Applied Soil Ecology 136 (2019) 122–138

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Plant and soil microfaunal biodiversity across the borders between arable and forest ecosystems in a Mediterranean landscape

L.E. Jackson[a,*], T.M. Bowles[b], H. Ferris[c], A.J. Margenot[d], A. Hollander[e], P. Garcia-Palacios[f], T. Daufresne[g], S. Sánchez-Moreno[h]

[a] *Department of Land, Air and Water Resources, University of California Davis, Davis, CA 95616 USA*
[b] *Department of Environmental Science, Policy and Management, University of California Berkeley, Berkeley, CA 94720 USA*
[c] *Department of Entomology and Nematology, University of California Davis, Davis, CA 95616 USA*
[d] *Department of Crop Sciences, University of Illinois Urbana-Champaign, Urbana, IL 61801 USA*
[e] *Information Center for the Environment, University of California Davis, Davis, CA 95616 USA*
[f] *Departamento de Biología y Geología, Física y Química Inorgánica y Analítica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, 28933 Móstoles, Spain*
[g] *Department of Soil Ecology, UMR 210 Eco&Sols, INRA, F-34060 Montpellier, France*
[h] *Unidad de Productos Fitosanitarios (DTEVPF), Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain*

ARTICLE INFO

Keywords:
Afforestation
Nematode metabolic footprint
Pasture
Predator-prey
Soil carbon
Succession

ABSTRACT

The distribution of organisms across ecosystem borders can be indicative of trophic interactions, food-web dynamics, and the potential for recovery after disturbance. Yet relatively little is known regarding patterns and ecology of belowground organisms across borders. Our hypothesis was that incremental zonation of vegetation and soil properties at the interface between cultivated fields and forests may facilitate the recolonization of a more complex soil faunal assemblage after disturbance ceases. Vegetation, soil characteristics, and soil nematodes (indicators of disturbance) were studied at the interface between arable and natural ecosystems (oak forest and maquis shrubland) in southwestern France. Sampling was along 23-m long transects, at six positions (center and edge of grain fields, both sides of field borders, and bands of shrub and forest vegetation) at four sites. Plant functional groups changed more markedly than species richness. Total soil carbon (C) and nematode biomass were 3.5 and 6 times higher in the forest than in the center of the cultivated fields. The nematode Structure Index gradually increased from fields to forests, along with higher total and labile soil C pools, litter, root C, and root C:N, and more negative root δ^{15}N. Microbivore nematodes were related to labile and total soil C. Structural equation modeling indicated that nematode predators and prey were both affected by total soil C, but proximity to the forest was important for predators, whereas plant community complexity was important for prey (i.e., microbivorous nematodes). The forested borders had minor effects on zonation of nematode assemblages and soil ecosystem services within the fields, yet woody vegetation may have facilitated recolonization by plants and soil fauna after tillage ceased and probably provided benefits for production of livestock (i.e., shade and erosion reduction) that were not measured. During plant succession, litter C and N apparently decomposed slowly into active forms in the soil, creating habitats for more K-selected, larger-bodied nematodes. Due to less cultivation and higher C inputs during the past 50 years, the more homogeneous landscape may promote more complex soil food webs, but less total agrobiodiversity, compared to the mosaic of diverse ecosystems that occurred in the ancient cultural landscape of the past.

1. Introduction

In agricultural landscapes, biodiversity and associated ecosystem services are enhanced by patches of natural vegetation, especially when they serve as corridors and movement channels that maintain species interactions and dispersion (Fischer et al., 2006; Mitchell et al., 2014). Complex landscapes composed of traditional agroecosystems adjacent to natural ecosystems are typically richer in biodiversity than

---

[*] Corresponding author.

E-mail addresses: lejackson@ucdavis.edu (L.E. Jackson), timothy.bowles@berkeley.edu (T.M. Bowles), hferris@ucdavis.edu (H. Ferris), margenot@illinois.edu (A.J. Margenot), adhollander@ucdavis.edu (A. Hollander), pablo.garcia.pala@gmail.com (P. Garcia-Palacios), tanguy.daufresne@supagro.inra.fr (T. Daufresne), sarasm@inia.es (S. Sánchez-Moreno).

https://doi.org/10.1016/j.apsoil.2018.11.015
Received 15 June 2018; Received in revised form 19 November 2018; Accepted 27 November 2018
Available online 08 January 2019

landscapes dominated by intensive agriculture (Concepción et al., 2012; Fischer et al., 2006; Jackson et al., 2012). The borders between ecosystems are places where the movement of organisms, by either passive or active transport, may cause changes in trophic interactions and food-web dynamics (Casini et al., 2012; Concepción et al., 2012; Tscharntke et al., 2005). As a result, ecosystem services may be enhanced by the propensity for these spillover effects (e.g., pest suppression, nutrient cycling, and recovery from disturbance) to occur on both sides of the border.

Soil biota discriminate among land use types in many types of landscapes (Cluzeau et al., 2012; Sánchez-Moreno et al., 2011). Forests tend to support more soil fungi, fungal-feeders, and a more structured soil faunal community than grasslands and meadows, while tilled, arable systems have lower soil biodiversity and abundance than these undisturbed ecosystems (Paula et al., 2014; Steel and Ferris, 2016; Villenave et al., 2013; Zhao and Neher, 2013). Greater soil biodiversity and biomass have been associated with increases in ecosystem functions and services, such as soil quality and crop productivity (Culman et al., 2010; Ferris, 2010; Ferris and Tuomisto, 2015; Nielsen et al., 2015).

Borders of natural and semi-natural ecosystems are hypothesized to serve as sources of biodiversity to restore the communities of soil biota in arable fields (French et al., 2017), but the dense particulate soil matrix may slow or deter this process. Most studies have focused on localized factors that contribute to higher diversity of microbes, nematodes, and other soil fauna, such as management occurring within a field. Such factors include organic matter additions and reduced or no tillage (Neher, 2010; Zhang et al., 2017), avoidance of synthetic pesticides and fertilizers (Hodson and Lewis, 2016; Song et al., 2016), and past legacies of a previous vegetation type (DuPont et al., 2014). Evidence exists for higher soil biodiversity in field margins and near forest edges (Culman et al., 2010; D'Acunto et al., 2016; Mueller et al., 2016; Sechi et al., 2017), yet little is known about the flux of soil biota across ecosystem interfaces, and the implications for ecosystem services.

Soil nematodes are excellent indicators because they are trophically diverse, indicative of the structure of the whole soil food web, and sensitive to environmental factors (Bongers, 1990; Ferris et al., 2001; Pulleman et al., 2012). Several metrics derived from nematode community data (e.g., functional indices, metabolic footprints) describe how management impacts the soil food web and its functions, such as predator–prey relationships and soil nutrient mineralization (e.g., Holtkamp et al., 2011; Ferris et al., 2001, Ferris et al., 2012). Tardigrades also play a role in the soil food web, such as by predation on nematodes (Sánchez-Moreno et al., 2008).

A recently proposed predator–prey power relationship indicates that the biomass pyramid becomes increasingly bottom-heavy (i.e., lower predator-prey ratio) in more productive ecosystems, based on abundant data from aboveground terrestrial and aquatic ecosystems (Hatton et al., 2015). No studies, to our knowledge, have tested this idea for the soil food web. Since cultivated and forest ecosystems would be expected to show differences in soil food webs (Culman et al., 2010; Tsiafouli et al., 2015), and because soil carbon (C) tends to be higher in undisturbed ecosystems (Steenwerth et al., 2002; Tsiafouli et al., 2015), nematode communities provide an opportunity to test this hypothesis. Microbivorous nematodes (i.e., bacterivores and fungivores) are prey for predator nematodes (Zhang et al., 2017), and a log-log model of the biomass of microbivores and predators may indicate that more C-rich soils (i.e., in forests) can support a higher ratio of prey to predators than more impoverished soils.

The Mediterranean Basin has a millennial history of heterogeneous landscapes composed of forest, shrubland, woodlots, pastures, and fields cultivated for grain, livestock, vineyards, and orchards. Traditional agroforestry systems were once widespread and included transhumance systems with extensive animal husbandry, seasonal movement of livestock, shelter belts for animals, and pollarding for fodder and wood (Marull et al., 2015; Smith et al., 2012). In some locations in southern France, where such heterogeneous landscapes still persist, plant species at the field-woodlot edge were variable among sites and influenced by history of forest cutting and coppicing, whereas ground beetle diversity at the edges was consistently a mix of species from both habitats (Alignier and Deconchat, 2013; Bassa et al., 2011; Roume et al., 2011). Vineyards in the region showed low soil biological activity and soil quality, but high structure of nematode species assemblages, especially in acidic soils, where fungal feeders were important (Coll et al., 2011; Salome et al., 2014).

This study examined vegetation, soil C, and soil nematodes at an ecosystem interface from arable to forest ecosystems in a traditional Catalan livestock system on acidic soils developed on schist parent material. The objectives of this study were to: 1) Describe the differences in soil properties (total and labile C, texture, and pH), vegetation (cover, taxa, and life forms), and nematode communities (taxa, indices, and metabolic footprints) at several positions along the disturbance gradient between cultivated fields and forest ecosystems. 2) Examine the ecological factors affecting the changes in soil nematodes with multivariate statistics. 3) Consider how the zonation of plant and soil faunal communities at ecosystem borders affects ecosystem services after disturbance in a heterogeneous landscape of arable fields and natural ecosystems.

The following hypotheses were made: 1) Gradual changes in nematode communities may occur across these distinct zones, reflecting incremental changes in soil properties and possibly directional movement and recolonization by soil fauna when disturbance ceases (Culman et al., 2010; Rossetti et al., 2015; Steenwerth et al., 2002). 2) As disturbance decreases and soil C increases from cultivated to forest ecosystems, microbivores may increase, along with generalist and specialist predators (Tsiafouli et al., 2015), causing changes in trophic relationships (De Roos et al., 2008; Saleem et al., 2012). And 3) The composition of the plant community and its root characteristics may influence the biomass and structure of nematode communities, or instead, more of the variation in nematode communities may be explained by soil C (Hu et al., 2016).

2. Materials and methods

2.1. Sites

The study area was a landscape of approximately 7 km^2 in area, situated south of the town of Ille-sur-Têt, reaching between Saint Michel de Llotes and Casefabre in the Pyrénées-Orientales department of southern France (Appendix A). It consisted of a triangular area on a ridge with hilly topography (42°36′46.86″N2°36′39.77″E (southwest corner) to 42°36′46.86″N2°36′39.77″E (north corner) to (42°37′12.01″N2°39′59.84″E) (southeast corner). Four sampling sites were chosen within this area (Sites 1 to 4, Appendix A). The elevation in the study area ranges from approximately 300 to 500 m above sea level.

The mild Mediterranean-type climate has mean annual minimum and maximum temperatures of 11.3 °C and 20.1°, respectively, and mean precipitation of 564.6 mm in the more coastal city, Perpignan-Rivesaltes, 20 km away, based on data collected 1981 to 2010 by Météo-France (accessed April 28, 2017 at https://www.infoclimat.fr/stations-meteo). The lowest amounts of precipitation occur in June, July, and August ($\leq$26 mm/month).

Evergreen holm oak (*Quercus ilex*) dominates the landscape, forming dense forests of short-statured trees with little understory. Also abundant is mid-successional maquis shrub vegetation composed of species such as rockrose (*Cistus* spp.), tree heath (*Erica arborea*), and leguminous shrubs (e.g., brooms such as *Genista cinerea*). Since the middle Neolithic, this vegetation mosaic has been influenced by agriculture and pastoralism (Heinz et al., 2004). Arable soils have probably been in cultivation for hundreds of years given the long anthropogenic history of the region (Brochier et al., 1998). In the flatter areas of the landscape, a few scattered fields are currently cultivated and seeded with grain for springtime grazing for cattle before summering them in pastures at higher elevations. According to local people, many of these fields were in cereals before the 19th century. Some were in vineyards until the mid-20th century, at which time they were either abandoned or intermittently in cereal production for seasonal cattle forage.

At the four sampling sites, tilled fields were adjacent to oak forest, the field margins displayed minimal livestock trampling, no road was present at the ecosystem interface, and no rock outcrops occurred in the non-cultivated zones. Slopes were close to level. Soils at all sites are classified as Luvisols (FAO/World Reference Base) or Alfisols (USDA Soil Taxonomy) and are developed on schist parent material. In the production system, soils are tilled to approximately 10 cm deep before the fall rains. Prior to tillage, amendments are occasionally added, such as lime, peach processing waste from nearby canneries, or as much as 50 kg N ha^{-1} as mineral fertilizer. No such amendments were added in the 2013–2014 growing season. The fall seeding rate was approximately 25 kg ha^{-1} for oats (*Avena sativa*), and for Sites 3 and 4, 10 kg ha^{-1} for vetch (*Vicia sativa*). No irrigation was available. At Sites 3 and 4, periods of two weeks of cattle grazing were followed by two weeks of no grazing during April and May 2014. For the cow-calf pairs, the stocking rate was approximately 1 animal unit month (AUM) per ha. The fields were withdrawn from grazing for the rest of the year, when cattle were moved to higher elevations in the mountains. For Sites 1 and 2, less detail on the grazing system was available.

To assess changes in the landscape through time, satellite and aerial images of the area were available to estimate the cover of cultivated land in the study area. With Landsat 5 and 8, satellite images were used for a 27-year comparison of 1987 vs. 2014 (Appendix A); 1987 was the earliest date when relevant data were available. With Géoportail (https://www.geoportail.gouv.fr/), a 50-year comparison was possible for ca. 1960 and 2015, the only two years for which aerial images were available for the area. The Géoportail images are finer resolution than the Landsat images, allowing more quantitative estimates of cultivated area.

Each site was located on the Landsat and Géoportail images. The relative change in the area of the cultivated field at each site was estimated for each time point (Appendix A). Since the finer resolution Géoportail aerial images were clear enough to distinguish features such as field rows, surface homogeneity indicative of recent tillage, and woody vegetation, the borders sampled in 2014 were examined for open ground, herbaceous vegetation, or woody vegetation. The borders could then be compared on the ca. 1960 and 2015 images (Appendix A).

The sampling design consisted of three 23-m transects per site with six positions along each transect, resulting in 72 sampling points in the study. The zonation includes an early successional agroecosystem (tilled and grazed grain fields), the edge of tilled ground, a mid-successional band of maquis shrub vegetation periodically cleared along the field edge, and late successional evergreen oak forest along transects. The sampling positions were situated from the line of current year's tillage (designated zero). The positive distances increase toward the center of the field and were in cultivated grain (+0.25 m, +4m, and +18 m). The negative distances progress away from the field and into the forest, and are therefore increasingly less disturbed (-0.25 m, -2.5 m, and -5m). Plots were centered at these exact distances from the line of tillage, except when an obstacle such as a fence or boulder was present. At -0.25 m, soils may have been tilled in the recent past when implements may have overreached the current line of tillage. At -2.5 m, shrubs were dominant, and at -5m, dense evergreen oak forest was present. Sampling further into the forest was avoided because the topography often became steeper and rockier, with high heterogeneity in soil (solum) thickness. Each plot was 6 m^2 (6 m × 1 m), centered in the transect sampling point, and extending 3 m perpendicular to the transect on each side (e.g., the -2.5 m sampling plot encompassed -2 to -3 m on the line of the transect). The exceptions were the +0.25 m and -0.25 m zones (6 m × 0.5 m) which were by necessity narrower to focus on the current cultivated/non-cultivated boundary. Sampling occurred from 27 to 30 April 2014, towards the end of the rainy season.

2.2. Data collection

Vegetation sampling consisted of estimating the percentage cover of all plant species in the 72 plots. Plant species were grouped into eight categories: annual graminoids; annual legumes; annuals in other families; perennial graminoids; perennial herbaceous legumes; perennial herbaceous species in other families; perennial woody legumes; or perennial woody species in other families. Species were identified according to Tison and de Foucault (2014).

Soil properties for each plot were determined for a composite soil sample from four cores (0 to 12 cm deep; 4 cm diameter) per 6 m^2 or 3 m^2 plot. A brass ring was pounded into the soil, and the surface litter was collected before removing the core. Soil from each composite soil sample was mixed and subsampled, then stored on ice for a maximum of 8 h before refrigerating up to three weeks prior to soil analysis or air-drying. Gravimetric water content (GWC) was measured on all samples by drying a subsample at 105 °C for 48 h. Soil particle size was determined by the laser diffraction method (Eshel et al., 2004). Soil pH and electrical conductivity (EC) were determined in a 1:2.5 soil:water solution (Thomas, 1996). Total soil C and nitrogen (N) were analyzed at the University of California Davis Stable Isotope Facility on an Elementar Vario EL Cube elemental analyzer. Permanganate-oxidizable C (POXC) was determined according to Culman et al. (2012) as an indicator of labile C. Available phosphorus (P) was measured using the Bray I method (Bray and Kurtz, 1945), which is a measure of P availability suited to the acidic pH of soils at the study sites.

Nematode and tardigrade extraction from fresh soils used a modification of the Baermann funnel method (Barker, 1985). A 175 g subsample from each of the 72 plots was soaked overnight prior to extraction. The total number of nematodes and tardigrades per sample was counted under a compound microscope. After counting, at least 150 nematodes were identified to genus or family according to (Bongers, 1994) under an inverted microscope. Data are expressed as nematodes or tardigrades per 100 g dry soil. Tardigrades were not identified.

Fine roots ($\leq$2mm diameter) were picked out of the soil–water solutions before extraction of nematodes. Roots were dried at 60 °C, ground, and analyzed for total soil C and N as described above and for $\delta^{13}C$ and $\delta^{15}N$ with the same analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer.

2.3. Nematode analysis

To categorize soil nematodes according to life history strategies and to estimate biomass, the NINJA program was used (Sieriebriennikov et al., 2014). The categories range from r-selected opportunists that are rapidly growing and reproducing to slow-growing K-selected taxa (Bongers, 1990). Soil food web indices (Ferris et al., 2001), which are based on life history strategies and trophic behavior, included the Basal Index (BI), an indicator of disturbance; the Enrichment Index (EI), an indicator of conditions supporting fast-growing bacterivores; the Channel Index (CI), an indicator of fungal-mediated dominance of organic matter decomposition; and the Structure Index (SI), an indicator of more highly structured soil food webs and enhanced ecological functions due to higher trophic links. The Plant Parasite Index (PPI) refers to plant parasitic nematodes.

The biomass or metabolic activity of species are often more useful measures of their abundance than numbers of individuals (Ferris, 2010; Ferris and Tuomisto, 2015). Nematode metabolic footprints were calculated according to the following equation (Ferris, 2010):

$$F = \sum (N_t(0.1\left(\frac{W_t}{M_t}\right) + 0.273(W_t^{0.75})))$$

where N_t is the number of taxa in each group of interest (for example predators), and W_t is the estimated weight of the taxa. The weight of life-time C mineralized by each taxon is derived from the molecular weights of C and O_2, as 12/44 or 0.273 of the mass of CO_2 evolved (Ferris, 2010). M_t is the cp classification of taxon t. The cp classification refers to 1 to 5 levels of a colonizer-persister series. In soil conditions just after resource addition or following a soil disturbance such as tillage, rapidly reproducing, low cp value nematodes flourish (Bongers and Bongers, 1998). In contrast, less disturbed and more resource-conserved communities support large bodied, slowly reproducing, high cp value nematodes, such as generalist and specialist predators.

For testing the log-log predator-prey power relationship of Hatton et al. (2015), biomass of microbivores was the summation of the biomass of bacterivores and fungivores, as classified according to Yeates et al. (1993). Biomass was based on the body size of female adults of each nematode species, calculated per Andrássy (1956) detailed in Ferris (2010), and provided in http://Nemaplex.ucdavis.edu. Note that nematodes classified as fungivores feed only on fungi, but those that are root associates may be feeding on either hyphae or root hairs. Both were categorized as microbivores herein. Summations of the biomass of generalist (omnivores feeding on diverse food sources) and specialist (carnivores feeding preferably on other nematodes) predators (Steel and Ferris, 2016) were used for predator biomass.

Species richness (R) is the number of nematode taxa (Ferris and Tuomisto, 2015). True species diversity, or the effective number of species or taxa, takes into account both the species richness and the degree of equality of their abundances (Ferris and Tuomisto, 2015; Jost, 2007, 2006; Tuomisto, 2010). When the species are equally abundant, the effective number of taxa (or true diversity) is R. For this calculation, we used q = 1 in the equation of Ferris and Tuomisto (2015) to weight each species by its proportional abundance.

The diversity-weighted abundance (θ) was proposed by Ferris and Tuomisto (2015) as the product of the diversity within a functional class and abundance parameters, for the purpose of comparing guilds performing the same function with different assemblages of like species, and serving as an indicator of the aggregate biomass of the effective number of species.

$$\theta = (({}^{q}D)^{b})\ .\ \sum_{i=1}^{R} Ai$$

where ${}^{q}D$ is the true diversity as calculated according to Ferris and Tuomisto (2015), b is a scalar that allows adjustment of the perceived importance of diversity (in the analyses herein we used b = 1), and A_i is the biomass or metabolic footprint abundance of the R species in the functional class of interest.

2.4. Statistical analyses

Mixed effects analysis of variance (ANOVA) was performed on soil, root, nematode, and tardigrade variables using the lme4 and lmerTest packages in R (Bates et al., 2015; Kuznetsova et al., 2016). Position (each of the six zones) was considered a fixed effect, while site and transect within a site were considered random effects. Diagnostic plots showed that most violations of assumptions of heteroscedasticity and normality were due to higher variance in the forest positions. A log transformation (or log + 1 if the variable contained zeroes) fixed these issues, and data were then back-transformed. Means, standard errors, F-statistics, and p values (Kenward-Roger approximation for degrees of freedom) were assessed for all variables. Regressions were conducted with the lm() function in R.

To examine the spatial distribution of plant and nematode communities, multivariate analysis of vegetation categories (percent cover) and, separately, nematode communities (biomass per unit of soil for each taxa) used non-metric multidimensional scaling (NMDS) with the Bray dissimilarity metric in the vegan package in R. The interpretation of stress value was made according to Clarke (1993). Confidence ellipses (95%) were calculated for each position. Correlations between the NMDS ordination of nematode communities and soil and root variables were tested with 1000 permutations in the *envfit* function in the vegan package in R (Oksanen et al., 2018).

To investigate the relationships between entire datasets of plants, nematodes, and soil properties, Mantel tests and partial Mantel tests were employed using the vegan package in R. The datasets consisted of cover of plant taxa, plant functional groups (i.e., eight categories above), biomass of nematode taxa, nematode metabolic footprints by functional group (i.e., herbivores, bacterivores, fungivores, generalist predators, and specialist predators), and soil properties (i.e., clay, silt, sand, EC, Bray P, total soil C and N, soil C:N ratio, POXC, and gravimetric moisture). Bray distance matrices were used.

Structural equation modeling (SEM) explored how predator and prey nematodes were influenced by disturbance, plant communities, and total soil C. We developed two similar models with either diversity-weighted biomass of predatory nematodes (model A) or prey nematodes (model B) as final endpoints, based on the following expectations. Distance (indicative of a disturbance gradient from arable to forest sites) was considered the first driver of our models, affecting plant richness and functional diversity, root biomass and C, and total soil C. Predatory and prey nematodes were expected to be differentially affected by distance, since large-bodied, predatory nematodes are more sensitive to physical and chemical disturbance than resistant, microbivorous nematodes (Ferris, 2010). Prey nematodes may be more affected by the plant community than predatory nematodes, based on previous work showing that the influence of the plant community composition on soil nematodes may surpass that of soil properties (Veen et al., 2010) and that plant community composition affects bacterivore and fungivore nematodes, through both underground root and aboveground litter plant inputs (Wardle et al., 2004). We also expected total soil C to increase from cultivated to forest ecosystems, positively affecting prey and predatory nematodes. Such positive effects, often mediated by increases in the fungivore-mediated channel, have been previously reported in planted and natural forests (Shao et al., 2015; Zhang et al., 2015).

The goodness-of-fit of the SEM models was assessed with the χ^2 test and the GFI and RMSEA indices (García-Palacios et al., 2011). High p-values for the χ^2 test indicate satisfactory model fit, and RMSI and GFI indices were interpreted following Schermelleh-Engel et al. (2003). Path coefficients, estimated by the maximum-likelihood technique, are interpreted as partial correlation coefficients of regressions, indicating the strength of each relationship. Aboveground plant community attributes (number of plant species and plant functional groups) were collapsed into a composite “Plant community complexity” variable, and belowground root characteristics (root biomass and C) into a single “Roots” variable. This allows conceptually related variables to be considered together and associated into a single path coefficient (García-Palacios et al., 2011), simplifying the model structure and aiding its interpretation. SEM models were run with the IBM SPSS AMOS 25 statistical package (Arbuckle, 2014).

3. Results

3.1. Landscape

Examination of the Landsat satellite images for the 7 km^2 study area indicates that 1987 had more open terrain and less woody cover than 2014 (Appendix A). Aerial images from Géoportail show less cultivated area in 2015 (approximately 5% of land cover) as compared to ca. 1960 (approximately 15% of land cover).

Sites 1 and 2 in the northern part of the landscape were single fields surrounded by broad expanses of forest (Appendix A). Both fields were larger in ca. 1960 than 2015 based on Géoportail images, and in 1987 compared to 2014 based on Landsat images; woody vegetation encroached with time into previously cultivated land. Sites 3 and 4 were slightly larger in ca. 1960 than in 2015. They were part of a network of fields often with narrow strips of forest in between them in 2014. More forest was present here in 1987 than 2014 based on Landsat images (Appendix A). The network of fields was more open in ca. 1960 than 2015 based on Géoportail images. Consequently, Sites 3 and 4 were surrounded by phases of expansion and reduction of cultivated area during the 50-year period. For the sampled transects, the shrub and forest zones at the four sites are occupied by woody vegetation in the 2015 Géoportail images, based on viewing at a fine resolution scale of 1:1066 (Appendix A). In the ca. 1960 images, these zones of the transects are usually occupied by cultivated or bare ground. Thus, sampling took place in situations where cultivated land was replaced by woody vegetation since ca. 1960.

3.2. Vegetation

A distinct change in plant functional groups occurred between the cultivated and non-cultivated zones with the most pronounced differences between the line of tillage and the forest, as indicated by the strong separation of confidence ellipses around field vs. forest positions in the NMDS biplot (Fig. 1). This biplot shows that annual plants dominated at +4 m and +18 m positions in the cultivated fields, mainly due to oat and vetch cover (Appendix B and C). At +0.25 m, however, annual cover decreased, with a small increase in cover of perennial species (Fig. 1; Appendix B). Less plant diversity tended to occur in the +0.25 m position, which was tilled in the year of the study, compared to the -0.25 m position, which was tilled less recently. Dominance of perennials occurred in the -2m and -5m positions, with perennial woody legumes more important in the shrub than forest positions. The ellipses for these vegetation types were very small, especially for the forest position, indicating high similarity within and between sites. The stress value of 0.131 indicates that the biplot gives a good representation of the dissimilarity in plant functional groups across the set of transects.

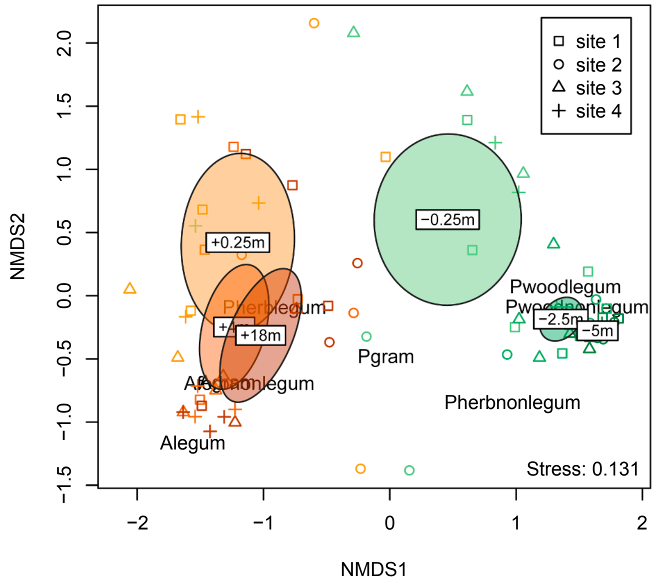


Fig. 1. Non-metric multidimensional scaling (NMDS) biplot showing the distribution of plant functional groups along the borders between arable and forest ecosystems on schist soils in the Pyrénées-Orientales, France. Distances are from the line of tillage; positive are cultivated and negative are towards the forest. Annual graminoid = Agram; Annual leguminous = Alegum; Annuals in other families = Anonlegum; Perennial graminoid = Pgram; Perennial herbaceous leguminous = Pherblegum; Perennial herbaceous in other families = Pherbnonlegum; Perennial woody leguminous = Pwoodlegum; Perennial woody in other families = Pwoodnonlegum. See Appendices B and C for the species composition and cover of the plant functional groups. n = 72 plots.

Plant cover was, on average, 96% in the forest at -5 m from the line of tillage, 74% in the shrub zone at -2m, and then decreased toward the line of tillage, with 34% and 39% cover at +4 m and +18 m, respectively, in the cultivated field (Appendix B). *Quercus ilex* was the dominant species in the forest, while *Cistus albidus* dominated the shrub zone, which also had the highest cover of perennial woody legumes. Plant species richness tended to be higher in the cultivated than non-cultivated zones, mainly due to high diversity of annuals in families other than the *Poaceae* and *Fabaceae* (Appendix C).

3.3. Soil properties and roots

Soil particle size fractions (sand, silt, clay) were remarkably similar at the four sites (Table 1). Soil texture was a silt loam at Sites 1, 3, and 4 and a sandy loam at Site 2. Sand content was higher in the shrub and forest positions than in the cultivated fields, and clay and silt content gradually decreased from the field to the forest. Gravimetric water content averaged 0.07 g H_2O g^{-1} dry soil in all positions, excluding the forest soil, which contained more moisture than any other zone (0.14 g H_2O g^{-1} dry soil on average). The soil pH was similar across all positions and sites, with a mean of 5.44. Soil EC, however, increased toward the forest, as did its variation. Higher mean Bray P occurred in the soil in the center of the field as compared to the forest soils. The accumulation of litter was higher under woody vegetation and little crop residue was present.

Total soil C was 3.5 times higher in the forest than the arable field (61 vs. 17 g C kg^{-1} soil, respectively), and for total soil N, the difference was more than two times higher (1.7 vs. 3.9 g N kg^{-1} soil, respectively) (Fig. 2). In the center of the arable field (+18 m), total soil C and N concentrations were higher than at +4 m from the line of tillage, but were not different from the line of tillage itself. For the non-cultivated positions, total soil C increased more rapidly toward the forest than did total soil N. The total soil C:N ratio increased from 10.3 to 15.2 (data not shown). The labile C pool represented by POXC showed the same general pattern as total soil C and N, although more variation tended to occur, especially in the cultivated zones (Fig. 2). A trend for a slightly lower ratio of POXC:total soil C occurred in the shrub and forest zones.

Fine root biomass was lowest near the line of tillage (+0.25 m and -0.25 m positions), and higher in the center of the cultivated field, and in the shrub and forest positions (Table 1). Roots in the non-cultivated zone had higher C content than roots in the cultivated zone, even in the -0.25 m position, where woody roots from the shrub zone were observed. Little change occurred in root $\delta^{13}C$ along the gradient. Root C:N was somewhat higher in the non-cultivated zones, gradually increasing from 24 in the center of the cultivated field to 35 in the forest. Root $\delta^{15}N$ was highest in the center of the cultivated field, with a gradual decrease toward the forest.

3.4. Soil nematodes

Twenty-six nematode taxa were identified at the study sites. Of them, 12 were bacterivores, 4 were fungivores, 3 were herbivores, and 7 were predators (3 generalist and 4 specialist predators). The total number of nematodes was similar across the positions, averaging 871 nematodes 100 g^{-1} soil (Table 1). Yet nematode biomass was six times higher in the forest than in the center of the cultivated field, reflecting larger body sizes on average in the forest. The bacterivore footprint in the -5m forest position was nearly three times higher than in the cultivated positions, whereas the fungivore biomass (Fig. 3) and footprint (Table 1) showed no differences along the transects. The percentage of fungivores was also similar, averaging 27% (data not shown). Metabolic footprints show greater functional importance of generalist predators

Table 1

Soil properties, nematodes, tardigrades, and roots in the top 12 cm of soil along transects from fields (+18 m, +4 m, and +0.25 m from the line of tillage) towards the forest (-0.25 m, -2.5 m, and -5 m from the line of tillage) from four sites on schist soils in the Pyrénées-Orientales, France. Different letters indicate significance at $p \leq 0.05$. See Fig. 3 for soil C and N, and Fig. 4 for Structure Index (SI). n = 72 plots.

Properties	Distance from line of tillage along the arable → forest transects																	
	+18 m			+4 m			+0.25 m			-0.25 m			-2.5 m			-5 m		
	mean	SE		mean	SE		mean	SE		mean	SE		mean	SE		mean	SE	
Soil																		
Sand (%)	42.8	3.1	**a**	41.3	3.5	**a**	42.6	3.1	**a**	44.6	2.8	**ab**	49.6	2.0	**bc**	52.7	1.6	**c**
Silt (%)	51.5	2.7	**bc**	52.4	3.0	**c**	51.6	2.7	**bc**	50.1	2.5	**bc**	46.1	1.8	**ab**	43.3	1.4	**a**
Clay (%)	5.8	0.5	**c**	6.3	0.6	**c**	5.8	0.5	**c**	5.3	0.4	**bc**	4.3	0.2	**ab**	4.0	0.2	**a**
Gravimetric moisture (g g^{-1})	0.06	0.00	**a**	0.06	0.00	**a**	0.07	0.01	**a**	0.08	0.02	**a**	0.07	0.01	**a**	0.14	0.01	**b**
pH	5.5	0.1		5.3	0.1		5.4	0.1		5.5	0.1		5.5	0.1		5.5	0.1	
EC (µS cm^{-1})	105.5	6.0	**a**	88.9	4.3	**a**	94.5	6.9	**a**	103.2	8.4	**a**	167.1	22.5	**b**	262.3	34.1	**c**
Bray P (µg g^{-1})	71.0	8.2	**b**	43.3	11.7	**a**	48.1	12.3	**ab**	49.2	13.6	**ab**	51.9	13.1	**ab**	26.1	3.6	**a**
Litter (mg cm^{-2})	74	32	**a**	73	41	**a**	187	87	**a**	897	322	**b**	3812	685	**c**	6070	605	**c**
Soil nematodes and tardigrades																		
Nematodes (No. 100 g^{-1})	854	245		793	165		977	269		923	195		1057	164		1350	237	
Tardigrades (No. 100 g^{-1})	0.00	0.00	**a**	0.08	0.08	**a**	0.08	0.08	**a**	0.58	0.36	**a**	3.25	1.33	**b**	2.00	1.24	**ab**
Nematode biomass (µg 100 g^{-1})	0.18	0.04	**a**	0.24	0.06	**a**	0.33	0.11	**a**	0.39	0.10	**ab**	0.90	0.33	**bc**	1.1	0.3	**c**
Bacterivore footprint (µg C 100 g^{-1})	30.9	9.9	**a**	28.7	10.8	**a**	31.1	9.1	**a**	35.2	10.4	**a**	44.8	8.0	**ab**	111.8	23.1	**b**
Fungivore footprint (µg C 100 g^{-1})	29.1	8.6		19.3	4.2		27.8	10.4		33.0	9.1		29.4	6.3		17.3	5.4	
Herbivore footprint (µg C 100 g^{-1})	13.9	2.6		21.8	5.7		23.6	5.0		17.6	3.9		23.3	4.8		28.9	6.3	
Gen. predator footprint (µg C 100 g^{-1})	3.8	1.7	**a**	13.7	7.1	**ab**	22.0	8.9	**ab**	32.4	10.8	**bc**	108.5	53.4	**c**	121.5	46.4	**c**
Spec. predator footprint (µg C 100 g^{-1})	0.0	0.0	**a**	0.0	0.0	**a**	0.0	0.0	**a**	1.0	1.0	**a**	7.9	6.2	**a**	1.2	0.5	**a**
Channel index (CI)	69.3	4.4	**b**	71.5	5.9	**b**	69.8	4.5	**b**	75.7	4.2	**b**	69.6	4.0	**b**	33.9	4.1	**a**
Enrichment index (EI)	47.6	2.7		42.6	4.7		45.3	2.7		45.1	2.3		43.8	2.0		48.0	2.8	
Basal index (BI)	51.5	2.8	**b**	53.7	4.3	**b**	52.3	2.9	**b**	50.7	2.0	**ab**	45.5	2.2	**ab**	39.2	3.0	**a**
Plant parasite index (PPI)	2.2	0.0	**b**	2.2	0.0	**b**	2.1	0.0	**ab**	2.1	0.0	**ab**	2.0	0.0	**a**	2.0	0.0	**a**
Roots																		
Biomass (mg g^{-1} soil)	5.7	0.8	**bc**	3.3	0.5	**ab**	3.0	0.6	**a**	2.4	0.3	**a**	5.8	0.8	**bc**	8.7	2.0	**c**
Carbon (%)	30.7	1.5	**a**	31.9	1.0	**a**	33.5	0.8	**a**	37.9	0.9	**b**	40.2	0.7	**bc**	44.3	1.0	**c**
$\delta^{13}C$ permil	-28.4	0.2	**ab**	-28.6	0.1	**a**	-28.3	0.3	**ab**	-28.6	0.2	**a**	-27.9	0.2	**ab**	-27.7	0.2	**b**
Nitrogen (%)	1.3	0.0		1.3	0.0		1.3	0.1		1.3	0.1		1.4	0.1		1.3	0.1	
$\delta^{15}N$ permil	0.15	0.22	**d**	-0.22	0.19	**cd**	-1.07	0.34	**bc**	-1.35	0.30	**ab**	-1.83	0.32	**ab**	-2.49	0.56	**a**
Carbon:Nitrogen (C:N)	23.6	1.1	**a**	24.8	0.9	**a**	26.8	2.0	**ab**	31.1	2.3	**ab**	31.2	2.8	**ab**	34.6	2.3	**b**

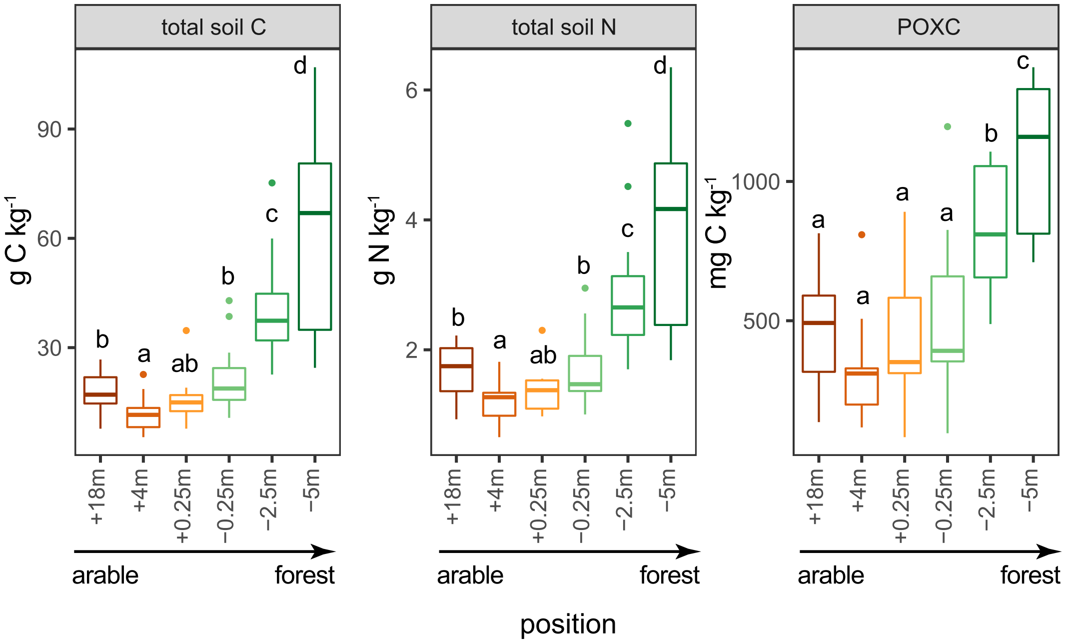


Fig. 2. Total soil carbon (C), nitrogen (N), and permanganate-oxidizable C (POXC) in the top 12 cm of soil along transects from arable to forest ecosystems on schist soils in the Pyrénées-Orientales, France. Distances are from the line of tillage; positive are cultivated and negative are towards the forest. Different letters indicate significant differences ($p \leq 0.05$). In the box plot graphs, the horizontal line is the median, and upper and lower "hinges" are the first and third quartiles, respectively. Upper and lower "whiskers" extend to the highest or lowest value, respectively, within 1.5 times the inter-quartile range (the distance between the first and third quartiles). Observations beyond this range are plotted as points. n = 72 plots.

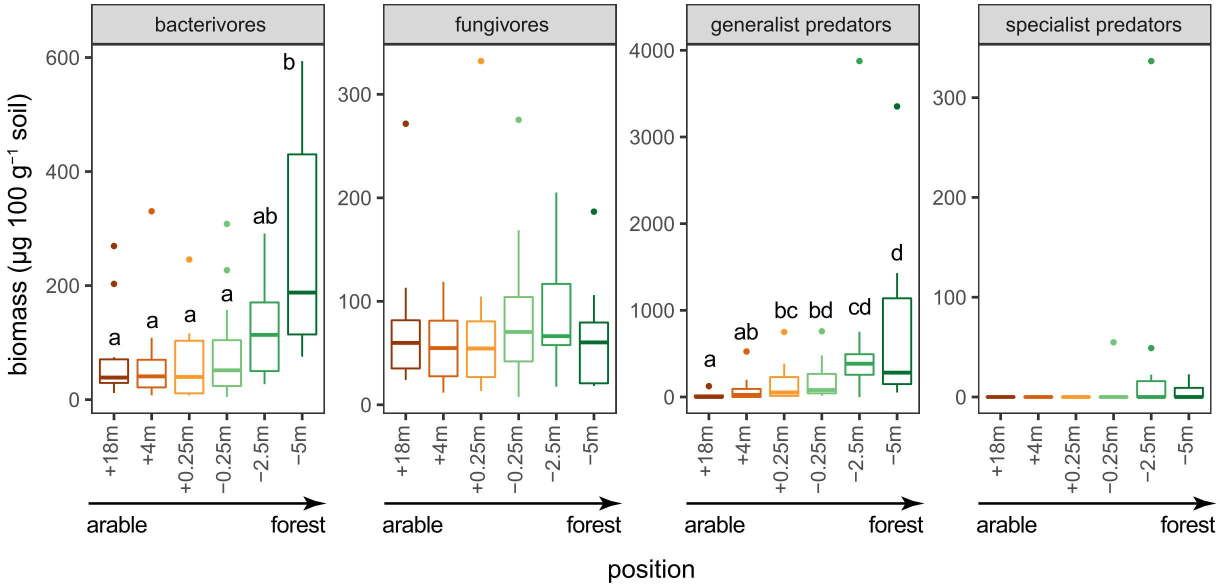


Fig. 3. Nematode biomass per 100 g of soil in the top 12 cm layer along transects from arable to forest ecosystems from four sites on schist soils in the Pyrénées-Orientales, France. Distances are from the line of tillage; positive are cultivated and negative are towards the forest. Biomass in four functional groups (bacterivores, fungivores, generalist predators, and specialist predators) was determined by counting nematodes by taxonomic grouping and calculating biomass (see text). Different letters indicate significant differences ($p \leq 0.05$). See Fig. 2. for plot format. n = 72 plots.

(i.e., omnivores) in the forest, while the metabolic footprints of the specialist predators were not different along the transect, due in part to the very high variation among the forest samples (Table 1). No specialist predators were found in the cultivated positions, and their biomass and the percentage of the total were highest in the forest (0.26%; data not shown).

Of the nematode functional indices, SI showed the most pronounced changes along the transect, with more structured nematode communities occurring in the shrub-dominated and forest zones, and gradually increasing from 4 in the center of the cultivated field to 36 in the forest (Fig. 4). Higher diversity-weighted biomass of generalist and specialist predators occurred in the shrub and forest positions, an indication of more effective species in these guilds in these locations. Tardigrades also increased in the forest (Table 1). Thus, the community became more complex and trophic structure became more developed toward the forest (Fig. 4). The CI was lowest in the forest, reflecting the high abundance of bacterivores in relation to fungivore abundance. Somewhat surprising is that no change in the EI was observed, but higher BI values, an indicator of depleted, perturbed food webs, were found in the arable areas compared to the forests. The PPI was highest in the center of the cultivated field and lowest in the shrub and forest positions.

Using regression, significant relationships were observed between soil C pools and microbivore (i.e., bacterivore + fungivore) biomass, true diversity, and diversity-weighted biomass. Here we present the

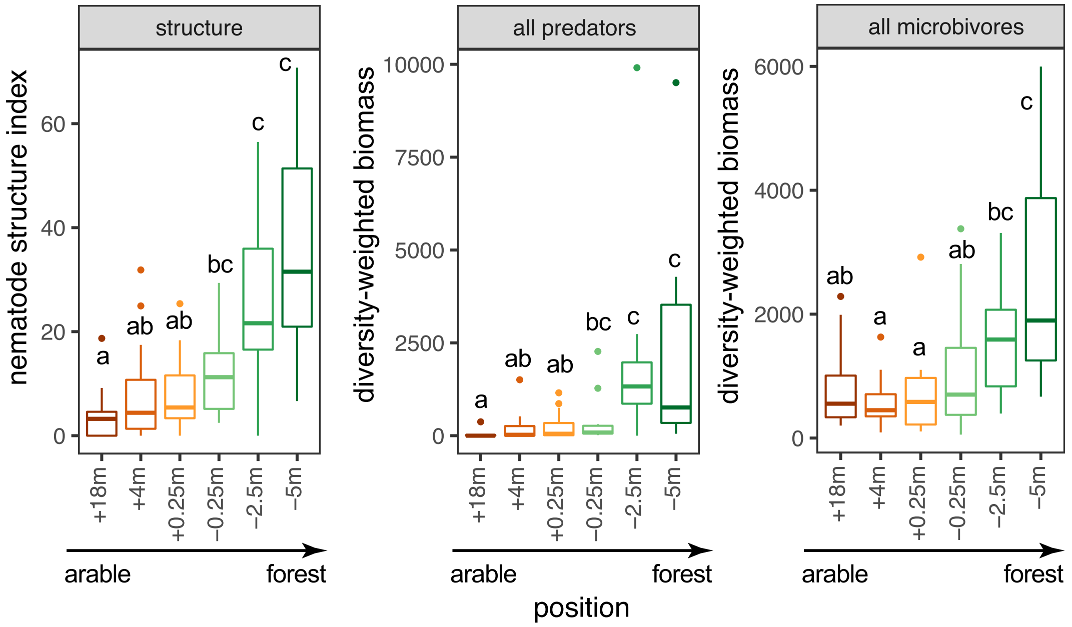


Fig. 4. Nematode diversity in the top 12 cm of soil along transects from arable to forest ecosystems from four sites on schist soils in the Pyrénées-Orientales, France. Distances are from the line of tillage; positive are cultivated and negative are towards the forest. Shown are Structure Index (maximum of 100), and diversity-weighted biomass of all predators and microbivores. Different letters indicate significant differences ($p \leq 0.05$). See Fig. 2 for plot format. n = 72 plots.

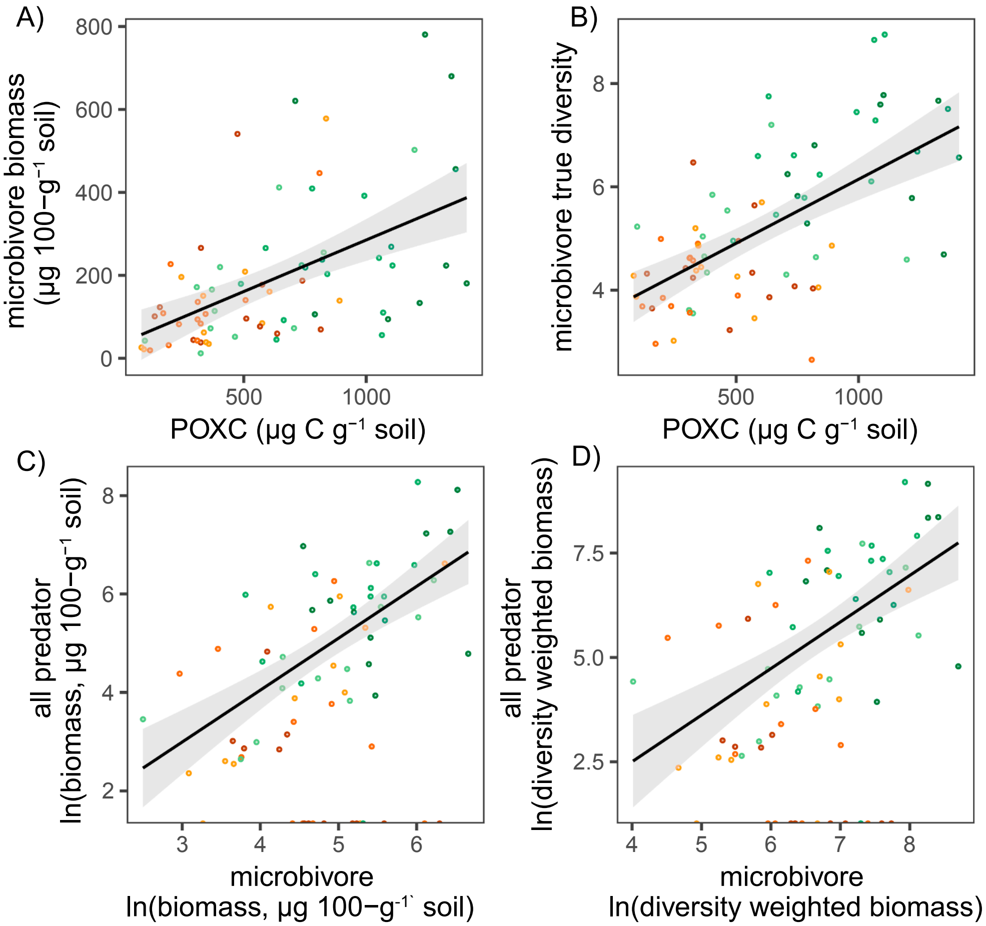


Fig. 5. Selected relationships between nematode biomass, diversity, and soil permanganate oxidizable carbon (POXC) across the arable to forest transects from four sites on schist soils in the Pyrénées-Orientales, France. For the predator – prey relationships, only samples with predators were included. a) microbivore (bacterivore + fungivore) biomass vs. POXC (slope = 0.248; $R^2 = 0.28$, $p < 0.0001$); b) microbivore true diversity vs. POXC (slope = 0.002; $R^2 = 0.38$; $p < 0.0001$); c) ln relationships between predator vs. microbivore (i.e., prey) biomass (slope = 1.03; $R^2 = 0.44$; $p < 0.05$); d) ln relationships between predator vs. microbivore (i.e., prey) diversity-weighted biomass (slope = 1.00; $R^2 = 0.32$; $p < 0.01$). n = 72 plots.

most noteworthy examples (Fig. 5). The biomass and true diversity of microbivores were related to POXC (slopes of 0.25 and 0.002, R^2 of 0.28 and 0.38, and $p < 0.0001$, respectively) (Fig. 5a and 5b). Total soil C shows a similar pattern but with lower R^2 for microbivore biomass (R^2 of 0.17 and $p < 0.01$), and higher R^2 for true diversity (R^2 of 0.44 and $p < 0.01$). Fungivore biomass was less responsive than bacterivore biomass to POXC (R^2 of 0.08 and $p < 0.05$ for fungivores; R^2 of 0.30 and $p < 0.01$ for bacterivores), as well as to total soil C ($p > 0.05$ for fungivores; R^2 of 0.23 and $p < 0.01$ for bacterivores).

A power function of predator biomass (i.e., generalist and specialist predators) vs. microbivore biomass (i.e., prey) shows a strong relationship, with a slope of 1.03, R^2 of 0.44, and $p < 0.05$ (Fig. 5c). A power function using diversity-weighted biomass of predators and prey had a similar relationship as for biomass (slope of 1.00, R^2 of 0.32, and $p < 0.01$) (Fig. 5d).

Multivariate analysis of biomass of nematodes, soil factors, and roots showed a gradual spatial directional change in nematode communities along the arable to forest transect (Fig. 6). The stress value was 0.155, indicating a good portrayal of relationships in the ordination. Patterns were consistent among the sites. Associated with nematode communities in the forest were high labile and total soil C concentrations, litter, root C and root C:N, and more negative root δ^{15}N. Root δ^{13}C values, which are indicative of the high water use efficiency of the woody vegetation, also had an effect. Notably, the specialist predatory nematodes, *Mylonchulus* and *Clarkus,* were associated with higher root C, whereas the specialist predators, *Mononchus* and *Tripyla*, and the bacterivores, *Wilsonema*, *Prismatolaimus*, *Acrobeles,* and *Eumonhystera*, were linked to higher total soil C and N. In contrast, nematode communities in the arable fields were very strongly associated with positive root δ^{15}N and available P concentrations, and the presence of the two herbivore nematodes, *Paratylenchus* and *Pratylenchus*. The biplot shows little distinction among the three cultivated positions, with only slight divergence of the -0.25 m on the forest side of the field edge. In such intermediate positions, the nematode community was characterized by the basal nematodes, *Aphelenchoides*, *Aphelenchus,* and *Acrobeloides*. Thus the NMDS showed pronounced differences in nematode taxa with soil properties across the borders between fields and forests. Mantel tests supported these findings, but also showed a very weak association between the plant and nematode variables, yet high association between plant and soil variables (Appendix D).

3.5. *Structural equation modeling*

A significant proportion of the variability of the data on the diversity-weighted biomass of predatory (46%) and prey (41%) nematodes was explained by the proposed SEM models (Fig. 7). Distance from the center of the fields to the inside of the forests exerted a large influence on the composition and functional diversity of the plant community, such that both plant species richness and functional diversity were reduced in the forest and thus with distance. On the contrary, total soil C and root C concentrations were positively and significantly affected by distance, while fine root biomass showed no relationship with the distance along the transect.

The direct effect of distance, acting as a proxy for other variables not included in the model (e.g., soil physical perturbation) determined the diversity-weighted biomass of predatory nematodes, which was also strongly governed by total soil C (Fig. 7a). The diversity of plant community and the attributes of plant roots did not affect the diversity-weighted biomass of predatory nematodes. Plant community complexity, however, did significantly influence the diversity-weighted biomass of prey, which, as for the predators, was affected by total soil C. In contrast to predators, the diversity-weighted biomass of prey did not

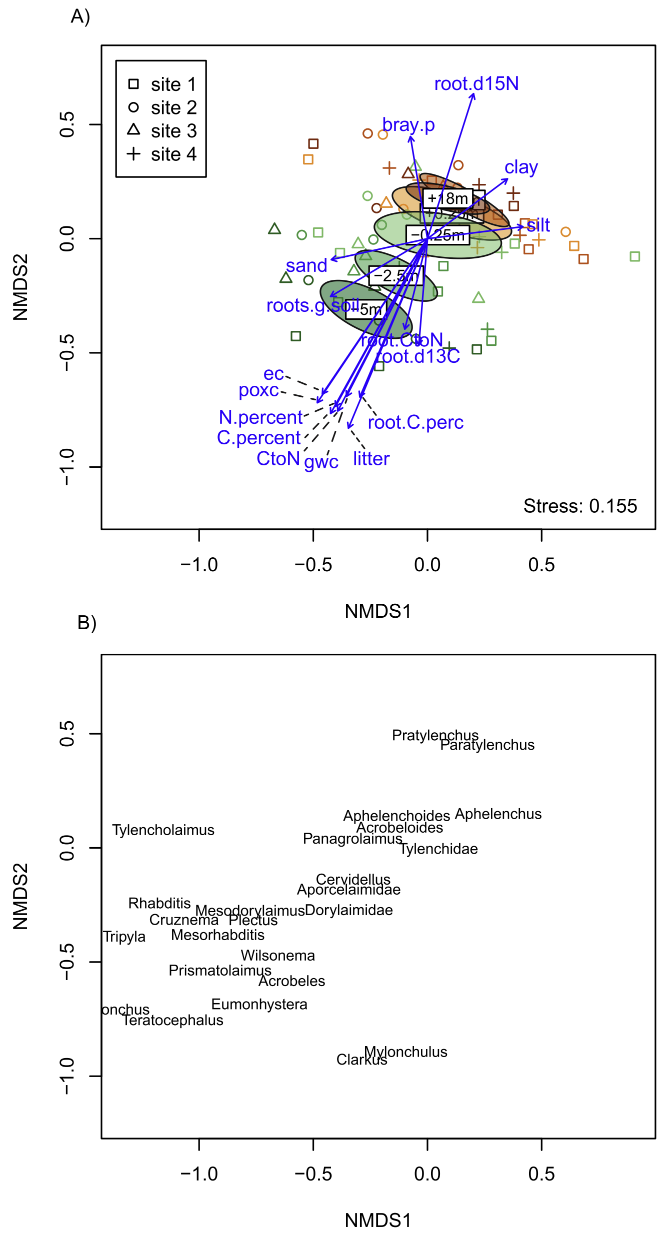


Fig. 6. Non-metric multidimensional scaling (NMDS) biplots for biomass of nematode taxa (μg per 100 g dry soil) in relation to environmental data (i.e., soil biogeochemical variables, fine root characteristics, and litter on the soil surface). Data are from four sites on schist soils in the Pyrénées-Orientales, France. a) biplot showing the similarity amongst the six positions (positive are cultivated and negative are non-cultivated) from forest to arable ecosystems. b) biplot showing the similarity amongst nematode taxa along the gradient.

respond to the distance gradient (Fig. 7b).

4. Discussion

Within the arable fields, minor changes occurred according to proximity to the forested border. Near the tilled edge (+4m position), total soil C and N, and available P were lower than in the center of the field. Yet a gradual increase in the nematode SI and the metabolic footprint of generalist predators began in this zone and increased across the tilled edge toward the forest, suggesting that both the structure and biomass of higher trophic links near the field edge are positively influenced by the undisturbed nature and resource availability of the forest. The woody vegetation likely provides other biophysical benefits to this agroecosystem, such as shade and cover for livestock, and protection from gully formation and erosion, which were observed but not measured. When the edge of the field is no longer tilled, the apparent shift of nematode taxa from more complex communities under woody perennial vegetation is slow and dependent on environmental conditions in the soil. Although recolonization by soil fauna may begin when disturbance ceases, the recovery of woody vegetation took decades based on the Géoportail images. With the onset of plant succession, plant C and N are apparently slowly deposited and decomposed into active forms in the soil (e.g., POXC), and habitats for more K-selected, larger-bodied nematodes are gradually created, delaying the spillover of nematode movement from more stable to more recently disturbed zones for years. At the landscape level the juxtaposition of cultivated and forest lands appears to facilitate the succession of both plant and nematode communities after disturbance.

4.1. Field borders and spillover effects

Pronounced differences in soil C occurred from the center of the arable fields to the forests in only 23 m. Since soils had developed on the same parent material (schist) and exhibited similar texture, the influence of soil physical properties on total soil C accumulation was probably negligible (Laganière et al., 2010; Six et al., 2002). The slow increase in labile and total soil C across the borders between arable fields and natural vegetation was accompanied by gradual changes in nematode biomass and functional groups. A different result occurred in the Netherlands, where field margins left undisturbed for at least four years supported relatively higher total soil C and predatory nematodes than at the line of tillage in our study, possibly due to higher clay content or to more mesic conditions there (Sechi et al., 2017). In the drier and warmer conditions of southern France, recovery of complex food webs is apparently less consistent and more dependent on site-specific conditions (Coll et al., 2012, 2011; Salome et al., 2014).

The higher concentrations of total soil C and N in the center of fields may be related to higher crop production than at the field edges in normal rainfall years. Roots of woody perennials were observed in soil collected in the fields at + 4 m and + 0.25 m from the border, but the biomass of surface litter did not differ from further inside the field, nor did the C:N ratio of roots or soil. An explanation that was suggested by the farmer of Sites 3 and 4 is that crop production in most years is higher in the field center than near the borders, due to shading and water uptake by woody vegetation. Plant responses to higher available P in the field center are more difficult to assess. The low pH is likely to cause P fixation but the Bray test indicates P is non-limiting for crop growth (Havlin et al., 2013). In this unusually dry spring, no difference was found in the cover of annual plants at + 18 m and + 4 m, and the farmer speculated that crop growth was moisture-limited in both positions. If crop production is typically higher in the center of the field, then gradual accumulation of root residue there could have caused an increase in total soil C (Gale et al., 2000). Also, higher grazing intensity might have caused the more positive soil δ^{15}N (Szpak, 2014), compared to the field edges.

As in other afforestation situations, total soil C accumulated slowly after the cessation of soil disturbance at the edge of the fields (Paul et al., 2002). The marked increase in total and labile soil C at -2.5 m in the maquis shrub zone (Fig. 2) may be due to the presence of broadleaf deciduous and N_2-fixing woody species whose litter is conducive to C and N retention in the soil (Alegre et al., 2004; Drinkwater et al., 1998; Paul et al., 2002). Additionally, the canopy could protect soil from moisture and temperature extremes that would adversely affect microbial processes and C sequestration (Laganière et al., 2010).

The gradual establishment of K-selected plants and nematodes on abandoned field edges has undoubtedly been facilitated by the close proximity of shrub and forest communities in the landscape. Conversion of arable land to maquis shrub and forest during the past few decades in the area, as evidenced by images of the landscape, is a continuation of a trend that began in the early 1900 s (Mayero, 1982). Historically, the

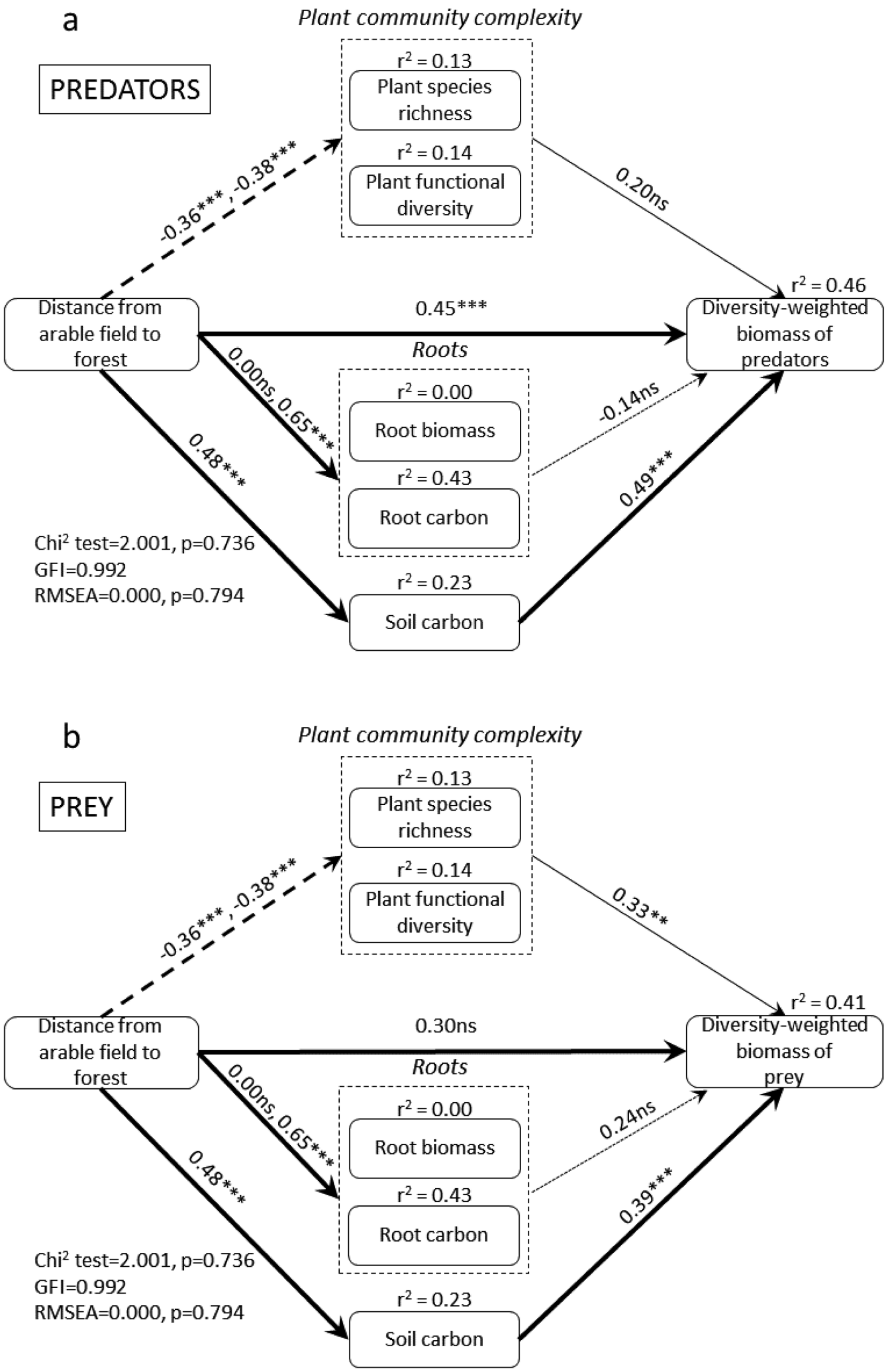


Fig. 7. Structural Equation Models exploring how the diversity-weighted biomass of a) nematode predator, and b) prey (i.e., microbivore) nematodes is related to distance along the transects from arable to forest ecosystems, soil C, plant community complexity, and plant roots. Data are from four sites on schist soils in the Pyrénées-Orientales, France, with six positions from arable to forest ecosystems. See text for details of the models. Thicker lines indicate significant relationships, and dotted lines indicate negative relationships.

multiple land-use strategy included pasture, rainfed grain, vineyards, olives, and terraced horticultural crops along waterways. Sheep, goats, and pigs grazed in oak forests, shrublands, and pastures, and acted as vectors of soil biota, propagules, and nutrients across the landscape, in greater densities than wild ungulates at present (Abbas et al., 2012). Thus, less opportunity currently exists for the movement of organisms across ecosystem interfaces. Even so, a gradual zonation from the undisturbed field edge to the shrub zone may increase recolonization of plants and nematodes, as compared to what might occur with an abrupt transition directly with forest. This connectivity may be important for restoration after major perturbations (e.g., tillage of abandoned fields, fire breaks, and after wildfire).

4.2. Soil food web

The progressive change toward a more complex nematode community from arable to forest zones was associated with ecosystem functions such as C sequestration in soil and in woody plants. A change in the magnitude of the function performed by upper guilds, for example, soil suppressiveness of pests, nutrient cycling and retention, and plant nutrition (Ferris, 2010; Trap et al., 2016), might be cautiously inferred by higher nematode metabolic footprints. Soil tardigrades, specialist predators previously associated with soil suppressiveness and extremely sensitive to soil disturbance (Sánchez-Moreno et al., 2008), also showed higher abundance toward the undisturbed forests. Associated with root C and litter, the active nematode hunters, *Mylonchulus* and *Clarkus*, appeared as the most characteristic nematodes of such areas.

The biomass of bacterivores, feeding on primary decomposers, significantly increased toward the forest, probably associated with more abundant resources (Ferris and Tuomisto, 2015). These included *Wilsonema*, *Prismatolaimus*, *Acrobeles*, *Teratocephalus*, and *Eumonhystera*, which are all bacterivore nematodes with extended lip modifications for grazing on decomposing organic matter and probably exploiting well-structured soils that facilitate active movement and access to resources (Briar et al., 2012). Bacterivores significantly contribute to soil N and P availability, and experimental approaches have shown that this results in higher plant biomass and assimilation of N and P (Gebremikael et al., 2016; Trap et al., 2016). Our SEM model shows, in agreement with previous work (Zhang et al., 2017), that higher diversity-weighted biomass of microbivorous nematodes was correlated with higher total soil C.

The arable fields were generally similar in soil food web indices to vineyards in the region (Coll et al., 2012, 2011; Salome et al., 2014), except that the SI of our arable fields was much lower, possibly reflecting greater tillage disturbance. Also, PPI in our fields was lower than in the vineyards. In fact, the only herbivore nematodes appearing at our sites, *Paratylenchus* and *Pratylenchus*, were clearly associated with the +18 m position in the center of the tilled fields. While continuous cropping commonly increases herbivore pressure (Li et al., 2016), these fields did not seem to be especially susceptible, which might be at least partially attributable to the suppressive service associated with a mosaic landscape with cropped fields inserted within natural vegetation forests (Bianchi et al., 2006).

Differences in litter quality between the fields and the forests may have affected microbes, microbivores, and the SI and CI indices (Margenot and Hodson, 2016). These marked differences with other zones suggest that a more stable, resource-rich soil environment may explain the forest's unique soil food web. Despite the narrow set of plant species in the forest and its similarity within and among sites, the nematode assemblages tended to be more variable in the forest soils, suggesting greater heterogeneity in microsites and nematode habitats, and possibly predator-mediated diversity of lower trophic levels. Since the forest appears to be a source of nematodes for re-colonizing disturbed areas, its diversity in taxa and microsites may provide assurance that some will survive the environmental fluctuations in a new location, consistent with the "insurance hypothesis" (Yachi and Loreau, 1999).

Previous work indicates that plant identity may determine nematode taxa distribution and community composition to a larger extent than plant species richness, and certain nematode species or functional guilds may be differentially linked to different plant species or plant functional groups (Viketoft, 2007; Viketoft et al., 2009). In their study on the effects of manipulated plant diversity on predator and prey nematodes, Kostenko et al. (2015) found no effect of plant diversity or identity on predators, while total plant diversity and legume abundance increased root, bacterial, and fungal-feeding nematodes. Similarly, we found a significant effect of plant community complexity on microbivorous but not on predatory nematodes. In our study, perennial woody legumes and non-legumes may be the key components of plant community complexity affecting higher diversity-weighted biomass of microbivores. These functional groups show more marked differences in these zones as compared to plant species richness. Relationships with plants were more discernible by separately assessing nematode functional groups with our SEM models, than with Mantel tests conducted with the entire nematode assemblage.

The main C pathway of root-derived C into the nematode community is the herbivore channel, followed by the bacterivore and fungivore channels, but only a very low amount of root C typically reaches higher trophic levels (Minoshima et al., 2007; Pausch et al., 2016). This, along with variability in biomass of fine roots across zones, may explain the absence of significant relationships between root attributes and diversity-weighted abundance of predators and prey in our dataset. In contrast, Hu et al. (2016), who measured total root biomass in densely planted shrubs at reforested sites of different ages in degraded calcareous soils, present an SEM showing a significant relationship between root biomass and nematode functional groups.

Across all sites and positions, the power function analysis of predators to prey was essentially 1:1, and did not show the $k = 0.75$ relationship typical of aboveground terrestrial and aquatic ecosystems (Hatton et al., 2015). This suggests that a top-heavy ecosystem structure may exist in our resource-rich environments that support the largest biomass of nematodes, i.e., forests. One explanation may be that the range of predator–prey abundances is relatively small despite the large changes in resource availability along the transects. Other reasons for the lack of consistency with aboveground terrestrial or aquatic ecosystems might include differential dispersion of small- and large-bodied nematodes within the soil matrix, lack of full accounting of other fauna (e.g., Collembola), or inadequate timing of sampling for considering the age structure of each population. Since the power function analysis of diversity-weighted biomass of predator and prey showed a similar or even weaker relationship than the power function based on biomass, it is unlikely that diversity has a big role in determining who is consumed by whom.

4.3. Conclusions

This study suggests that maintaining stages of successional zonation within the borders between arable and forested ecosystems may be conducive to recolonization by soil fauna after disturbance ceases. If tillage had repeatedly created an abrupt edge with the forest vegetation, nematodes from higher trophic levels would be less likely to establish. The gradual change in soil properties also increased the soil ecosystem services in the borders. Future studies should focus on whether other ecosystem services are affected by gradual transitions between arable and forest ecosystems (e.g., crop productivity, forage quality, livestock habitat, or pest suppression for plants) and the implications for management of field margins (Luedeling et al., 2016; Marshall and Moonen, 2002; Sánchez et al., 2009). More of the land in the study area may be inhabited by a complex soil food web now that it is dominated by maquis shrub and holm oak forest, following the rural exodus and abandonment of agriculture during the past century. Yet despite the increase in soil biodiversity, total agrobiodiversity now is lower than in the past (Marull et al., 2015; Otero et al., 2015). When and if people decide to re-create food production systems in the area, heterogeneity of land use types and the borders between them could promote more complex soil food webs and soil ecosystem services across the landscape.

Acknowledgements

Much appreciation goes to Ann Dennis of Ille-sur-Têt for her help with project design and field sampling, and her hospitality during the field season. We are very grateful for the cooperation of Daniel Moragas of Le Monistrol (Casefabre). Thanks go to the UMR 210 Eco&Sols (Ecologie fonctionelle et biogéochimie des sols et des agroécosystèmes) in Montpellier for hosting the research project, and to Gérard Souche for his help with site selection. The interest and contributions of colleagues at the UMR 1248 AGIR (Agroécologie-Innovations-Territoires) in Toulouse are highly appreciated, with special thanks to Jean-Pierre Theau and Michel Duru. Pierre-Olivier Cochard's expertise with plant identification was immensely helpful. Valuable discussions occurred with Eric Garnier and Marie-Laure Navas to plan the research. Stephen Wood generously helped with field work.

Appendix A

Analysis of satellite and aerial images of the study area in the Pyrénées-Orientales, France. 1) Landscape images in 1987 (Landsat 5) and 2014 (Landsat 8). 2) Site description methods using Géoportail in ca. 1960 and 2015.

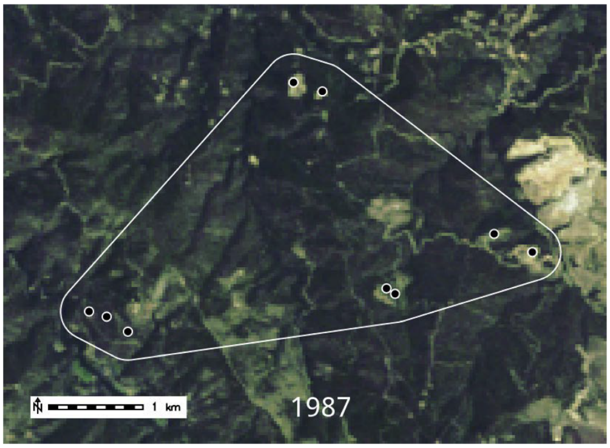
1) Landscape images of the study area in 1987 (Landsat 5) and 2014 (Landsat 8)

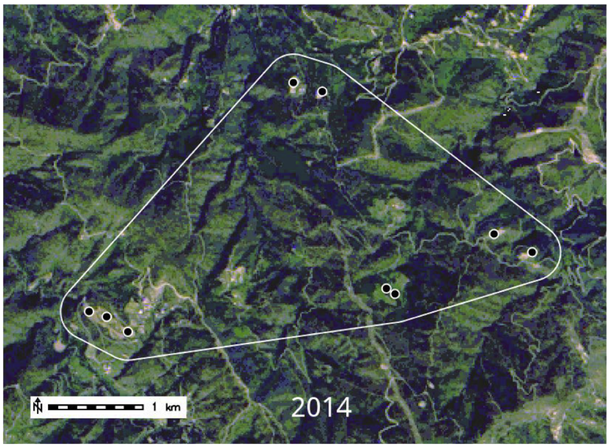
The study area was approximately 7 km^2 in area, and was situated south of the town of Ille-sur-Têt, reaching between Saint Michel de Llotes and Casefabre in the Pyrénées-Orientales department of southern France. It consisted of a triangular area on a ridge with hilly topography (42°36'46.86“N2°36'39.77”E (southwest corner) to 42°36'46.86“N2°36'39.77”E (north corner) to (42°37'12.01“N2°39'59.84”E) (southeast corner).

Landsat 5 was used for the 1987 (image ID LT51970301987179XXX02) and Landsat 8 for the 2014 image (image ID LC81970312014125LGN00). The Landsat 5 image used the natural color bands 1, 2, and 3 at 30 m resolution. The Landsat 8 image used the natural color bands 2, 3, and 4 at 30 m resolution together with the panchromatic band 8 at 15 m resolution combined through an image fusion algorithm (https://landsat.gsfc.nasa.gov/). The images were from the spring season at the peak of biomass production, because during the rest of the year, bare areas might be confounded with senescent vegetation. Darker colors indicate evergreen oak forest and maquis shrubland. Early successional grasslands and cultivated fields are lighter in color. It is not possible to distinguish between them due to Landsat's resolution. In 2014, we searched the landscape for all fields that had been tilled in the past year. Fields marked with a dot on the Landsat images were visually confirmed in the field as tilled in 2014.

Sites 1 and 2 were in the most northern fields (east and west dots, respectively). In the cluster of fields in the southwestern corner, Site 3 was in the middle field and Site 4 was in the southernmost field.

The image from the spring of 1987 has lighter colors and more open and more even distribution of vegetation in the study area than in 2014. It is unlikely, however, that 1987's lighter colors are due to water-stressed perennial vegetation since precipitation and temperature were close to normal in 1987, whereas in 2014, spring precipitation was 50% lower and mean temperature was 2°C higher than normal (https://www.infoclimat.fr/stations-meteo).





2) Site description methods using Géoportail in ca. 1960 and 2015.

Aerial images from Géoportail (https://www.geoportail.gouv.fr/) for the study area were only available for ca. 1960 and in 2015. The resolution is clear enough to distinguish features of fields such as rows, edges, and surface homogeneity indicative of recent tillage. The 7 km^2 study area was accessed by locating the same area as in the Landsat images above. By moving down and up in scale, it was possible to identify the cultivated fields, and then estimate their area as a percentage of the total land cover.

To inspect the four sites in ca. 1960 and in 2015, each site was located on Géoportail aerial images for the two time points. Using Site 1 as an example: 1) On the Géoportail website, search for Saint Michel de Llotes. 2) Select three layers of maps: i) Photographies aériennes; ii) Culture et patrimoine > Photographies aériennes 1950-1965; and iii) Territoires et Transport > Foncier, Cadastre et Urbanisme > Parcelles cadastrales. 3) Choose the layers for Photographies aériennes and Parcelles cadastrales. 4) Locate the cultivated field between Mas d'en Grau and Fournas, along the jurisdictional boundary of Saint Colombe (Site 1). 5) Trace the perimeter of the field at 1:1066 resolution for 2015 as this is the date for the aerial photograph of this layer. 6) Choose the layer for Photographies aériennes 1950-1965. 6) Trace the perimeter of the field at 1:1066 resolution for ca. 1960 (approximate date of the layer). 7) Overlay the traces of the field perimeters and examine the differences including shrinkage or expansion of the cultivated area.

The sampled transects were located on the two sets of aerial photographs at a resolution of 1:1066. Since the overlays of traced perimeters almost always showed a wider cultivated field in ca. 1960 than 2015 for these sampled locations, we examined the sampled sections of the field borders for bare soil, herbaceous vegetation, or woody vegetation, and compare status in ca. 1960 vs. 2015 (with the assumption that the field edges were similar in 2014 (sampling) and 2015 (Géoportail photograph). Using Site 1 as an example, the sampled transects were in the easternmost edge of the field, along the center part of the 'panhandle'.

Appendix B

Cover of plant species per plot (mean and standard deviation) and frequency per plot across the six zones along transects from cultivated fields to evergreen oak forest, compiled by groups. Data are from four sites on schist soils in the Pyrénées-Orientales, France. n = 72 plots.

Plant species by functional group	Percent cover Mean	Percent cover Std Dev	Frequency Number of plots
Annual graminoid species			
Aira caryophyllea L.	0.0819	0.3853	4
Avena sativa L.	5.3721	7.1766	40
Bromus madritensis L.	1.3058	4.0912	18
Bromus rubens L.	0.0004	0.0005	4
Hordeum spp.	0.0003	0.0005	3
Lamarckia aurea (L.) Moench.	0.0001	0.0003	1
Secale cereale L.	2.3574	2.8982	11
Vulpia bromoides (L.) Gray	1.0130	1.5126	16
Vulpia muralis (Kunth) Nees	2.6694	6.3881	6
Annual leguminous species			
Ornithopus compressus L.	0.1224	0.4709	5
Vicia sativa L.	9.0946	14.6730	25
Annual species in other families			
Agrostemma githago L.	0.0010	0.0000	4
Anarrhinum bellidifolium (L.) Willd.	0.0100	–	1
Anchusa arvensis (L.) M. Bieb. Arvensis	0.0001	0.0003	1
Anthemis arvensis L.	0.0084	0.0257	3
Arabidopsis thaliana (L.) Hyenh.	0.0173	0.0535	4
Arenaria serpyllifolia L.	0.3340	0.5768	3
Capsella bursa-pastoris (L.) Medik	0.0010	–	1
Carduus pycnocephalus L.	0.3799	0.6161	16
Carlina L. spp.	0.0033	0.0045	4
Cerastium ramosissimum Boiss.	0.0018	0.0082	12
Chondrilla juncea L.	0.0494	0.1938	17
Corrigiola littoralis L.	0.0002	0.0004	2
Crepis sancta (L.) Bornm.	1.2324	2.3989	11
Erodium cicutarium (L.) L'Hér.	0.0010	–	1
Filago pyramidata L.	0.4248	1.1684	17
Foeniculum vulgare Mill.	0.0001	0.0003	1
Galium aparine L.	0.0334	0.1414	2
Galium spp. 1	0.0005	0.0005	7
Geranium rotundifolium L.	0.2807	1.1778	4
Lamium amplexicaule L.	0.0002	0.0004	2
Linaria arvensis (L.) Desf.	0.0008	0.0007	6
Lysimachia arvensis (L.) U. Manns & Anderb.	0.0008	0.0012	6
Malva neglecta Wallroth	0.0010	–	1
Papaver rhoeas L.	0.0001	0.0003	1
Plantago lanceolata L.	0.1651	0.8341	8
Polygonum aviculare L.	0.3368	0.6358	9
Raphanus raphanistrum L.	0.0001	0.0004	4
Reseda phyteuma L.	0.0048	0.0085	5
Rumex acetosella L.	0.6292	1.0267	14
Rumex bucephalophorus L.	0.7858	1.7119	6
Rumex L. spp.	0.2004	0.6323	5
Senecio vulgaris L.	0.0018	0.0055	5
Sherardia arvensis L.	2.4004	5.3546	18
Silene gallica L.	0.0838	0.2885	7
Silybum marianum (L.) Gaertn.	0.0010	0.0000	2
Sisymbrium officinale (L.) Scop.	0.0010	–	1

Sonchus oleraceus L.	0.0001	0.0003	1
Spergula pentandra L.	0.0001	0.0003	1
Unknown Brassicaceae	0.0001	0.0003	2
Unknown Caryophyllaceae	0.0005	0.0005	6
Unknown Compositae	0.1669	0.6044	8
Unknown Forb A	0.0742	0.3849	4
Unknown Forb B	0.0010	0.0000	2
Unknown Forb C	0.0010	0.0000	4
Unknown Forb D	0.0010	0.0000	2
Veronica hederifolia L.	0.0001	0.0003	1
Perennial graminoid species			
Agrostis spp.	0.1112	0.3233	4
Arrhenaterum elatius (L.) J. & C. Presl	0.2779	0.9582	5
Brachypodium retusum (pers.) P. Beauv.	1.2942	2.0845	10
Carex spp.	1.0000	–	1
Dactylis glomerata subsp. *hispanica* (Roth) Nyman	0.0002	0.0004	2
Elytrigia campestris (Godr. & Gren.) Kerguélen	0.2630	0.4919	4
Festuca L.	0.0010	–	1
Lolium perenne L.	0.9491	2.0734	28
Poa bulbosa L.	0.0001	0.0003	1
Unknown perennial grass A	1.7779	4.9693	3
Unknown perennial grass B	0.0090	0.0169	4
Unknown perennial grass C	0.0001	0.0003	1
Perennial herbaceous leguminous species			
Aspaltium bituminosa (L.) Fourr.	0.0010	0.0000	3
Lotus corniculatus L.	0.0010	0.0000	2
Perennial herbaceous species in other families			
Aristolochia pistolochia L.	0.0010	0.0000	2
Asparagus acutifolius L.	1.6365	3.8858	13
Asplenium onopteris L.	0.0001	0.0003	1
Clematis flammula L.	0.5837	1.1643	7
Convolvulus arvensis L.	1.0000	–	1
Convolvulus L. spp	0.0001	0.0003	1
Cytinus hypocistus (L.) L.	0.0002	0.0004	2
Dittrichia viscosa (L.) Greuter	0.0022	0.0067	1
Euphorbia segetalis L.	0.0004	0.0005	4
Euphorbia serrata L.	0.0022	0.0067	1
Galium maritimum L.	0.0003	0.0005	3
Hedera helix L.	0.4445	1.3382	3
Lonicera etrusca Santi	1.0390	3.0436	11
Rubia peregrina L.	0.1102	0.4156	20
Senecio inaequidens DC.	1.0860	4.0151	29
Unknown Forb E	0.0010	–	1
Unknown Forb F	0.0010	–	1
Unknown Umbelliferae	0.0002	–	4
Perennial woody leguminous species			
Calicotome infesta (C. Presl.) Guss.	7.6004	8.2941	5
Genista cinerea (Vill.) DC	1.8000	4.4062	8
Ononis L. spp.	0.0011	0.0033	1
Spartium junceum L.	4.0003	4.3355	6
Ulex europaeus L.	2.7778	6.4128	6
Perennial woody species in other families			
Cistus albidus L.	5.5016	13.3438	20
Cistus monspeliensis L.	2.8667	10.2360	11
Cistus salviifolius L.	3.4695	4.6236	11
Erica arborea L.	3.7917	7.0771	10
Euphorbia characias L.	0.4547	1.4712	6
Phyllyrea media L.	0.0010	–	1
Quercus ilex L.	35.2251	37.8027	27
Quercus pubescens Willd.	13.2000	12.6372	5
Rhamnus alaternus L.	0.3333	0.7071	2
Rosa spp.	0.0010	–	1
Rubus spp. A	1.7191	5.0046	20
Rubus spp. B	0.1112	0.3234	3
Rubus spp. C	0.0556	0.2357	2
Smilax aspera L.	0.0556	0.1667	1
Sorbus domestica L.	1.6667	5.0000	1
Thymnus vulgaris L.	0.3340	0.5768	3
Vitis vinifera L.	0.0373	0.1924	6

Appendix C

Number of plant species and cover of plant functional groups in the six positions from cultivated fields to evergreen oak forest. Cultivated positions are at +18 m, +4 m, and +0.25 m from the line of tillage, and non-cultivated positions are at -0.25 m, -2.5 m, and -5 m from the line of tillage. Data are from four sites on schist soils in the Pyrénées-Orientales, France. n = 72 plots.

	Position on interface between ecosystem types					
	Cultivated field		Line of tillage		Shrub or forest	
Plot distance to field-forest edge	+18 m	+4 m	+0.25 m	-0.25 m	-2.5 m	-5 m
Plant functional groups						
Mean number of species in each functional group per plot						
Annual graminoids	2.42	2.83	2.08	1.17	0.00	0.08
Annual legumes	0.67	0.75	0.75	0.25	0.08	0.00
Annual other families	6.50	5.83	4.67	2.25	0.42	0.00
Perennial graminoids	0.92	1.00	0.83	0.83	0.92	0.83
Perennial herbaceous legumes	0.00	0.00	0.00	0.00	0.00	0.00
Perennial herbaceous other families	1.50	0.92	0.33	0.17	1.33	3.08
Perennial woody legumes	0.08	0.08	0.25	0.50	1.17	0.08
Perennial woody other families	0.30	0.92	0.58	0.58	2.00	4.00
Mean total number of species per plot	12.52	12.42	11.42	9.33	8.33	9.67
Mean percent cover in each functional group per plot						
Annual graminoids	15.31	13.96	5.34	2.45	0.00	0.00
Annual legumes	16.08	15.83	2.37	0.00	0.00	0.00
Annual other families	4.64	2.01	1.65	0.94	0.33	0.00
Perennial graminoids	1.46	1.63	1.33	0.58	1.75	0.25
Perennial herbaceous legumes	0.00	0.00	0.00	0.00	0.00	0.00
Perennial herbaceous other families	0.09	0.00	1.50	1.75	5.17	2.67
Perennial woody legumes	0.001	0.00	0.01	2.96	10.00	0.42
Perennial woody other families	1.32	0.75	0.30	14.68	57.09	92.54
Mean total percent cover per plot	38.89	34.19	12.52	23.37	74.34	95.89

Appendix D

Mantel tests for relationships among nematode, plant, and soil property matrices. The data are from six positions along transects from cultivated fields to evergreen oak forest. Bray distances of each matrix were used. Data are from four sites on schist soils in the Pyrénées-Orientales, France. Shown are Mantel statistics (r). Significance values were $p \leq 0.001$ or 0.0001 for all tests. $n = 72$ plots.

Explanation:

Using the complete datasets for nematode taxa and nematode metabolic footprints in Mantel tests, matrices were highly associated with the matrix of soil properties. Plant taxa and functional group matrices were also highly associated with the matrix of soil properties. Yet there was only a very weak association between the plant and nematode variables. Nematode metabolic footprints showed a slightly higher association with plant taxa and functional groups than did nematode taxa.

The similarity of a partial Mantel test between nematode variables and soil variables, conditioned on plant functional group cover (Mantel r: 0.2219, $p < 0.001$) and the previous Mantel test, suggests that the correlation between soil variables and the complete set of nematode taxa is unique; "taking out" the association between plant and nematode variables does not change the correlation, when based on the entire community of both types of taxa.

Matrices	Nematode taxa	Nematode metabolic footprints	Plant taxa	Plant functional groups	Soil variables
Nematode taxa	1				
Nematode metabolic footprints	0.74	1			
Plant taxa	0.1	0.13	1		
Plant functional groups	0.08	0.14	0.82	1	
Soil variables	0.24	0.3	0.33	0.36	1

References

Abbas, F., Merlet, J., Morellet, N., Verheyden, H., Hewison, A.J.M., Cargnelutti, B., Angibault, J.M., Picot, D., Rames, J.L., Lourtet, B., Aulagnier, S., Daufresne, T., 2012. Roe deer may markedly alter forest nitrogen and phosphorus budgets across Europe. Oikos 121, 1271–1278.

Alegre, J., Alonso-Blázquez, N., De Andrés, E.F., Tenorio, J.L., Ayerbe, L., 2004. Revegetation and reclamation of soils using wild leguminous shrubs in cold semiarid Mediterranean conditions: Litterfall and carbon and nitrogen returns under two aridity regimes. Plant Soil 263, 203–212.

Alignier, A., Deconchat, M., 2013. Patterns of forest vegetation responses to edge effect as revealed by a continuous approach. Ann. For. Sci. 70, 601–609.

Andrássy, I., 1956. Die Rauminhalst and Gewichtsbestimmung der Fadenwurmer (Nematoden). Acta Zool. Acad. Sci. 2, 1–15.

Arbuckle, J.L., 2014. Amos (Version 23.0). [Computer Program]. IBM SPSS, Chicago.

Barker, K.R., 1985. Nematode extraction and bioassays, in: Barker, K.R., Carter, C.C., Sasser, J.N. (Eds.), An Advance Treatise on Meloidogyne, Vol. 2 Methodology. North Carolina State University Graphics, Raleigh, NC, USA, pp. 19–35.

Bassa, M., Boutin, C., Chamorro, L., Sans, F.X., 2011. Effects of farming management and landscape heterogeneity on plant species composition of Mediterranean field boundaries. Agric. Ecosyst. Environ. 141, 455–460.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Bianchi, F.J.J., Booij, C.J., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc. R. Soc. B Biol. Sci. 273, 1715–1727.

Bongers, T., 1994. Nematodes of the Netherlands (De Nematoden van Nederland). Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht, The Netherlands.

Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14–19.

Bongers, T., Bongers, M., 1998. Functional diversity of nematodes. Appl. Soil Ecol. 10, 239–251.

Bray, R.H., Kurtz, L.T., 1945. Determination of total, organic, and available forms of phosphorus in soils. Soil Sci. 59, 39–46.

Briar, S.S., Culman, S.W., Young-Mathews, A., Jackson, L.E., Ferris, H., 2012. Nematode community responses to a moisture gradient and grazing along a restored riparian corridor. Eur. J. Soil Biol. 50, 32–38.

Brochier, J.E., Claustre, F., Heinz, C., 1998. Environmental impact of Neolithic and Bronze Age farming in the eastern Pyrenees forelands, based on multidisciplinary investigations at La Caune de Bélesta (Bélesta Cave), near Perpignan, France. Veg. Hist. Archaeobot. 7, 1–9.

Casini, M., Blenckner, T., Mollmann, C., Gardmark, A., Lindegren, M., Llope, M., Kornilovs, G., Plikshs, M., Stenseth, N.C., 2012. Predator transitory spillover induces trophic cascades in ecological sinks. Proc. Natl. Acad. Sci. 109, 8185–8189.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.

Cluzeau, D., Guernion, M., Chaussod, R., Martin-Laurent, F., Villenave, C., Cortet, J., Ruiz-Camacho, N., Pernin, C., Mateille, T., Philippot, L., Bellido, A., Rougé, L., Arrouays, D., Bispo, A., Pérès, G., 2012. Integration of biodiversity in soil quality monitoring: baselines for microbial and soil fauna parameters for different land-use types. Eur. J. Soil Biol. 49, 63–72.

Coll, P., Le Cadre, E., Blanchart, E., Hinsinger, P., Villenave, C., 2011. Organic viticulture and soil quality: a long-term study in Southern France. Appl. Soil Ecol. 50, 37–44.

Coll, P., Villenave, C., Le Cadre, E., 2012. How are nematode communities affected during a conversion from conventional to organic farming in southern French vineyards? Nematology 14, 665–676.

Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tscharntke, T., Verhulst, J., 2012. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. J. Appl. Ecol. 49, 695–705.

Culman, S.W., Snapp, S.S., Freeman, M.A., Schipanski, M.E., Beniston, J., Lal, R., Drinkwater, L.E., Franzluebbers, A.J., Glover, J.D., Grandy, A.S., Lee, J., Six, J., Maul, J.E., Mirksy, S.B., Spargo, J.T., Wander, M.M., 2012. Permanganate oxidizable carbon reflects a processed soil fraction that is sensitive to management. Soil Sci. Soc. Am. J. 76, 494.

Culman, S.W., Young-Mathews, A., Hollander, A.D., Ferris, H., Sánchez-Moreno, S., O'Geen, A.T., Jackson, L.E., 2010. Biodiversity is associated with indicators of soil ecosystem functions over a landscape gradient of agricultural intensification. Landsc. Ecol. 25, 1333–1348.

D'Acunto, L., Semmartin, M., Ghersa, C.M., 2016. Uncultivated margins are source of soil microbial diversity in an agricultural landscape. Agric. Ecosyst. Environ. 220, 1–7.

De Roos, A.M., Schellekens, T., Van Kooten, T., Persson, L., 2008. Stage-specific predator species help each other to persist while competing for a single prey. Proc. Natl. Acad. Sci. 105, 13930–13935.

Drinkwater, L.E., Wagoner, P., Sarrantonio, M., 1998. Legume-based cropping systems have reduced carbon and nitrogen losses. Nature 396, 263–265.

DuPont, S.T., Beniston, J., Glover, J.D., Hodson, A., Culman, S.W., Lal, R., Ferris, H., 2014. Root traits and soil properties in harvested perennial grassland, annual wheat, and never-tilled annual wheat. Plant Soil 381, 405–420.

Eshel, G., Levy, G., Mingelgrin, U., Singer, M., 2004. Critical evaluation of the use of laser diffraction for particle-size distribution analysis. Soil Sci. Soc. Am. J. 68, 736–743.

Ferris, H., 2010. Form and function: Metabolic footprints of nematodes in the soil food web. Eur. J. Soil Biol. 46, 97–104.

Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18, 13–29.

Ferris, H., Griffiths, B.S., Porazinska, D.L., Powers, T.O., Wang, K.-H., Tenuta, M., 2012. Reflections on plant and soil nematode ecology: past, present and future. J. Nematol. 44, 115–126.

Ferris, H., Tuomisto, H., 2015. Unearthing the role of biological diversity in soil health. Soil Biol. Biochem. 85, 101–109.

Fischer, J., Lindenmayer, D.B., Manning, A.D., 2006. Biodiversity, ecosystem function and resilience: ten guiding principles for off-reserve conservation. Front. Ecol. Environ. 4, 80–86.

French, K.E., Tkacz, A., Turnbull, L.A., 2017. Conversion of grassland to arable decreases microbial diversity and alters community composition. Appl. Soil Ecol. 110, 43–52.

Gale, W.J., Cambardella, C.A., Bailey, T.B., 2000. Root-derived carbon and the formation and stabilization of aggregates. Soil Sci. Soc. Am. J. 64, 201–207.

García-Palacios, P., Bowker, M.A., Maestre, F.T., Soliveres, S., Valladares, F., Papadopoulos, J., Escudero, A., 2011. Ecosystem development in roadside grasslands: Biotic control, plant-soil interactions, and dispersal limitations. Ecol. Appl. 21, 2806–2821.

Gebremikael, M.T., Steel, H., Buchan, D., Bert, W., De Neve, S., 2016. Nematodes enhance plant growth and nutrient uptake under C and N-rich conditions. Sci. Rep. 6, 32862.

Hatton, I.A., McCann, K.S., Fryxell, J.M., Davies, T.J., Smerlak, M., Sinclair, A.R.E., Loreau, M., 2015. The predator-prey power law: Biomass scaling across terrestrial and aquatic biomes. Science 369 (6252), aac6284.

Havlin, J.L., Tisdale, S.L., Nelson, W.L., Beaton, J.D., 2013. Soil fertility and nutrient management: an introduction to nutrient management, 8th Edition. Pearson, Upper Saddle River, New Jersey, USA.

Heinz, C., Figueiral, I., Terral, J.-F., Claustre, F., 2004. Holocene vegetation changes in the northwestern Mediterranean: new palaeoecological data from charcoal analysis and quantitative eco-anatomy. The Holocene 14, 621–627.

Hodson, A., Lewis, E., 2016. Managing for soil health can suppress pests. Calif. Agric. 70, 137–141.

Holtkamp, R., van der Wal, A., Kardol, P., van der Putten, W.H., de Ruiter, P.C., Dekker, S.C., 2011. Modelling C and N mineralisation in soil food webs during secondary succession on ex-arable land. Soil Biol. Biochem. 43, 251–260.

Hu, N., Li, H., Tang, Z., Li, Z., Tian, J., Lou, Y., Li, J., Li, G., Hu, X., 2016. Community diversity, structure and carbon footprint of nematode food web following reforestation on degraded Karst soil. Sci. Rep. 6, 28138.

Jackson, L.E., Pulleman, M.M., Brussaard, L., Bawa, K.S., Brown, G.G., Cardoso, I.M., de Ruiter, P.C., García-Barrios, L., Hollander, A.D., Lavelle, P., Ouédraogo, E., Pascual, U., Setty, S., Smukler, S.M., Tscharntke, T., Van Noordwijk, M., 2012. Social-ecological and regional adaptation of agrobiodiversity management across a global set of research regions. Glob. Environ. Chang. 22, 623–639.

Jost, L., 2007. Partitioning diversity into independent alpha and beta components. Ecology 88, 2427–2439.

Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375.

Kostenko, O., Duyts, H., Grootemaat, S., De Deyn, G.B., Bezemer, T.M., 2015. Plant diversity and identity effects on predatory nematodes and their prey. Ecol. Evol. 5, 836–847.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2016. lmerTest: Tests in linear mixed effects models. R Package. Version 2.0-33. https://CRAN.R-project.org/package=lmerTest.

Laganière, J., Angers, D.A., Paré, D., 2010. Carbon accumulation in agricultural soils after afforestation: a meta-analysis. Glob. Chang. Biol. 16, 439–453.

Li, X., Lewis, E.E., Liu, Q., Li, H., Bai, C., Wang, Y., 2016. Effects of long-term continuous cropping on soil nematode community and soil condition associated with replant problem in strawberry habitat. Sci. Rep. 6, 30466.

Luedeling, E., Smethurst, P.J., Baudron, F., Bayala, J., Huth, N.I., van Noordwijk, M., Ong, C.K., Mulia, R., Lusiana, B., Muthuri, C., Sinclair, F.L., 2016. Field-scale modeling of tree-crop interactions: Challenges and development needs. Agric. Syst. 142, 51–69.

Margenot, A.J., Hodson, A.K., 2016. Relationships between labile soil organic matter and nematode communities in a California oak woodland. Nematology 18, 1231–1245.

Marshall, E.J.P., Moonen, A.C., 2002. Field margins in northern Europe: Integrating agricultural, environmental and biodiversity functions. Agric. Ecosyst. Environ. 89, 5–21.

Marull, J., Otero, I., Stefanescu, C., Tello, E., Miralles, M., Coll, F., Pons, M., Diana, G.L., 2015. Exploring the links between forest transition and landscape changes in the Mediterranean. Does forest recovery really lead to better landscape quality? Agrofor. Syst. 89, 705–719.

Mayero, L., 1982. Population et vie rurale dans le bassin de la Têt Pyrénées Orientales. Rev. Geogr. du Pyrénées du Sud-Ouest 53, 305–324.

Minoshima, H., Jackson, L.E., Cavagnaro, T.R., Ferris, H., 2007. Short-term fates of carbon-13-depleted cowpea shoots in no-till and standard tillage soils. Soil Sci. Soc. Am. J. 71, 1859.

Mitchell, M.G.E., Bennett, E.M., Gonzalez, A., 2014. Forest fragments modulate the provision of multiple ecosystem services. J. Appl. Ecol. 51, 909–918.

Mueller, R.C., Rodrigues, J.L.M., Nüsslein, K., Bohannan, B.J.M., 2016. Land use change in the Amazon rain forest favours generalist fungi. Funct. Ecol. 30, 1845–1853.

Neher, D.A., 2010. Ecology of plant and free-living nematodes in natural and agricultural soil. Annu. Rev. Phytopathol. 48, 371–394.

Nielsen, U.N., Wall, D.H., Six, J., 2015. Soil biodiversity and the environment. Annu. Rev. Environ. Resour. 40, 63–90.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2018. Vegan: community ecology package. R Package. Version 2. 4-6. https://doi.org/10.1093/molbev/msv334.

Otero, I., Marull, J., Tello, E., Diana, G.L., Pons, M., Coll, F., Boada, M., 2015. Land abandonment, landscape, and biodiversity: Questioning the restorative character of the forest transition in the Mediterranean. Ecol. Soc. 20 (2), 7.

Paul, K.I., Polglase, P.J., Nyakuengama, J.G., Khanna, P.K., 2002. Change in soil carbon following afforestation. For. Ecol. Manage. 168, 241–257.

Paula, F.S., Rodrigues, J.L.M., Zhou, J., Wu, L., Mueller, R.C., Mirza, B.S., Bohannan, B.J.M., Nüsslein, K., Deng, Y., Tiedje, J.M., Pellizari, V.H., 2014. Land use change alters functional gene diversity, composition and abundance in Amazon forest soil microbial communities. Mol. Ecol. 23, 2988–2999.

Pausch, J., Hofmann, S., Scharroba, A., Kuzyakov, Y., Ruess, L., 2016. Fluxes of root-derived carbon into the nematode micro-food web of an arable soil. Food Webs 9, 32–38.

Pulleman, M., Creamer, R., Hamer, U., Helder, J., Pelosi, C., Pérès, G., Rutgers, M., 2012. Soil biodiversity, biological indicators and soil ecosystem services-an overview of European approaches. Curr. Opin. Environ. Sustain. 4, 529–538.

Rossetti, I., Bagella, S., Cappai, C., Caria, M.C., Lai, R., Roggero, P.P., Martins da Silva, P., Sousa, J.P., Querner, P., Seddaiu, G., 2015. Isolated cork oak trees affect soil properties and biodiversity in a Mediterranean wooded grassland. Agric. Ecosyst. Environ. 202, 203–216.

Roume, A., Deconchat, M., Raison, L., Balent, G., Ouin, A., 2011. Edge effects on ground beetles at the woodlot-field interface are short-range and asymmetrical. Agric. For. Entomol. 13, 395–403.

Saleem, M., Fetzer, I., Dormann, C.F., Harms, H., Chatzinotas, A., 2012. Predator richness increases the effect of prey diversity on prey yield. Nat. Commun. 3, 1305.

Salome, C., Coll, P., Lardo, E., Villenave, C., Blanchart, E., Hinsinger, P., Marsden, C., Le Cadre, E., 2014. Relevance of use-invariant soil properties to assess soil quality of vulnerable ecosystems: the case of Mediterranean vineyards. Ecol. Indic. 43, 83–93.

Sánchez-Moreno, S., Ferris, H., Guil, N., 2008. Role of tardigrades in the suppressive service of a soil food web. Agric. Ecosyst. Environ. 124, 187–192.

Sánchez-Moreno, S., Ferris, H., Young-Mathews, A., Culman, S.W., Jackson, L.E., 2011. Abundance, diversity and connectance of soil food web channels along environmental gradients in an agricultural landscape. Soil Biol. Biochem. 43, 2374–2383.

Sánchez, I.A., Lassaletta, L., McCollin, D., Bunce, R.G.H., 2009. The effect of hedgerow loss on microclimate in the Mediterranean region: An investigation in Central Spain. Agrofor. Syst. 78, 13–25.

Schermelleh-Engel, K., Moosbrugger, H., Müller, H., 2003. Evaluating the fit of Structural Equation Models: Tests of significance and descriptive Goodness-of-Fit measures. Methods Psychol. Res. Online 8, 23–74.

Sechi, V., De Goede, R.G.M., Rutgers, M., Brussaard, L., Mulder, C., 2017. A community trait-based approach to ecosystem functioning in soil. Agric. Ecosyst. Environ. 239, 265–273.

Shao, Y., Bao, W., Chen, D., Eisenhauer, N., Zhang, W., Pang, X., Xu, G., Fu, S., 2015. Using structural equation modeling to test established theory and develop novel hypotheses for the structuring forces in soil food webs. Pedobiologia 58, 137–145.

Sieriebriennikov, B., Ferris, H., de Goede, R.G.M.M., 2014. NINJA: An automated calculation system for nematode-based biological monitoring. Eur. J. Soil Biol. 61, 90–93.

Six, J., Conant, R.T., Paul, E.A., Paustian, K., 2002. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. Plant Soil 241, 155–176.

Smith, J., Pearce, B.D., Wolfe, M.S., 2012. A European perspective for developing modern multifunctional agroforestry systems for sustainable intensification. Renew. Agric. Food Syst. 27, 323–332.

Song, M., Li, X., Jing, S., Lei, L., Wang, J., Wan, S., 2016. Responses of soil nematodes to water and nitrogen additions in an old-field grassland. Appl. Soil Ecol. 102, 53–60.

Steel, H., Ferris, H., 2016. Soil nematode assemblages indicate the potential for biological regulation of pest species. Acta Oecologica 73, 87–96.

Steenwerth, K.L., Jackson, L.E., Calderón, F.J., Stromberg, M.R., Scow, K.M., 2002. Soil microbial community composition and land use history in cultivated and grassland ecosystems of coastal California. Soil Biol. Biochem. 34, 1599–1611.

Szpak, P., 2014. Complexities of nitrogen isotope biogeochemistry in plant-soil systems: implications for the study of ancient agricultural and an mal management practices. Front. Plant Sci. 5, 1–19.

Thomas, G.W., 1996. Soil pH and soil acidity, in: Sparks, D.L. (Ed.), Methods Soil Anal. Part 3 - Chem. Methods. Soil Sci. Soc. Amer. Book Ser. 5. Soil Sci. Soc. Amer. Madison, WI, USA. pp. 475–490.

Tison, J.-M., de Foucault, B., 2014. Flora Gallica: Flore de France. Biotope éditions. Mèze, France.

Trap, J., Bonkowski, M., Plassard, C., Villenave, C., Blanchart, E., 2016. Ecological importance of soil bacterivores for ecosystem functions. Plant Soil 398, 1–24.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management. Ecol. Lett. 8, 857–874.

Tsiafouli, M.A., Thébault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten, W.H., Birkhofer, K., Hemerik, L., de Vries, F.T., Bardgett, R.D., Brady, M.V., Bjornlund, L., Jørgensen, H.B., Christensen, S., Hertefeldt, T.D., Hotes, S., Gera Hol, W.H., Frouz, J., Liiri, M., Mortimer, S.R., Setälä, H., Tzanopoulos, J., Uteseny, K., Pižl, V., Stary, J., Wolters, V., Hedlund, K., 2015. Intensive agriculture reduces soil biodiversity across Europe. Glob. Chang. Biol. 21, 973–985.

Tuomisto, H., 2010. A diversity of beta diversities: Straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography (Cop.) 33, 2–22.

Veen, G.F., Olff, H., Duyts, H., Van Der Putten, W.H., 2010. Vertebrate herbivores influence soil nematodes by modifying plant communities. Ecology 91, 828–835.

Viketoft, M., 2007. Plant induced spatial distribution of nematodes in a semi-natural grassland. Nematology 9, 131–142.

Viketoft, M., Bengtsson, J., Sohlenius, B., Berg, M.P., Petchey, O., Palmborg, C., Huss-Danell, K., 2009. Long-term effects of plant diversity and composition on soil nematode communities in model grasslands. Ecology 90, 90–99.

Villenave, C., Jimenez, A., Guernion, M., Pérès, G., Cluzea, D., Mateille, T., Martiny, B., Fargette, M., Tavoillot, J., 2013. Nematodes for soil quality monitoring: Results from the RMQS BioDiv Programme. Open J. Soil Sci. 03, 30–45.

Wardle, D.A., Walker, L.R., Bardgett, R.D., 2004. Ecosystem properties and forest decline in contrasting long-term chronosequences. Science 305, 509–513.

Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proc. Natl. Acad. Sci. 96, 1463–1468.

Yeates, G.W., Bongers, T., De Goede, R.G., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera-an outline for soil ecologists. J. Nematol. 25, 315–331.

Zhang, X., Guan, P., Wang, Y., Li, Q., Zhang, S., Zhang, Z., Bezemer, T.M., Liang, W., 2015. Community composition, diversity and metabolic footprints of soil nematodes in differently-aged temperate forests. Soil Biol. Biochem. 80, 118–126.

Zhang, X.K., Ferris, H., Mitchell, J., Liang, W.J., 2017. Ecosystem services of the soil food web after long-term application of agricultural management practices. Soil Biol. Biochem. 111, 36–43.

Zhao, J., Neher, D.A., 2013. Soil nematode genera that predict specific types of disturbance. Appl. Soil Ecol. 64, 135–141.