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Crop management strategies shape the shared temporal dynamics of soil food web structure and functioning

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ABSTRACT

In recent decades, there has been growing interest in exploring the soil biota, highlighting the significance of soil organisms' networks in soil functioning. Here, we use a modeling approach to investigate how changes in cropping practices influence the soil food web dynamics and it relates to that of soil functioning. In an experimental trial, we tested for change in topsoil food webs after shift from conventional to alternative practices (changes in tillage intensity, amount of residues returned and N fertilization rate). Samplings were made in 16 plots of a randomized complete block design during spring of year 0, 2 and 4 after the onset of the trial. Microorganisms, microfauna, mesofauna and macrofauna were sampled, identified and grouped into trophic groups. We built a general soil food web describing plausible carbon flows between these trophic groups and computed several network indices. At the same dates, soil functions linked to C and N dynamics were measured from soil samples. We used a COSTATIS analysis to investigate relationships between temporal sequences of soil functions and soil food web indices. Significant interactive effects of the date and of agricultural systems were found on the mean and the maximum trophic level, the bacterial-to-fungal path ratio, the total biomass and the way biomass accumulates across trophic levels, the number of trophic groups and the functional redundancy in trophic groups. Similarly, organic matter transformations and enzymatic activities showed differences across date and agricultural systems. Results show that temporal changes in soil food web structure and in soil processes related to N and C cycling co-vary following changes in agricultural management practices. Management practices related to tillage exerted stronger effects on soil food web functioning than those related to the export of crop residues or reduction in mineral N fertiliser. For instance, reduced tillage lead to more complex food webs, with increased C and N mineralization in the upper soil layer (0–5 cm), in which most of the residues accumulate. Our results provide insights on soil food webs temporal dynamics, even within a restricted panel of agricultural practices. Our results suggest that changes in agricultural practices influence feedbacks between organisms and the functions they perform, so that a temporal co-structure can be observed in the studied site. Such work could help better understand the mechanisms of resistance or ecological debt during agroecological transition, which could limit or delay expected Nature-based solutions.

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1. Introduction

The hidden world of the soil biota has been increasingly investigated in the last decades revealing the importance of soil organisms for soil functioning, notably organic matter decomposition and nutrient cycling (Bardgett and van der Putten, 2014; Crowther et al., 2019). At the same time, concern has grown about the unfavorable or declining state of soil biodiversity worldwide, particularly in agro-ecosystems (Geisen et al., 2019; Tsiafouli et al., 2015). Therefore, improved understanding of how multitrophic soil communities respond to changes in land use intensification and agricultural practices and how their functional structure relates to soil functioning has been identified as a key challenge for scientific research (de Vries et al., 2013). Indeed, the soil biota displays a multi-dimensional and richly connected structure (Bloor et al., 2021), with trophic interactions among soil organisms being intimately linked to the cycling of nutrients (Brondani et al., 2022; Whalen et al., 2013).

The study of soil food webs has been used to investigate how environmental and anthropogenic changes affect ecosystem functioning (Calderón-Sanou et al., 2022; Morris, 2010). The amount of time and effort needed to collect the data or the lack of explicit trophic interaction matrices have limited their study in soil ecology. Recently, the metabarcoding of environmental DNA has offered new possibilities to model soil food web topology (Bloor et al., 2021; Calderón-Sanou et al., 2022). However, the eDNA metabarcoding does not allow to characterize taxa biomass, a major limitation for modeling energy fluxes between trophic groups (Tsiafouli et al., 2015). Modeling energy fluxes in the food webs allows deriving quantified indices of community structure, such as fungal-to-bacterial path ratio which can be related in turn to measures of soil functioning (de Vries et al., 2013), with more efficiency than soil food web topology alone.

In cropped systems, the role of soil organisms has long been supplemented by the use of external inputs, such as fertilizers and pesticides. Studies on the effects of agricultural practices on soil food webs and associated functioning have been developed in 1990's (de Ruiter et al., 1993; Hunt et al., 1987; Moore and de Ruiter, 2012). Agricultural intensification drives modifications in taxonomic, functional and trophic group diversity (Bloor et al., 2021), thereby compromising soil biodiversity potential to contribute to soil functioning. Several studies have shown that contrasting land uses in agroecosystems can greatly affect soil food web structure and biomass distribution (Barnes et al., 2014; Potapov et al., 2019; Tsiafouli et al., 2015), which can co-vary with important soil functions (de Vries et al., 2013). However, while the development of alternative agricultural practices has been identified as a key challenge for sustainable food production (Tilman et al., 2002), we still need to investigate how changes in agricultural management practices influence the links between soil food web and soil functions (Bach et al., 2020). Indeed, most existing studies focus so far on distinct land uses (e.g. grasslands, extensive and intensive rotations in (Tsiafouli et al., 2015); rainforest, rubber and oil palm plantations in (Potapov et al., 2019)) rather than on effects of management practices in each crop system. Another issue is the need to deal with soil food webs temporal dynamics, as it is crucial for forecasting future management strategies. For example, temporal variability is of great significance for the persistence of populations, the coexistence of species and thereby species interactions.

Hence, in addition to previous studies focusing on the effect of land use without taking temporal dynamics into account (e.g. Tsiafouli et al., 2015), herein we investigated how agricultural practices shape the soil food webs and ecological functions over time. We use food web modeling to investigate how changing agriculture practices influence the structure of soil communities over time and how its dynamics relates to that of soil functioning. For this, we tested for a change in topsoil food webs after shift from conventional to alternative practices (changes in tillage intensity, residues management and N fertilization). Soil organisms from microorganisms (bacteria and fungi), microfauna (protists and nematodes), mesofauna (collembola and mites) and macrofauna

(annelids, mollusks, arthropods), as well as C and N soil functions, were studied during four consecutive years in an agricultural long-term experiment after the adoption of new practices. We estimated the energy fluxes between the trophic groups calculated a set of food web indices and tested for their variation over years., We hypothesized that less intensive management would (*i*) increase the total biomass of soil organisms and decrease the dominance of bacteria over fungi and reduce the predominance of bacteria compared to fungi in the energy pathway, (*ii*) increase the number of trophic groups and the functional redundancy within groups, and (iii) shift food webs from bottom-heavy (most of the biomass at the bottom of the food web) towards top-heavy. We also postulated that soil food webs and soil functioning would follow similar temporal patterns.

2. Materials and methods

2.1. Study site

The study was conducted on the 'arable crops' site of the long-term experiment ABCB (Agriculture, Biogeochemical Cycles and Biodiversity). It is implemented by the INRAE (French national research institute for agriculture, food and environment) and located at Estrées-Mons, Northern France (49.873 N, 3.032 E). The experiment was established on a 11 ha field previously managed with conventional practices for at least 25 years. Prior to the onset of the experiment, a complete homogenization of the field was done during 2 years (wheat in 2008 then barley in 2009 followed by a mustard intercropping), during which plots were managed under conventional tillage and residues incorporation with mouldboard ploughing (CONV treatment, see below). A six-year rotation was initiated in March 2010 (T0) and six treatments were set up with four replicates within a randomized block design (Fig S1). The crop rotation was spring pea (*Pisum sativum*, L.), winter wheat (*Triticum aestivum*, L.), rapeseed (*Brassica napus*, L.), spring barley (*Hordeum vulgare*, L.), maize (*Zea mays*, L.) and winter wheat (*Triticum aestivum*, L.). Four of six treatments were investigated in the present study (Table 1): CONV (conventional practice with full inversion tillage), RT (reduced tillage), RT-RR (reduced tillage and residues removal) and RN (reduced N fertilization). The CONV treatment is the continuation of the previous management system, and the other treatments are deviations from it.

In the RT-RR treatment, crop residues were removed after harvest using a hay baler after cereal crops and a silage harvester for maize. In the other treatments, crop residues were incorporated in soil using disk plowing in the RT treatment and mouldboard ploughing in the CONV and RN treatments. Tillage depth was about 25 cm in the ploughed treatments and 7 cm in the reduced tillage treatments. In the other treatments, crop residues were incorporated in soil using disk ploughing in the RT treatment and mouldboard ploughing in the CT and RN treatments. The reference rate of N fertilization was calculated for each

Table 1

Description of the investigated treatments within LTER ABCB (Agriculture, Biogeochemical Cycles and Biodiversity) dedicated to arable crops.

Code	Traitment	Soil tillage	Crop residue management	N fertilization rate
CONV	Conventional	Full-inversion tillage	Returned	Reference[a]
RT	Reduced tillage	Shallow tillage	Returned	Reference
RT-RR	Reduced tillage and residue removal	Shallow tillage	Exported	Reference
RN	Reduced Nitrogen	Full-inversion tillage	Returned	32 % of the Reference

[a] The reference rate was calculated for each crop each year, according to a N balance-sheet method

crop each year, based on a N balance-sheet method. Over the full rotation, the mean fertilization rate was 134 kg N ha^{-1} yr^{-1} for CONV, RT and RT-RR treatments and 43 kg N ha^{-1} yr^{-1} only in RN treatment. Initial soil physico-chemical parameters and their spatial variability were measured at the onset of the trial on a 270-points grid, independent of blocks (Coudrain et al., 2016). No significant differences in any characteristics between treatments were detected at the onset of the experiment.

The total amount of C returned to soil through aerial crop residues during the studied period was 13.7, 12.5, 13.7 and 6.8 Mg C ha^{-1} in the CONV, RN, RT and RT-RR treatments, respectively. However the ranking was different in the 0–5 cm soil layer studied here. Taking into account the mixing depth of crop residues in soil by tillage (7 cm for RT and RT-RR, 25 cm for CONV and RN), and the consequent dilution of organic matter inputs in the soil, the annual input of aerial crop residue-C in the 0–5 cm layer was estimated at 0.68, 0.62, 2.45 and 1.22 Mg C ha^{-1} yr^{-1} in the CONV, RN, RT and RT-RR treatments respectively, during the first four years.

2.2. Soil biota collection

The sampling procedure was fully described by (Coudrain et al., 2016). Soil organisms were sampled in each of the sixteen plots, in March 2010, 2012 and 2014 at the start of the growing season. Microorganisms were collected from five soil cores (0–20 cm depth) pooled to obtain one sample per plot for each year. Microbial DNA was extracted from 1 g of soil (Terrat et al., 2012). Bacterial and fungal diversities were determined by 454 pyrosequencing of ribosomal genes. For bacteria, a 16 S rRNA gene fragment with sequence variability and the appropriate size (about 450 bases) for 454 pyrosequencing was amplified by PCR using primers F479 and R888. For fungi, a 18 S rRNA gene fragment of about 350 bases was amplified using primers FR1 and FF390. Primers and PCR conditions were as described in Tardy et al. (Tardy et al., 2014). The PCR products were purified using a MinElute gel extraction kit (Qiagen, Courtaboeuf, France) and quantified using the PicoGreen staining Kit (Molecular Probes, Paris, France). A second PCR of 9 cycles was then conducted under similar PCR conditions with purified PCR products and ten base pair multiplex identifiers added to the primers at 5' position to specifically identify each sample and avoid PCR bias. Finally, the PCR products were purified and quantified. Pyrosequencing was then carried out on a GS FLX Titanium (Roche 454 Sequencing System). Taxonomic units were derived from high-quality reads that were obtained using GnS-PIPE developed by the GenoSol platform (INRAE, Dijon, France) (Tardy et al., 2014).

Microfauna (Nematoda and Protozoa) was sampled in five soil cores taken in each plot at each sampling date using steel cylinders (5 cm diameter, depth 5 cm). All samples were transported to the laboratory in cool boxes, and stored at 4 °C before further treatments. Protozoan abundance was determined using a 5 g (fresh mass) sub-sample of sieved soil; the total number of Protozoa was estimated using the most probable number method (Ronn et al., 1995). In short, we first added 100 ml Tryptic Soy broth (TSB, 0.1 gl-1) to each of the wells in a 96 (12×8) well microtiter plate. Next, we mixed the 5 g of soil and 100 ml TSB in a blender for 1 min to produce a soil suspension. Then we transferred 50 ml soil of the suspension to each well in row 1 in the micro titre plate using a multichannel pipette, mixed thoroughly and transferred 50 ml to row 2, etc. until row 12. We stored plates in darkness in zipped plastic-bags (to avoid evaporation) at 12 °C, and inspected the wells for presence/absence of protozoa after 7 and 21 days using an inverted microscope (40 times magnification, phase contrast). We finally converted presence/absence data from the microtiter plates to "most probable number" of protozoa (MPN) using a computer program (Ekelund unpublished, based on Fisher, 1922). Nematodes were wet-extracted from approximately 300 g wet soil and then identified, using ISO 23611–4). The composition of the soil nematofauna was determined after fixing in a formaldehyde-glycerol mixture and

transferring to slides. On average, 185 nematodes per sample slide were identified to the family or genus level at 400X magnification.

Mesofauna (Collembola, Acari) was sampled at three sampling points using steel cylinders (5 cm diameter, depth 5 cm). Microarthropods were extracted by the dry-funnel method and stored in 70 % ethyl alcohol. Under the dissecting microscope, Collembola, Oribatida and Gamasinae were sorted out and enumerated. Soil-dwelling macroinvertebrates were hand-sorted from a 25 ×25×25 cm monolith of soil, preserved in alcohol and identified at least at the family level. Fauna Europaea was used as standard for invertebrate taxonomy (https://fauna-eu.org/).

2.3. Food web modelling

Different papers already described the response of soil organisms to agricultural practices in this site. However, herein, our aim was to analyse the functional dimension of the soil biodiversity, what was not the purpose of Coudrain et al. (Coudrain et al., 2016), focused on taxonomic diversity, nor of Coulibaly et al. (Coulibaly et al., 2017), dedicated to the sole group of Springtails. We chose to use this food-web approach because it allows to depict trends in C fluxes or pathways (e.g. green to brown pathway metric), this was possible by focusing on the biomass of each group, a novelty compared to the previous papers.

We built a general food web describing plausible trophic interactions between the soil taxa sampled during the experiment. Soil taxa were categorized into trophic groups that represented the nodes of the food web (Table S2). Trophic groups were defined as containing taxa sharing the same prey and predators (Bloor et al., 2021). To determine with the best accuracy to which trophic group each identified taxa belongs, an analysis of literature was made and eventually completed by taxa specialists of the consortium. Our final consensus soil food web contained 29 nodes (Figure S3).

Following previous studies on soil food webs, we estimated the energy fluxes between the trophic groups of the food webs by making a mass-balance assumption, meaning that for each trophic group growth equals loss (de Vries et al., 2013). With this assumption, material fluxes to each trophic group can be calculated using the biomasses of observed trophic groups in a given plot and year and the feeding preferences and physiological parameters of each trophic group. We considered that trophic group losses were equal to losses due to metabolism and predation (Barnes et al., 2014). The overall feeding rate of trophic group j on trophic group i (F_{ij}) is then expressed as:

$$F_{ij} = g_{ij} \frac{M_j + \sum_{k=0}^{n} F_{jk}}{a_j}$$

$$\text{with } g_{ij} = \frac{\omega_{ij} B_i}{\sum_{k=0}^{n} \omega_{kj} B_k}$$

where M_j is the metabolic demand of group j a_j is its assimilation efficiency n is the number of trophic groups and g_{ij} corresponds to the fraction represented by each prey i in the diet of trophic group j. g_{ij} depends on predator relative feeding preferences (w_{ij}) weighted by prey biomasses (B_i) The trophic group biomasses were calculated from observed taxa abundance [ind m^{-2}] and mean taxa body mass [mg] taken from literature data, except for the groups "detritus", "plant material", "bacteria" and "fungi" for which measured data did not allow appropriate estimation of biomass. This lack of data for basal trophic groups did not affect overall estimation of energy fluxes for other trophic groups since total feeding rates are estimated starting from the top of the food web. When detritus or plant material was part of the diet of some trophic groups, we considered that the diet fraction coming from these sources was fixed (i.e. g_{ij} = constant). When bacteria and/or fungi were part of trophic group diet, the fractions coming from these sources were estimated from total microbial carbon data (observed data obtained

from fumigation) and the relative proportion of bacterial 16 S rRNA copy numbers and fungal 18 S rRNA gene copy numbers (see S4). Parameters used for feeding preferences and body size were obtained from expert opinion completed with literature sources and data for assimilation efficiencies were obtained from literature sources (Table S2). Metabolic demand was calculated based on taxa fresh weight [mg] and taxa-specific metabolic constants (according to (Hoste-Danyłow et al., 2013)) and adjusted for a temperature of 8 °C, corresponding to the average March temperatures in our study site (details are given in S5).

We modeled the food web of each sampling plot (16 plots x 3 years = 48 food web models). From the food web models we calculated several complementary indices, focusing on nodes, fluxes trophic levels and trophic pathways. t. The number of nodes in the networks informs about how many trophic groups composed the network, while the mean number of taxa per trophic group informs on functional redundancy in the network. The number of links refers to the trophic flux number (how many groups interact). Link diversity can be measured in multiple ways, depending on the importance given to large fluxes. We used a unified approach that estimates the diversity profile (Chao et al., 2014), based on the Hill number ^qD where q measures the sensitivity of the links to the relative abundance. When $q = 0$, the links are equally weighted and ^0D equals link richness. Increasing orders of q emphasizes the relative weight of links, taking into account all links at low values of q to describing the diversity of only the stronger links at higher values of q. Hill numbers are continuous and can be portrayed on a single graph as a decreasing function of q, leading to a "link diversity profile" (Marcon and Hérault, 2015). The mean and the maximum trophic level depict the mean and the maximum postion of trophic groups in the network, corresponding to the distance from the basal energy sources. The total biomass is the sum of all organisms biomass in the network. We analyzed the cumulative distribution of biomass through the trophic levels and computed the area under curve (AUC) to synthesize these distributions. Higher values of AUC reflected more bottom-heavy food webs (i.e. relatively less biomass at the top of the food web). Finally, we computed the ratio of the proportion of total flux through the bacterial path vs fungal path (bacterial/fungal path log ratio) and through the plant path vs the detritus path (green/brown path log ratio). These two later indices allow to depict the modification of predominance of some of path of energy flow.

2.4. Soil function measurements

The potential gross N fluxes, C mineralization and enzymatic activities were measured in the soil layer 0–5 cm in the laboratory, with 4 replicates per treatment corresponding to the four blocks. The soils come from the same samples as those collected for nematode fauna. Gross N fluxes were quantified by the ^{15}N pool dilution technique[54] using a soil amendment of ^{15}N-NH$_4$. This approach allows simultaneous assessment of N mineralization, N immobilization and nitrification. The protocol used here was described in detail by Attard et al. (Attard et al., 2016). Briefly, for each sampling date and treatment, a sub-sample of fresh soil (42 g equivalent dry soil), sieved at 2 mm and adjusted to 20 % humidity by spreading it thinly and spraying it with a ^{15}(NH$_4$)$_2$SO$_4$ solution (15 mg NH-N kg^{-1} soil enriched at 10 atom% ^{15}N) using an atomizer. The soil was then mixed, separated into two sub-samples, placed in glass vessels and incubated at 15 °C, one vessel was removed after 2 h and the second sub-sample was removed after 74 h. NH$_4^+$ and NO$_3$ in soil were extracted with KCl and sequentially transferred to a filter using a micro diffusion technique (Fillery and Recous, 2001). The NH$_4^+$ and NO$_3$ contents of the supernatants and the organic N concentrations of the soil pellets, along with their ^{15}N abundances, were measured by mass spectrometry (N analyser Euro EA, Eurovector, Milano, Italia and Delta Avantage, Thermo- Electron, Bremen, Deutschland). Gross mineralization and nitrification were calculated using the classical isotopic dilution equations (Geens et al., 1991) while gross immobilization was calculated using the enrichment in ^{15}N of the soil organic N according to Mary

and Recous (Mary and Recous, 1994). All fluxes were expressed in mg N per kg of dry soil and per day at 15 °C.

C mineralization was calculated from the C-CO$_2$ emitted from soil samples during the 74 h incubation used to determine gross N fluxes, and was used as a proxy of soil heterotrophic microbial activity. Soil samples were placed in jars containing a beaker with water and a 20 ml vial filled with 0.25 M of a NaOH solution to absorb CO$_2$ produced. Sodium hydroxide contained in the vials was back titrated with 0.025 M HCl, at the end of incubation.

β-glucosidase and urease activity measurements were performed in microplate less than 48 h after sample collection, according to Cheviron et al. (2022). Briefly, activities were measured in triplicates in 4 g soil samples mixed during 10 min at 250 rpm with 25 ml water. For β-glucosidase activities, soil solutions were incubated respectively with 4-nitrophenyl β-D-glucopyranoside (50 mM, 1 h). Reaction was stopped with 0.5 M CaCl$_2$ and 0.1 M Tris at pH 12. For urease activity, soil solutions were mixed with 0.4 M urea. NH$_4^+$ formed was revealed with ammonium salicylate and ammonium cyanurate. After the reactions, each plate was centrifuged 5 min at 2000 g, and absorbance was measured on a microplate reader Genius (SAFAS). The amounts of p-nitrophenol (PNP) and NH$_4^+$ formed were obtained by measuring the absorbance at 405 nm and 610 nm with comparison to calibration curve. Results were expressed as mU g^{-1} dry soil.

2.5. Statistical analysis

For each of the food web indices and the soil function measurements mentioned above, we investigated temporal differentiation between agricultural practices using linear mixed effect models. Food web indices and soil functions were individually considered as the response variable, year and agricultural treatment as the fixed effect and plot within block as random effect to account for annual resampling of the same plots. We considered a significant interaction between "year" and "treatment" to be indicative of temporal differentiation. Post-hoc test of differences among treatments was conducted using Dunn test. Model assumptions were visually checked. Log-transformation was used if it improved residual distribution.

To investigate the temporal co-variation between soil food web properties and soil functions following changes in agricultural practices, we used a descriptive approach which (i) does not need definition of dependent and independent variables as in predictive approaches and (ii) can be used without constraint on the ratio between the number of samples and the number of variables. We constructed a temporal sequence (over $k = 3$ sampling dates) of paired ecological tables with similar rows (the studied plots), and with columns corresponding to either (i) soil function variables or (ii) soil food web indices. We used a COSTATIS analysis to investigate relationships between this pair of k-tables (Thioulouse, 2011). More precisely, COSTATIS first performed two Partial Triadic Analyses (PTA) to compute the temporal compromises of each k-tables, and then a Co-Inertia analysis (CoI) that studies the co-structure of the PTAs. PTA can be seen as the PCA of a series of PCAs. Significance of CoI was assessed using permutation tests. Analyses and graphs were realized using lme4, ggplot2 and ade4 libraries for R software.

3. Results

3.1. Food web temporal dynamics

The variations of food web indices are displayed in Fig. 1 and the significance of the effects of agricultural treatments and year on these indices are depicted in Table 2. Significant interactive effect of "year" and of "treatment" was found on the mean and the maximum trophic level, the bacterial-to-fungal path ratio ($p < 0.001$), the area under the biomass-to-trophic level curve ($p < 0.01$), functional redundancy, the number of trophic groups and total biomass ($p < 0.1$).
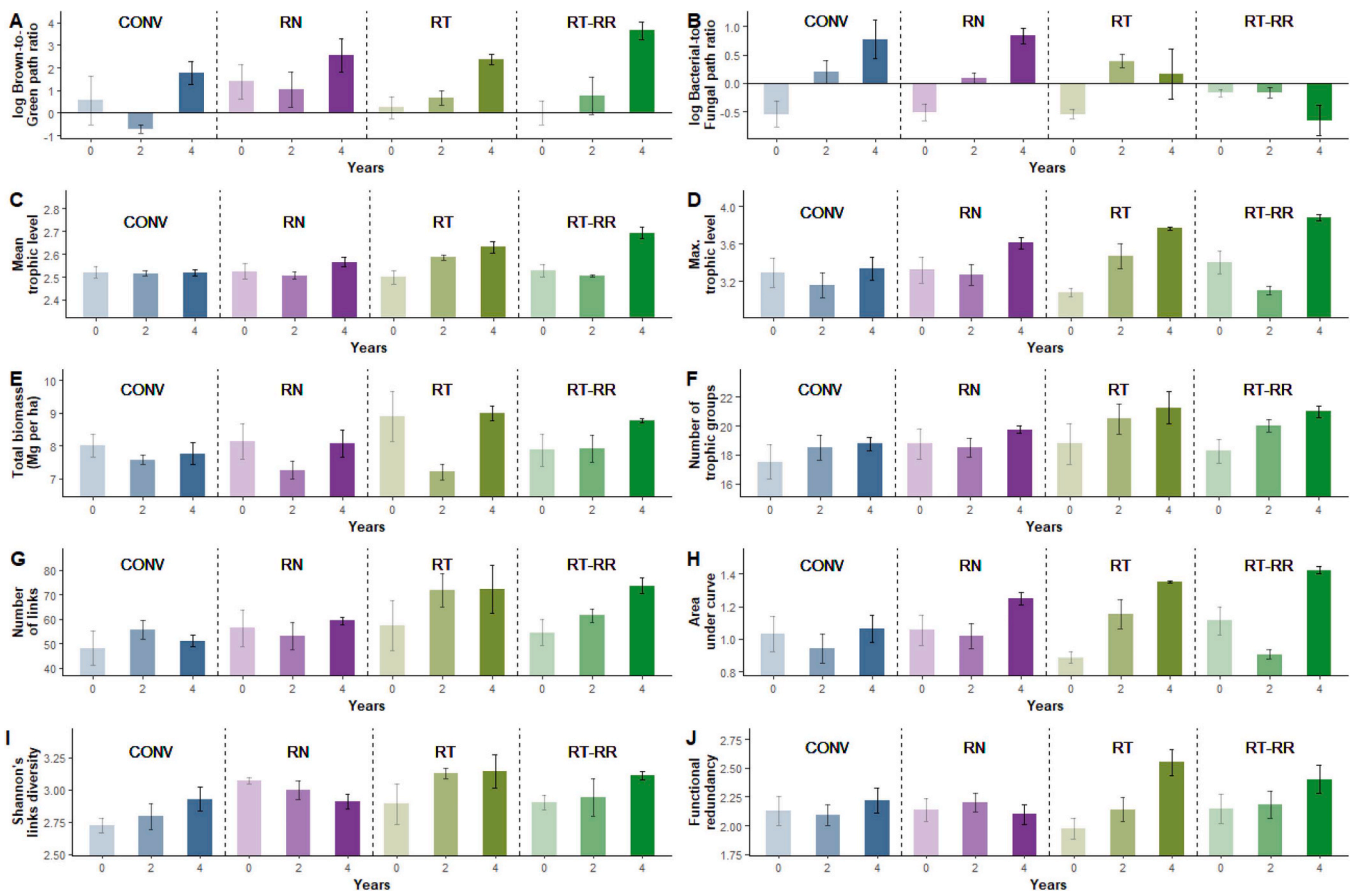
Fig. 1. Temporal dynamics of food web indices under the four agricultural managements. Agricultural management: CONV = conventional (inversion) tillage and residues incorporation with mouldboard, RN = same as CONV with reduced N fertilization, RT = same as CONV with reduced tillage, RT-RR = same as RT with crop residues removal.

Table 2
Significance of the effects of agricultural treatment, year and their interactions on food web indices, C-based and N-based functions.

		Treatment	Year	Ttt x Year
Food web indices	Brown-to-green path ratio	$	***	ns
	Bacteria-to-fungi path ratio	***	***	***
	Mean trophic level	***	***	***
	Maximum trophic level	***	***	**
	Total biomass	***	***	$
	Number of trophic groups	***	**	$
	Number of links	***	*	ns
	Area under curve	***	***	**
	Shannon's link diversity	***	ns	ns
	Functional redundancy	***	**	$
C-based functions	C mineralization	***	***	$
	Glucosidase	***	***	***
N-based functions	N mineralization	***	$	$
	N immobilization	***	***	*
	Nitrification	***	***	**
	Urease	***	***	***

*** $p < 0.01$,
** $p < 0.01$,
* $p < 0.05$,
$ $p < 0.10$.

The log-transformed brown-to-green path ratio only varied across years, being significantly higher after 4 years (Fig. 1A). The log-transformed bacterial-to-fungal path ratio was higher in the treatments with inversion tillage (CONV and RN) compared to the treatments with superficial tillage (RT and RT-RR) (Fig. 1B). Post-hoc tests indicated that in the last year (year 4), the mean trophic level was significantly lower in treatments with inversion tillage (2.52 – 2.57) than in the two others (2.63 – 2.69) (Fig. 1C), and similar results were found for the maximum trophic level (3.3 – 3.6 *vs* 3.8 – 3.9) (Fig. 1D). The total biomass of soil organisms was lower at year 2 than at the two other dates (7.4 *vs* 8.2 – 8.4 Mg ha^{-1} or 740 *vs* 820 – 840 kg m^{-2}; at year 4, it was significantly higher in treatments with superficial tillage (8.8 – 9.0 Mg ha^{-1} or 880 – 900 kg m^{-2}) than in treatments with inversion tillage (7.1 – 8.1 Mg ha^{-1} or 710 – 810 kg m^{-2} (Fig. 1E). The number of trophic groups was influenced by both date and treatments but without significant interaction (Fig. 1F).

The number of links (Fig. 1G) and the Shannon diversity of links (Fig. 1I) were affected only by treatments, with lower values in CONV than in RT-RR (and RT in the case of links number). On year 4, the area under the biomass-to-trophic level curve (Fig. 1H) was lower in RT than CONV, and the functional redundancy (Fig. 1J) was lower in RN than in RT-RR (2.5 and 2.1 species per group, respectively), the other treatments displaying intermediate values.

Temporal differentiation in the energy fluxes diversity was marked for the RT and RT-RR treatments, whereas they remained almost identical over time for the CONV and RN treatments (Fig. 2). For the RT and RT-RR treatments, differentiation occurred at $q <1$, which indicates that temporal differences in link diversity were mainly due to the increased presence of small fluxes. For all treatments, the steepness of the curve's slope indicates that large fluxes dominated the food webs.

The cumulative distribution of biomass over the trophic levels of the soil food web in the CONV treatment showed a similar pattern over time:
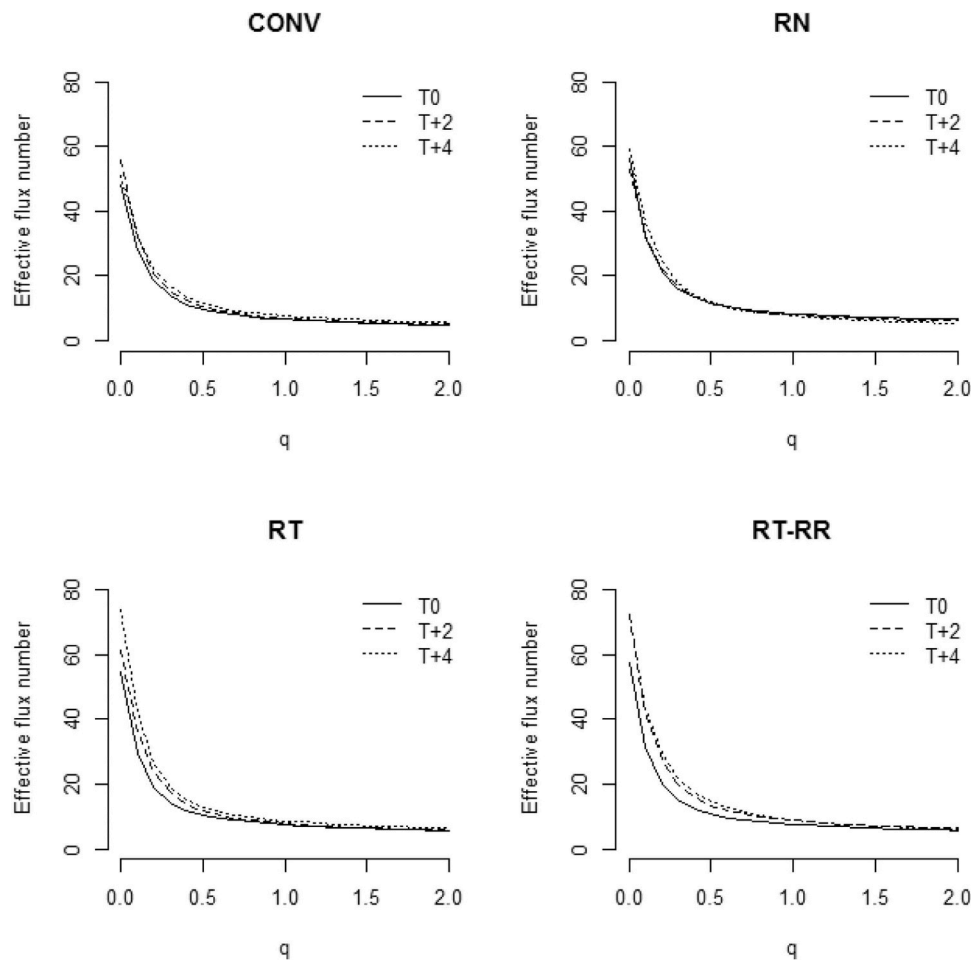
Fig. 2. Temporal dynamics of the the effective flux diversity under the four agricultural managements.

60–65 % of the biomass was concentrated in trophic levels lower than 2 and the whole biomass was contained in trophic levels smaller than 3.5 (Fig. 3). Conversely, the biomass distribution in RT-RR significantly changed over time. The proportion of biomass represented by organisms at the bottom of the food web significantly decreased with time, and the trophic level at which the curve saturated increased with time. The same result could be observed for RN, but with a lower magnitude and only at year 4. The RT treatment was also characterized by biomass distributions that significantly differed over years. However, the dynamic was not unidirectional. The food web became bottom-heavier at year 2 but reversed to a top-heavier pattern at year 4.

3.2. Temporal dynamics of soil C and N functions

C mineralization significantly varied across treatment and year and according to the interaction of both factors (Table 2). C mineralization increased with years, more in the RT and RT-RR treatments than in the CONV and RN ones (Fig. 4A). The glucosidase activity was also influenced by factors (treatment, date) and their interaction (Fig. 4B). After an increase at year 2, it saturated in the CONV and RN treatments on year 4 whereas it continued to increase in the RT and RT-RR treatments.

Nitrification rate ranged from 2.58 to 6.84 N kg soil^{-1} day^{-1}, and significantly responded to treatment and date (Fig. 4C). The lowest rate occurred in RN compared to CONV, RT and RT-RR which were not significantly different). The N mineralization rate varied from 0.68 to 2.73 mg N kg soil^{-1} day^{-1} and was influenced by treatment and the interaction treatment x date (Fig. 4D) with significant higher values in RT than in CONV. N immobilization rate ranged from 0.51 to 1.91 mg N kg soil^{-1} day^{-1} (Fig. 4E) and significantly varied with both factors and

their interaction). The temporal pattern was hump-shaped (maximum value reached at year 2) in RN, RT and RT-RR and decreased in CONV. N immobilization rate was significantly greater in the treatments with reduced tillage (RT-RR and RT) than in CONV and RN. Urease activity was significantly affected by the treatment, date and their interaction (Fig. 4F). Maximum values were observed on year 4, and were also higher in reduced tillage than in ploughed treatments.

3.3. Temporal covariation of food web parameters and soil functions

Results from the COSTATIS analysis revealed a significant co-structure between 'food web indices' and 'soil functions' *k*-tables (*RV* = 0.48, *p* < 0.001). Ordination of the compromises on the first factorial plan highlighted a clustering of the sampling plots according to treatments, with a clear separation between conventionally ploughed (CONV and RN) and reduced tillage (RT and RT-RR) treatments (Fig. 5). On the first axis, the conventionally plowed treatments were characterized by a higher bacterial-to-fungal path ratio and a bottom-heavy food web while the reduced tillage treatments were linked with high values of the other food web indices (except the functional redundancy) and of N mineralization, N immobilization and urease activity. The second axis mostly opposed RT to the other treatments. On this axis, RT was negatively correlated to bacterial-to-fungal path ratio and characterized by higher total biomass, link diversity, functional redundancy, brown-to-green path ratio and by higher C mineralization, nitrification and glucosidase activity.
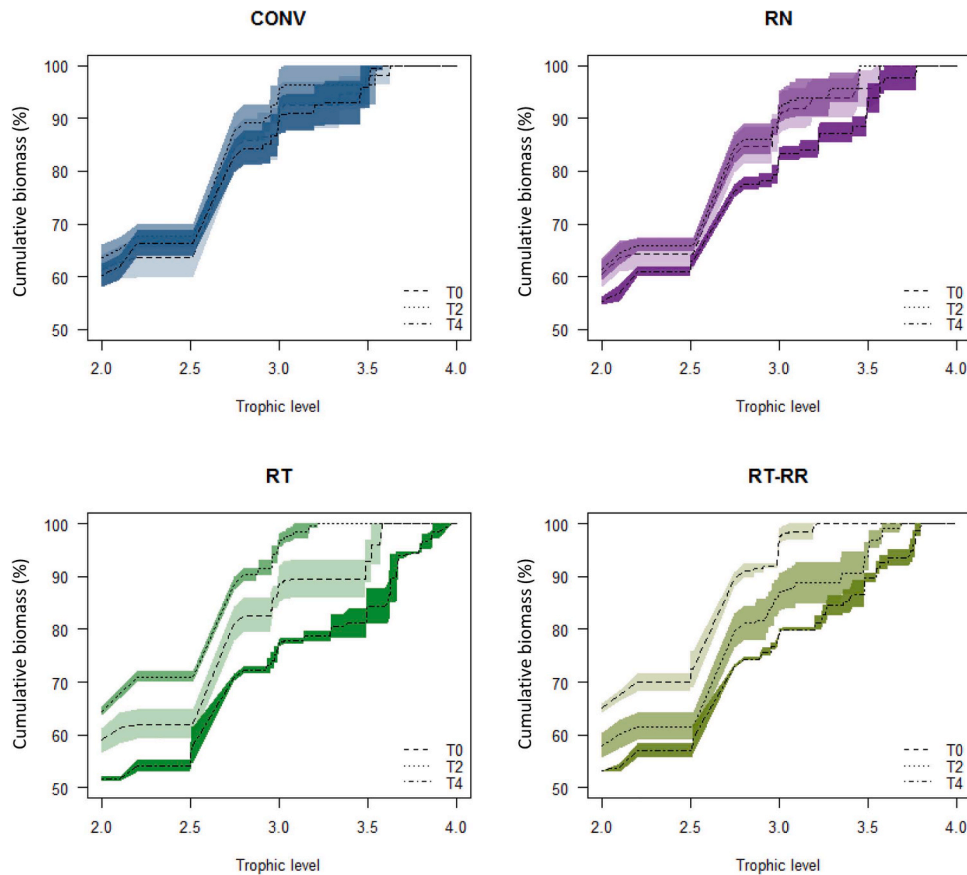
Fig. 3. Cumulative distribution of biomass over the trophic levels of the food web in the four agricultural managements. Lines represent the mean values, pinkish envelopes correspond to the 95 % confidence interval. Non-overlapping confidence interval envelopes reveal significant differences (p< 0.05).

4. Discussion

4.1. Temporal dynamics of soil food web under changing agricultural management

Our results show that in fields where tillage has been reduced for four years, soil food webs become more complex in the upper soil layer. Our results are in agreement with studies which found that soil food web complexity and redundancy within trophic groups decreased when land-use intensity increased (Barnes et al., 2014; Bloor et al., 2021; Tsiafouli et al., 2015). Such strong differences in land use are known to affect soil food web, while little is known about the impact of changes in agricultural management practices applied to a given cropping system. Our study demonstrates that changing agricultural management practices can also consistently affect soil food web complexity and related energy fluxes.

Our results confirm that the food webs of agricultural soils are dominated by a few large fluxes- (Fig. 2), mainly at the bottom of the network (Fig. 3). This reflects simplified communities in annual cropping systems compared to other agroecosystems (Bloor et al., 2021) and a high level of omnivory (Digel et al., 2014). As expected, we observed differences in bacterial-to-fungal path ratio according to agricultural management practices. While still dominated by bacteria-based energy pathways, a higher proportion of fungal-based in food webs may reflect both a decrease in tillage intensity and an increase in stabilized soil organic matter (Bloor et al., 2021).

Higher trophic levels may contribute little to total fluxes but have an important indirect effect on soil functioning (Koltz et al., 2018). The presence of higher trophic level species can change the relation between soil biota and soil processes, in a "positive" or "negative" way (Nielsen et al., 2011; Osler and Sommerkorn, 2007). For instance, higher trophic

levels (predators and micro-predators) and larger-size organisms (such as earthworms) are important in renewing/ stimulating basal levels (microorganisms), e.g. through their grazing activity, transportation of material and organisms and structuration of the soil habitat (Brondani et al., 2022; Erktan et al., 2020).

The shape of the biomass pyramid in food webs showed that reduced tillage leads to less bottom-heavy food webs, i.e. to food webs with relatively more biomass at the top trophic levels compared with full-inversion tillage. Changes in the shape of the biomass pyramid of soil food webs might reflect changes in the relative importance of top-down and bottom-up controls on food web dynamics (Oksanen, 1991). The changes in the biomass pyramid shape under reduced tillage was related to increases in link diversity through the addition of small energy fluxes. Although these additional links represent a small part of total energy fluxes in the food webs, they might significantly affect food web dynamics and stability, as predicted by theory (Mccann et al., 1998).

We found that changes in soil tillage produced the greatest effect on soil food web. This result may be explained by two reasons. (1) Soil tillage is recognized to be deleterious for many soil organisms, either directly by hurting, killing or exposing them to predators or indirectly by modifying their habitat (Neher et al., 2019; Pelosi et al., 2014). Reduced tillage promotes the growth of fungi and their consumers (Coulibaly et al., 2017; Hedlund et al., 2004). Full inversion tillage exerts harmful effects of on ecosystem engineers like earthworms, while the roles of ecosystem engineers on non-trophic energy fluxes in soil (bioturbation, nutrient availability, etc) largely overpass their biomass (Jones et al., 1994). (2) An indirect effect is linked to residues distribution in soil. Reduced tillage concentrates organic residues in the upper soil layer (0–5 cm) in which most measurements (microfauna, mesofauna, C and N fluxes) were made. We have mentioned the much greater input of residues-C in this layer in the reduced tilled treatments: 2.45 t C ha^{-1}
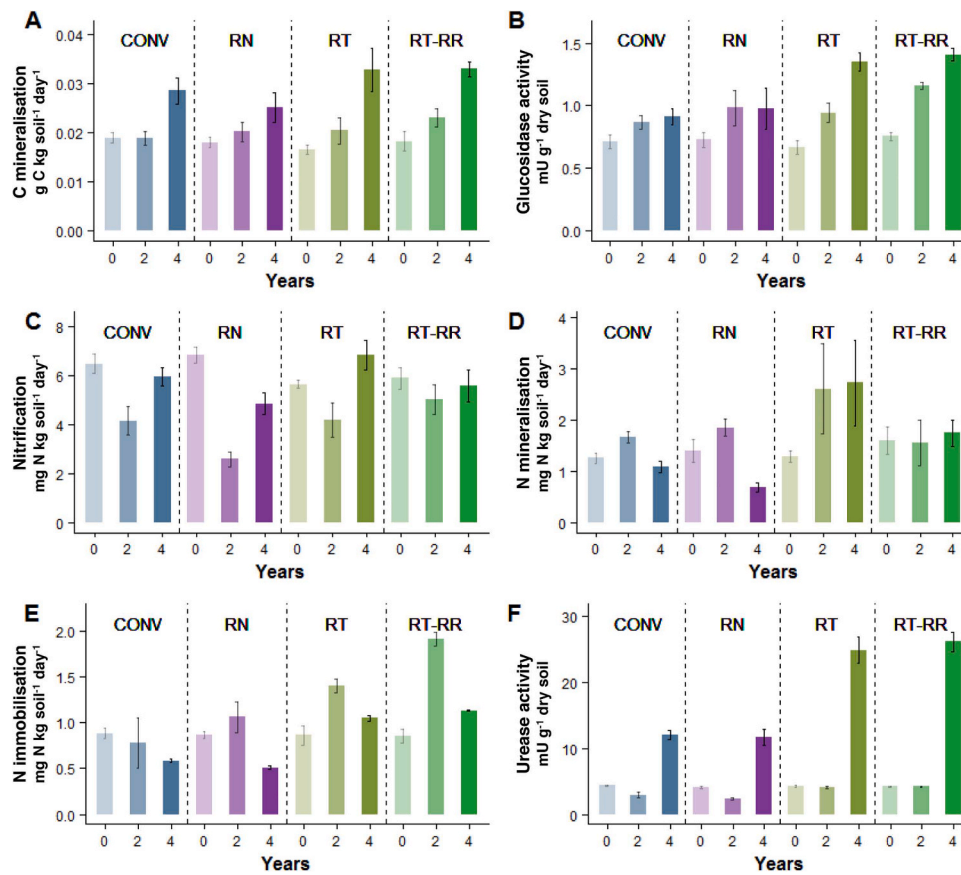
Fig. 4. Temporal dynamics of C-based and N-based soil functions in the four agricultural managements in the 0–5 cm layer. The significance of factors (treatment, date and their interaction) is given at Table 2.
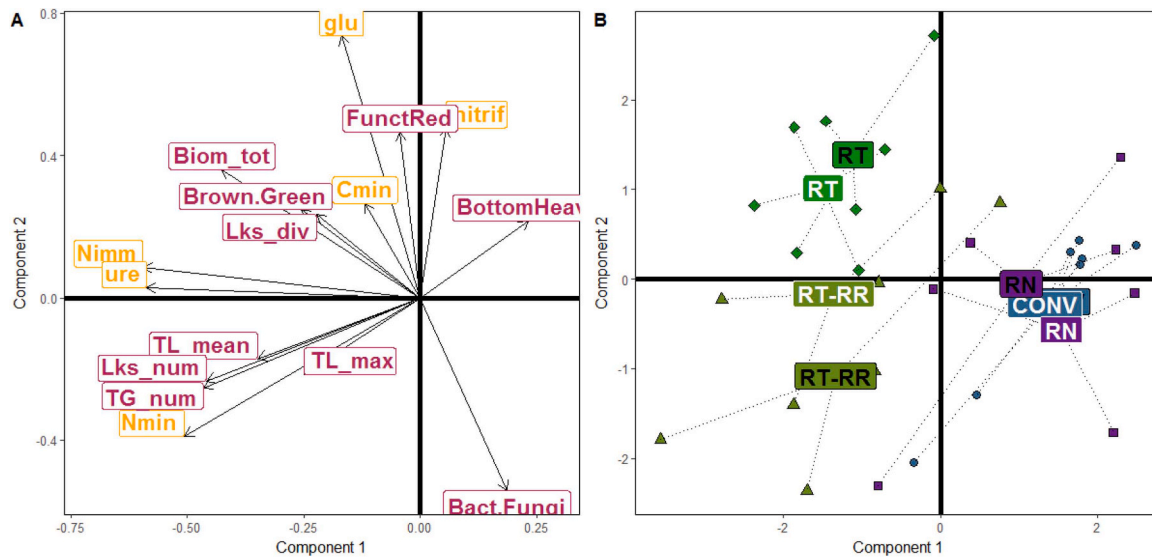

Fig. 5. Results of the COSTATIS analysis (mapping of the first two axes). Biplot of the co-inertia analysis between the compromises of the two Partial Triadic Analyses for soil function and food web indices (5 A). The coordinates of plots of the four agricultural managements from each PTA are displayed on Fig. 5B. Cmin = C mineralisation; glu = glucosidase activity; nitrif = nitrification, Nimm = N immobilisation; Nmin = N mineralisation; ure = urease activity; TL_mean = mean trophic length; Lks_div = diversity of links; Lks_num = number of links; TG_num = number of trophic groups; Biom_tot = total biomass; Brown.Green = Brown-to-green path ratio; Bact.Fungi = Bacterial-to-fungal path ratio; FunctRed = functional redundancy.

yr^{-1} in RT and 1.22 t C ha^{-1} yr^{-1} in RT-RR versus 0.68 t C ha^{-1} yr^{-1} in CONV.

It is difficult to disentangle the two effects which are simultaneously affected by soil tillage. Analyzing a long-term experiment, Mary et al.

(Mary et al., 2020) demonstrated that the C mineralization rate of the soil was strongly linked to the C input rate, much more than to the soil disturbance. The greater availability of crop residues in RT and RT-RR sustained higher trophic levels and more abundant predators in the

soil food webs at the end of the four years of changes in management practices, in agreement with theory that generally predicts that the number of trophic levels is limited by energy in ecosystems (Oksanen, 1991). Conversely, the treatment with reduced N inputs (which had the same C addition rate than the conventional) did not affect food web structure during the course of our study. This suggests that soil food web productivity is (still) not limited by nitrogen in the agricultural fields studied here.

The modeling of C fluxes in trophic networks is by nature a simplification of reality, linked to technical or modelling constraints which in turn imply specific impacts on the results. It should be regarded with the benefits it brings in our understanding of soil biodiversity, without denying its limitations linked to various parameters (e.g. biomass or assimilation rate). One inherent limitation of our study lies in the indirect estimation of organism biomass within the soil food web. We applied an average mass per taxon, which does not account for the intra- and inter-specific variability in the model. One other limitation in our food web model arises from the scarcity of data on assimilation rates across all trophic groups. For example, the assimilation rates for earthworms used herein may appear low, despite falling within the known range of values (Blanchart et al., 2009; Chertov et al., 2017). As assimilation rates are a cornerstone of the model, altering their values could lead to significant differences in the model output. While we have made efforts to address this limitation through careful parameterization and sensitivity analyses, it remains an important consideration in the interpretation of our results. We also chose to use trophic groups that are commonly defined by expertise (Hunt et al., 1987; de Vries et al., 2013; Potapov et al., 2019), while alternative approaches are available (Bloor et al., 2021; Hedde et al., 2022; Le Guillarme et al., 2023). Additionally, the sampling of invertebrates at different depths within the soil profile may further complicate the interpretation of our results. The differences in sampling depths are mainly due to the fact that, to limit the time needed to extract, count and identify organisms, the organisms are sampled in the relevant layer where they are most abundant and diversified. While soil biota presents decreasing abundance/biomass with depth, differences in this pattern exist (Moradi et al., 2020). Variations in sampling depths may lead to differences in community composition and biomass distribution, potentially influencing the dynamics of the soil food web. However, the layers sampled correspond to those that host the most organisms and biomass (Moradi et al., 2020).

While we acknowledge the limitations of our modeling approach may potentially alter absolute values within our study, we maintain confidence in the robustness of the relative differences observed between treatments. Despite these challenges, the fundamental changes in soil ecosystem dynamics induced by different agricultural practices are likely to manifest in discernible shifts in relative biomass distributions and food web structures.

4.2. Soil food web and soil functioning co-variation over time

Relating the dynamics of soil biotic communities to that of soil functioning has proven difficult so far. Because of indirect mechanisms and retroactions, the relationship between soil functioning and any single trophic group or trophic level may appear nonexistent or inconsistent (Filser et al., 2002). For instance, short term potential fluxes or enzymatic activities are snapshots of soil functions that may be difficult to relate with the density or biomass of organisms which are likely to follow seasonal dynamics. By studying the temporal co-variation rather than a direct one-off correlation between soil food webs and soil functions, we shed light on an existing co-dynamics.

The temporal co-dynamics between soil food web properties and soil functions supports the hypothesis that energy fluxes may serve as good indicators of ecosystem functioning. Even within a restricted range of practices, we detected changes in how soil food web and ecosystem functions correlate, thereby adding a significant contribution to other studies that mostly compared contrasted land uses or did not incorporate

large soil invertebrates (de Vries et al., 2013; Hunt et al., 1987).

Parallel dynamics of soil functions and soil community may reflect underlying feedback mechanisms, resembling an autocatalytic process. Indeed, in agricultural land, soil organisms can be limited by the low availability of trophic resources, while soil functions can be boosted by the presence/activity of organisms, by species complementarity or by interactions among organisms in the trophic networks. For example, microcosm experiments suggested that soil processes rates were primarily influenced by positive species interactions, such as facilitation or complementarity, occurring either between (Heemsbergen et al., 2004) or within soil invertebrate guilds (Hedde et al., 2010).

Temporal co-variation between soil functions and food web properties was observed on two axes related to tillage regime and amount of returned residues. Reducing drastically mineral N fertilization (by 68 %) did not result in a further variation compared to the conventional treatment. This may involve that at least during the first years, full-inversion ploughing shapes more drastically the links between food-webs and C- and N-based functions, as compared to mineral N fertilization. Our results highlight a positive association between N-based functions (urease activity, mineralisation and immobilization) and food webs characterized by higher links number and diversity, as well as increased biomass, mean trophic level and proportion of top predator (less bottom-heavy webs), associated with reduced tillage. Under such management, crop residues were buried into the topsoil only (0–7 cm), increasing concentration of crop residues and lowering mechanical soil disturbance, both processes providing more favorable environmental conditions for fungi than with full-inversion tillage. This first axis hence shows that soil N-based functions are related to bottom-up regulations as being favored by higher organic matter inputs. Previous studies showed that higher N mineralization is usually accompanied by higher N immobilization, because both processes are dependent, the Mineralization-Immobilization Turnover MIT (Jansson, 1971) being linked to soil organic matter content (Attard et al., 2016; Luxhøi et al., 2008). The higher inputs of plant residue-C and N in the top layer of the reduced tillage treatments enabled to increase the MIT and the enzyme activities in the RT and RT-RR treatments. Simultaneously, more complex trophic interactions arose in reduced tillage systems. N-based functions appeared to be correlated with the increase in mean trophic level and proportion of top predators (less bottom-heavy web) on the first axis, which indicates a possible top-down regulation of N-based processes. Despite the usually smaller biomass of higher trophic level organisms, whether a top-down regulation of the N cycle exists is a long-standing question (Verhoef and Brussaard, 1990). Predators might have cascading effects on the grazing pressure of microbivores on microorganisms (top-down control) and thereby patterns of N processing by microorganisms. Nematodes grazing on bacteria have been shown to boost N mineralization (Brondani et al., 2022; Standing et al., 2006).

We showed that glucosidase activity, C mineralisation, nitrification, total biomass and functional redundancy pointed in a similar direction in contrast to bacterial to fungal pathway ratio. Accordingly, exportation of residues may negatively affect predator abundance and relieve their control of microbivores, allowing increased N mineralization, while this is not strictly corroborated by our results. However, bottom-up effects of crop residue retention certainly further contribute to the association between soil food webs and soil functions. By offering particular habitat conditions and additional food resources, crop residues favor population growth of specific soil organisms. This is in agreement with our results, whereby the presence of crop residues diverts energy fluxes towards the brown pathway, usually related to an expanding fungal biomass and larger detritivore assemblages (Moore, 1994).

5. Conclusion

This study shows how soil food web structure and soil processes related to N and C fluxes co-vary following changes in agricultural

management practices. Both components varied with time and their variation was detectable even during a short period of four years of differentiation. We found that adapting management practices to reduced tillage had strong effects on soil food web functioning. Reduced tillage lead to more complex food webs with increased C and N mineralization in the upper soil layer (0–5 cm), in which most of the residues accumulate. This works open up questions on the mechanisms behind the observed patterns. It appears that in this trial, the interaction networks among organisms and the functions they carry out statistically co-vary, yet the feedback loops between them remain unsolved. Elucidating theunderlying mechanisms, like temporal mismatch or ecological debt—instances where habitat modification occurs without corresponding changes in communities or functions— is important to support the transition to agroecological practices. Understanding these temporal dynamics is crucial as they may impede or postpone the realization of anticipated Nature-based solutions.

CRediT authorship contribution statement

Valérie Coudrain: Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Pierre-Alain Maron:** Writing – review & editing, Methodology. **Matthieu Chauvat:** Writing – review & editing, Project administration, Methodology. **Nathalie Cheviron:** Writing – review & editing, Methodology. **Flemming Ekelund:** Writing – review & editing, Methodology. **Christian Mougin:** Writing – review & editing. **Bruno Mary:** Writing – review & editing. **Sylvie Recous:** Writing – review & editing, Project administration, Funding acquisition. **Cécile Villenave:** Writing – review & editing, Methodology. **Elisa Thébault:** Writing – review & editing, Writing – original draft, Conceptualization. **Mickael Hedde:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Conceptualization.

Declaration of Competing Interest

On behalf of all the authors of a submission, I disclose any financial and personal relationships with other people or organizations that could inappropriately influence our work.

Data Availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109058.

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