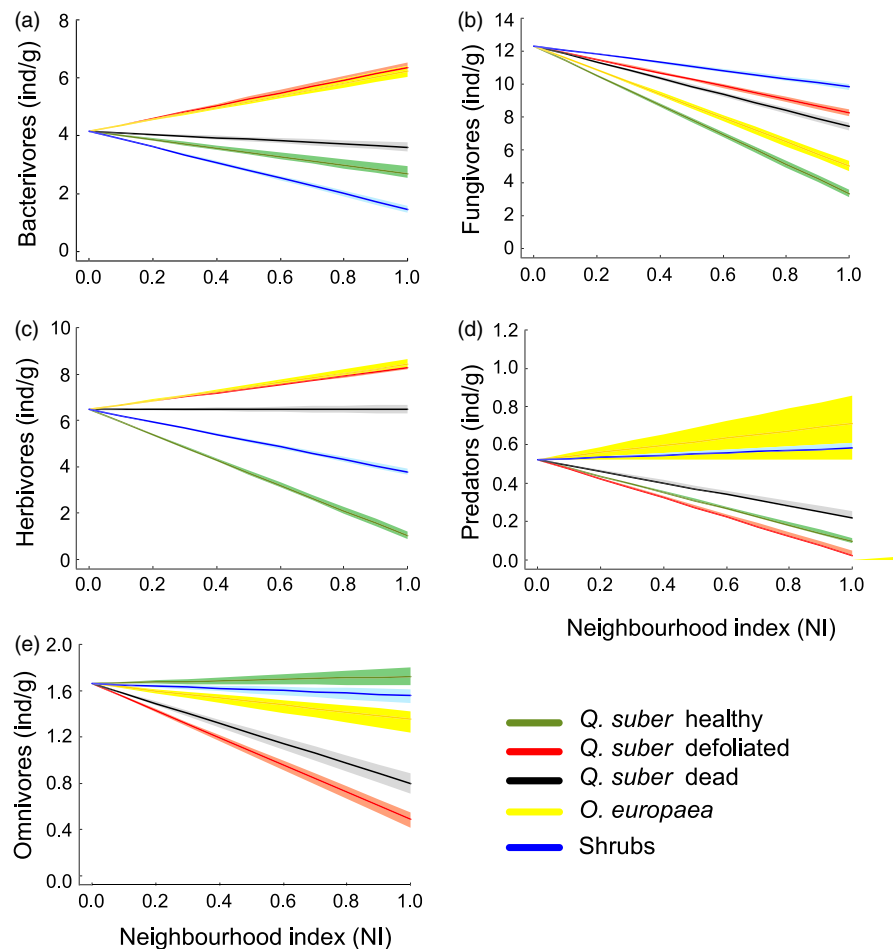


FIGURE 1 Predicted effect of variation in the neighbourhood index (NI) on the abundance of the nematode trophic groups for the best models in open woodlands. Neighbour effects were calculated using equations and parameter values for best models reported in Table 2 and Supporting Information Table S7. Nematode abundance was expressed as number of individuals per gram of soil dry wt number of individuals per gram of soil dry wt (ind/g). Shaded areas represent the higher and lower supporting intervals of the predicted effects [Colour figure can be viewed at wileyonlinelibrary.com]

and health status) in mixed forests affected by pathogen-driven tree decline.

4.1 | Impacts of *Q. suber* decline on the soil food web structure

Our results did not support our expectation of an impact of *Q. suber* decline on the total abundance, richness, or diversity of soil nematodes. However, in agreement with our first hypothesis, we found strong changes in the abundance of the different trophic groups. In particular, the abundance of bacterivore and mainly fungivore nematodes tended to increase in neighbourhoods dominated by defoliated and/or dead *Q. suber* trees. For example, in closed forests, the abundance of fungivores was five times higher in neighbourhoods dominated by dead than by healthy *Q. suber* trees (i.e., c. 16 vs. 3 ind/g, Figure 2b). The decline of *Q. suber* in our study area is mainly caused by the exotic oomycete *P. cinnamomi*, which destroys fine roots and causes the progressive defoliation of tree canopies (Camilo-Alves, et al., 2013). The high inputs of organic matter and

nutrients derived from dead roots, litterfall, and decaying wood that accumulate under defoliated and dead trees could have promoted the proliferation of saprophytic micro-organisms (both bacteria and fungi) under those trees and hence bacterial and fungal-feeding nematodes. In fact, these neighbourhoods tend to have more C-enriched soils than neighbourhoods dominated by healthy *Q. suber* trees (J.M. Ávila, unpubl. results).

Our results also demonstrated that *Q. suber* decline influenced the abundance of herbivore nematodes, although only in open woodlands. Previous experimental studies conducted with soil from the same open woodlands have shown strong negative effects of soil pathogens on root biomass of *Q. suber* (Gómez-Aparicio et al., 2017). Therefore, we expected a lower abundance of herbivore nematodes in neighbourhoods of defoliated and dead *Q. suber* linked to a loss in tree performance and root biomass. However, we found just the opposite pattern. We propose that this result could be explained by post-mortality alterations of microclimatic conditions in open woodlands. In this type of forest, gaps opened after tree death are of larger than in closed forests due to their lower tree

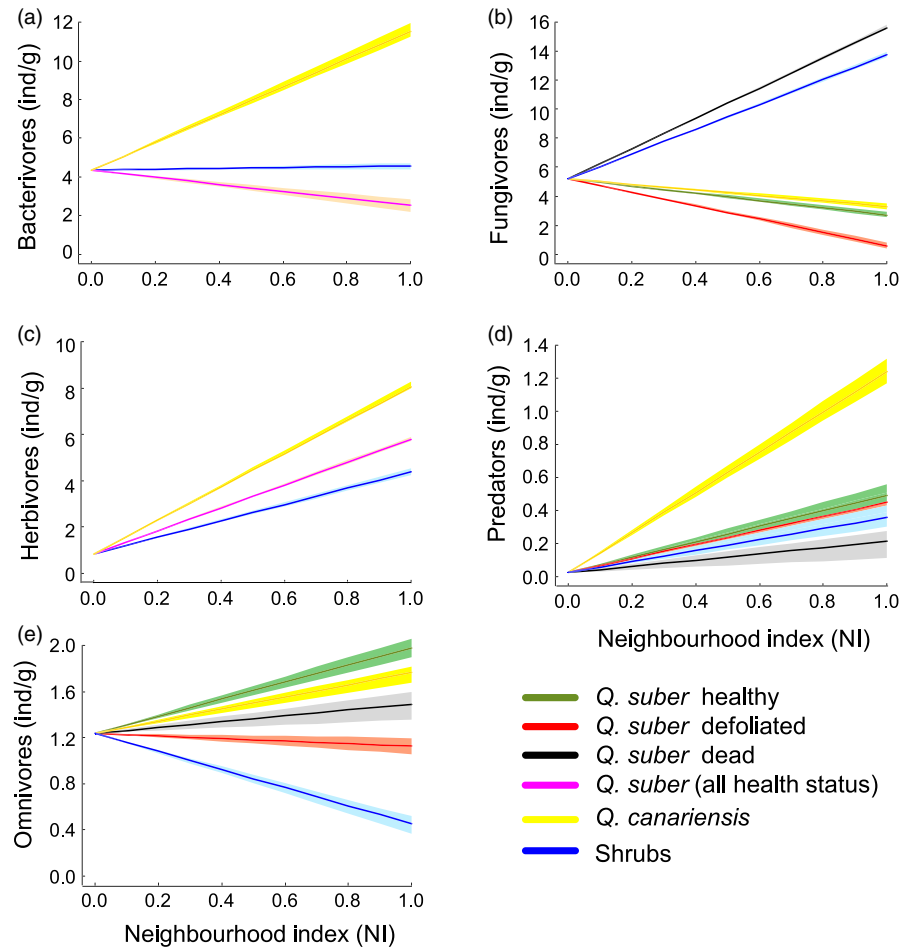


FIGURE 2 Predicted effect of variation in the neighbourhood index (NI) on the abundance of the nematode trophic groups for the best models in closed forests. Neighbour effects were calculated using equations and parameter values for best models reported in Table 2 and Supporting Information Table S8. Nematode abundance was expressed as number of individuals per gram of soil dry wt number of individuals per gram of soil dry wt (ind/g). Shaded areas represent the higher and lower supporting intervals for the predicted effects [Colour figure can be viewed at wileyonlinelibrary.com]

density, leading to stronger increases in light levels accompanied by higher cover of herbaceous vegetation (Rodríguez et al., 2017). This hypothesis is supported by the much larger abundance (c. 6 vs. 2 ind/g) of herbivore nematodes found in gaps (i.e., NI = 0) than in neighbourhoods dominated by healthy *Q. suber* trees (i.e., NI_{*Q. suber* healthy} = 1) in the open woodland (Figure 1c). Previous studies have also reported a higher abundance of herbivore nematodes in gaps between woody species, likely due to the role of herbaceous vegetation as a higher nutrient sink in spring compared to trees (Biederman & Boutton, 2010; Cesarz et al., 2013; Renčo, Čerevková, Homolová, & Gömöryová, 2015).

Contrary to the pattern found for bacterivores, fungivores, and herbivores, the decline of *Q. suber* caused a decrease in the abundance of predators and omnivores in the nematode community. Nematodes in these trophic groups are mainly k-strategist nematodes (i.e., belonging to cp-4 and cp-5 groups). Because of their large size, long life cycles, low fecundity, and permeable cuticles they are highly susceptible to environmental changes and fluctuations (Wilson & Kakouli-Duarte, 2009). They are the first nematodes to disappear after unfavourable conditions, and have been shown to decrease in soils altered by pollutants and other disturbances (Forge & Simard, 2000; Freckman & Ettema, 1993; Korthals et al., 1996). Overall, our results suggest that *Q. suber* decline implies significant changes in the structure of the soil food web of disturbed systems,

increasing the abundance of the groups at the lower trophic levels and decreasing the abundance of the higher trophic levels.

Our neighbourhood approach allowed us to gain valuable insights into the role of tree size and distance to neighbour trees as determinants of the nematode community. This type of information is not frequent in the literature on soil organisms (but see Bach, Grytnes, Halvorsen, & Ohlson, 2010; Nacke et al., 2016; Saetre & Bååth, 2000; Weber & Bardgett, 2011), despite the recognized relevance of incorporating the spatial dimension into studies of below-ground communities (Coyle et al., 2017; Ettema & Wardle, 2002) and their feedback effects (Kardol, de Deyn, Laliberté, Mariotte, & Hawkes, 2013). Our models supported the significant role of tree size as determinant of the abundance of soil nematodes, with larger trees supporting more abundant communities likely due to larger resource inputs (Gallardo, 2003). Moreover, some trophic groups (i.e., bacterivores, predators) showed disproportionate responses (i.e., $\alpha > 2$) to large trees. Because mortality caused by *Phytophthora* mainly affects trees of medium to large size (Cobb, Filipe, Meentemeyer, Gilligan, & Rizzo, 2012), our results support a large capacity of pathogen-driven mortality to alter nematode communities in forest systems. Regarding the role of distance, it strongly varied among trophic groups and indices. In general, the spatial extension of tree effects was more clearly detected in closed forests than in open woodlands, where other factors (e.g., high abundance of herbaceous

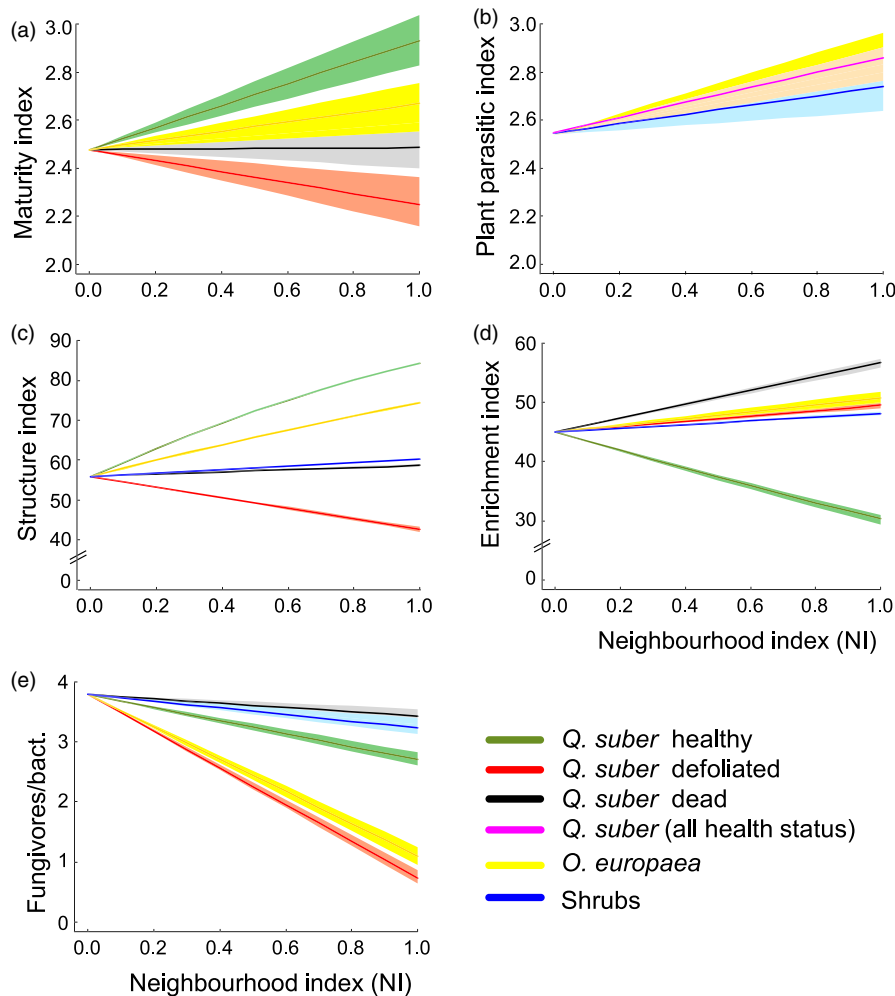


FIGURE 3 Predicted effect of variation in the neighbourhood index (NI) on the maturity index (MI), plant parasitic index (PPI), structure index (SI), enrichment index (EI), and the fungivores/ bacterivores ratio (F/B) for the best models in open woodlands. Neighbour effects were calculated using equations and parameter values for best models reported in Table 2 and Supporting Information Table S7. Shaded areas represent the higher and lower supporting intervals for the predicted effects [Colour figure can be viewed at wileyonlinelibrary.com]

vegetation) could have obscured the decrease in tree influence with distance. Moreover, the different trophic groups varied in their response to distance effects, showing significant differences in their scale of spatial variation likely related to differences in top-down vs. bottom-up control forces (Robertson & Freckman, 1995; Viketoft, 2013).

4.2 | Impacts of *Q. suber* decline on the successional status and complexity of the soil food web

In agreement with our second hypothesis, our results indicated that the decline of *Q. suber* translated into a setback of the ecological succession in the soil food web to an earlier stage (lower maturity index or higher plant parasitic index) and simplified, less structured soil food webs (lower structure index). These changes were likely determined by the sustained nutrient enrichment produced by defoliated and dead trees, which increased the abundance of opportunistic nematodes in the lower c-p groups (supported by the higher values of the enrichment index under those trees). Previous studies have reported similar trends in the modification of the values of these indices associated to disturbances such as windstorms (Renčo & Čerevková, 2017), floodings (Wagner, Eisenhauer, &

Cesarz, 2015), experimental warming (Thakur et al., 2014), or fires (Pen-Mouratov, He, & Steinberger, 2004). Functionally, lower values of the maturity index and higher values of the plant parasitic and enrichment indices frequently reflect a high microbial abundance and activity that translate into faster N mineralization and soil respiration rates (Bongers & Bongers, 1998; Ferris & Matute, 2003).

The lower values of the maturity and structure indices are also considered indicative of a shift towards simplified soil food webs, less regulated by top-down effects (i.e., predation and competition) due to lower abundance of predators and omnivores (Ferris & Matute, 2003). Predator and omnivore nematodes can feed at more than one trophic level of the soil food web, and play a regulatory function by feeding on the most dominant prey, increasing biodiversity (Bongers & Bongers, 1998). Their loss can therefore translate into a lower connectivity (i.e., the proportion of links among nodes in the food web) in the food web. A lower abundance of trophic linkages usually implies a decrease in functional redundancy and, consequently, less functional resilience to disturbances (Ferris et al., 2001). Overall, these results indicate that *Q. suber* decline is creating less stable soil food webs with low capacity to recover from further disturbances (Bongers & Bongers, 1998).

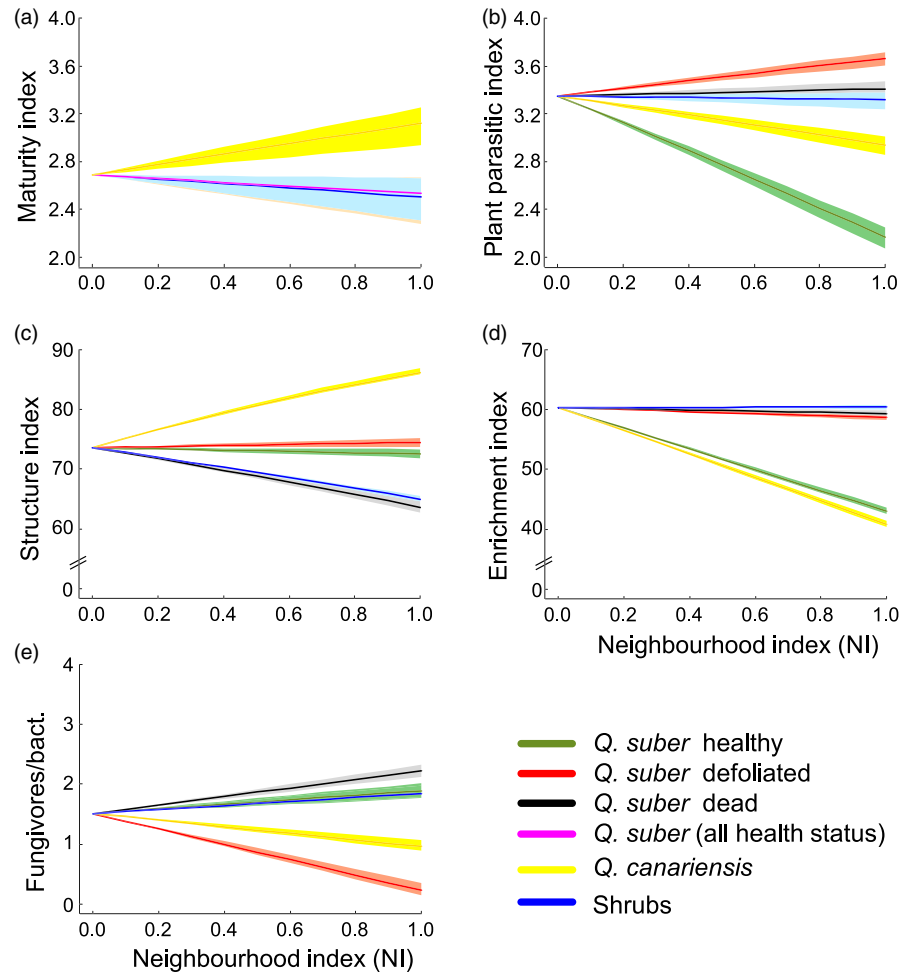


FIGURE 4 Predicted effect of variation in the neighbourhood index (NI) on the maturity index (MI), plant parasitic index (PPI), structure index (SI), enrichment index (EI), and the fungivores/bacterivores ratio (F/B) for the best models in closed forests. Neighbour effects were calculated using equations and parameter values for best models reported in Table 2 and Supporting Information Table S8. Shaded areas represent the higher and lower supporting intervals for the predicted effects [Colour figure can be viewed at wileyonlinelibrary.com]

4.3 | Impacts of *Q. suber* decline on the predominant decomposition pathway

In our third hypothesis, we predicted the decline of *Q. suber* to increase the “fast” bacterial decomposition channel typical for disturbed ecosystems with high-nutrient availability, instead of the “slow” fungal channel characteristic of late-successional, undisturbed ecosystems (Van der Heijden et al., 2008). Our results, however, suggested that the shifts in the predominant decomposition channel (as indicated by bacterivore and fungivore nematodes) imposed by the process of oak decline was more complex than this. Specifically, we found a shift towards bacterial-dominated food webs in neighbourhoods dominated by defoliated *Q. suber* trees (indicated by lower fungivores/bacterivores values than in healthy neighbourhoods), but an increase in the fungal channel under dead *Q. suber* trees. These results suggest that the impacts of *Q. suber* dieback on the predominant decomposition channel were highly influenced by the temporal changes in the quantity and quality of energy inputs to the soil. First, the dead roots and litterfall accumulated under defoliated trees could have stimulated the bacterial activity. Besides, defoliated plants usually enhance the exudation of organic soluble compounds (easily metabolized by bacteria) to the soil (Hamilton & Frank, 2001; Paterson & Sim, 1999). Therefore, the dominance of

bacterial-based food webs was probably due to the increase in labile compounds under defoliated trees. Later, when a *Q. suber* tree dies, rhizodeposition ends, deadwood logs start to accumulate and, since most labile compounds have already been decomposed by bacteria, decomposition tends to be fungal-dominated. Fungi have a higher capacity than bacteria to degrade recalcitrant molecules such as cellulose, hemicellulose, and lignin (Strickland & Rousk, 2010; Van der Heijden et al., 2008). Consequently, fungal decomposition predominates in soils with high inputs of organic material with high C:N ratio (Ferris & Bongers, 2006; Van der Heijden et al., 2008) such as the deadwood under dead trees (Baldrian, 2016). An increase in the soil C:N ratio is usually related to a high N immobilization and low N mineralization, resulting in lower N availability for plants (Ferris & Matute, 2003). Overall, our results suggest that *Q. suber* decline could produce significant changes in the spatial pattern of predominant decomposition pathways, eventually leading to a strong dominance of the slow fungal decomposition channel.

4.4 | Long-term impacts of *Q. suber* decline on soil food webs due to species replacements

In the long term (i.e., at decades scale, following Hicke et al., 2012), the process of plant species replacement after tree mortality could

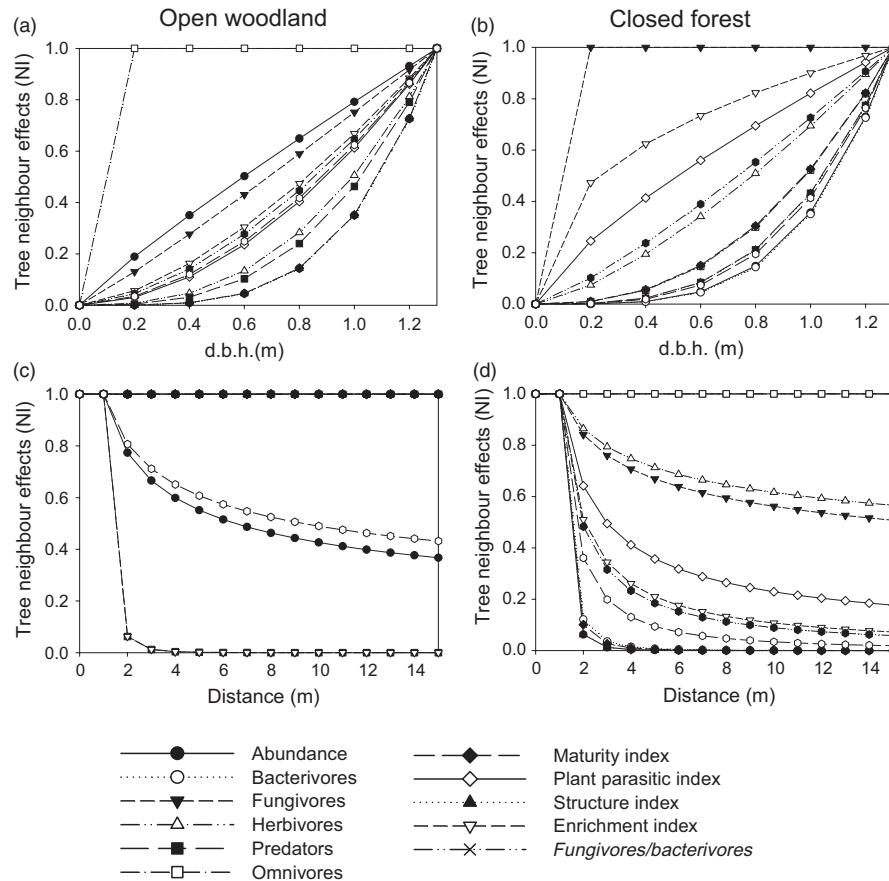


FIGURE 5 Predicted variation in tree neighbour effects (estimated as NI_{Tree}) as a function of neighbour size (DBH) and distance in open woodlands (a, c) and closed forests (b, d). Size effects were calculated using Equation 1, α values for best models (Supporting Information Tables S7 and S8) and setting $\beta = 0$ for simplicity, whereas distance effects were calculated using Equation 1, β values for best models (Supporting Information Tables S7 and S8) and setting $\alpha = 0$. NI values are shown standardized (i.e., divided by the maximum values for each variable) to facilitate comparison among characteristics of the nematode community

lead to important indirect impacts on soil food webs (e.g., Loo, 2009; Lovett, Canham, Arthur, Weathers, & Fitzhugh, 2006). This is because the abundance and diversity of soil organisms are tightly linked to plant species identity and diversity (De Deyn, Raaijmakers, van Ruijven, Berendse, & van der Putten, 2004; Eisenhauer et al., 2013) due to close host-guest relationships (e.g., mycorrhizal fungi, soil-borne pathogens), as well as to local adaptations of the free-living decomposer community to litter produced by the plant species above them (the “home-field advantage”; Ayres et al., 2009; Gholz, Wedin, Smitherman, Harmon, & Parton, 2000; Strickland, Lauber, Fierer, & Bradford, 2009). Here, we used a space-for-time approach to explore potential implications of the replacement of dead *Q. suber* trees by co-existing species. In agreement with our fourth hypothesis, we found significant differences among species in their impacts on nematode communities. Therefore, our results support strong potential for large long-term impacts of *Q. suber* decline on soil food webs under the likely scenario of a loss of *Q. suber* dominance in favour of non-declining shrub and tree species.

In both forest types, shrubs exhibited soil nematode communities largely similar to those of dead trees and were characterized by

low index values indicative of altered, degraded food webs dominated by fungi. Pioneer shrubs tend to occupy the gaps open after tree death in declining Mediterranean forests, due to their faster growth and better ability than most tree species to tolerate the increase in radiation levels and drought stress derived from the loss of the canopy cover (Ibáñez, Gómez-Aparicio, Ávila, Pérez-Ramos, & Marañón, 2017). This shrub-dominated successional stage can become remarkably persistent, a condition called arrested succession (Acácio, Holmgren, Jansen, & Schrotter, 2007). In this scenario, we could expect that the long-term indirect effects of *Q. suber* decline on soil food webs due to shrub dominance would maintain the short-term direct effects of tree mortality, leading to simplified and unstable soil food webs with slow recovery of the initial conditions characteristic of a healthy forest. Our results also suggest that the eventual recovery of these degraded food webs will very much depend on the identity of the tree species that can establish in shrub-dominated microsites, with tree species characterized by high-quality litter (e.g., *Q. canariensis*) counteracting the negative effects of tree mortality and leading to faster recoveries of soil functionality.

5 | CONCLUSIONS

This work shows for the first time that changes in nematode communities can provide important insights into the sensitivity of soil food webs and soil functioning to the process of decline of a dominant tree species in mixed forests. Specifically, our findings demonstrate that the decline of *Q. suber* in Mediterranean forests invaded by the aggressive exotic pathogen *P. cinnamomi* could lead to simplified, degraded food webs, with lower resilience to disturbances. Moreover, these changes in soil food webs would have important consequences for soil biogeochemical processes, potentially causing transient increases in N and C mineralization, but eventually leading to nutrient cycles strongly dominated by the slow fungal decomposition channel, characterized by low nutrient turnover and availability for plants that could limit post-mortality recovery of plant cover (Ávila et al., 2016). Overall, our findings are not only pertinent to Mediterranean *Q. suber* forests, but also to the increasing forest cover affected by *P. cinnamomi* and many other *Phytophthora* species world-wide (Cahill, Rookes, Wilson, Gibson, & McDougall, 2008; Hansen, 2015), showing the strong implications that an ongoing deterioration of tree health will have for soil food webs in both the short- and long term.

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AUTHORS' CONTRIBUTIONS

J.D.B. and L.G.A. conceived the ideas and designed methodology. J.D.B. conducted the nematode extraction and identification. G.D. and N.E. provided critical support for nematode identification. J.D.B., assisted by L.G.A., conducted the data analysis. J.D.B. and L.G.A. led the writing of the manuscript, and all authors substantially contributed to the subsequent drafts.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository, <https://doi.org/10.5061/dryad.q5p514v> (Domínguez-Begines, De Deyn, García, Eisenhauer, & Gomez-Aparicio, 2018).

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