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# Effets des changements de pratiques agronomiques sur la diversité des vers de terre et collemboles- conséquences sur leurs fonctions associées.

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Normandie Université

## THÈSE

**Pour obtenir le diplôme de doctorat**

**Spécialité : Sciences de la vie et de la santé**

**Préparée au sein de « Université de Rouen Normandie »**

**Effets des changements de pratiques agronomiques sur la diversité des vers de terre et des collemboles – Conséquences sur leurs fonctions associées**

**Présentée et soutenue par  
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## Avant-propos

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Cette thèse a été menée au sein (i) du laboratoire d'écologie de l'Université de Rouen Normandie (Ecodiv URA/EA 1293, IRSTEA, FED Scale CNRS 3730), dirigé par le professeur Michaël AUBERT et (ii) de l'unité Aghyle (UniLaSalle, Aghyle UP 2018.101, FED NORVEGE 4277), dirigé par Isabelle GATTIN.

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Le présent manuscrit comprend une introduction générale répartie en quatre parties, quatre chapitres de résultats et une conclusion générale. Les chapitres de résultats ont été rédigés en anglais sous la forme d'articles scientifiques. Chaque article est précédé par une courte présentation rédigée en français.

## Résumé

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Le sol est une des composantes essentielles au soutien du fonctionnement de l'écosystème. Il est le support de la production primaire, un habitat pour la diversité biologique et remplit de nombreux processus écologiques. Les activités anthropiques, et parmi elles, les pratiques agricoles intensives, ont conduit à des déséquilibres au sein du sol causant un fort déclin de leur biodiversité. En réponse à ces effets, de nouvelles pratiques agricoles ont été développées pour préserver les sols et les services écosystémiques qu'ils fournissent. Ces pratiques dites innovantes s'appuient principalement sur la réduction du travail du sol, une gestion intégrée des résidus de culture, l'installation d'un couvert végétal permanent ou encore l'introduction de légumineuses dans les rotations de culture. C'est dans ce contexte de mutation des pratiques agricoles que s'inscrit ce sujet de thèse qui vise à mieux comprendre les effets de l'adoption de ces gestions innovantes sur (i) la diversité des communautés de la macro- et de la mésofaune du sol et (ii) sur le fonctionnement du sol en termes de stockage du carbone organique (source de nourriture de base), de structure du sol et de distribution de la taille des pores (milieu de vie). Au cours des différents chapitres de ce travail, nous avons mis en évidence trois actions liées à des pratiques agricoles innovantes combinant des approches expérimentales in et ex situ. L'objectif de la première action visait à étudier l'effet combiné de l'introduction de légumineuse (féverole) et de la réduction du travail du sol sur le compartiment endogé. Pour y répondre, nous avons développé une conception expérimentale empirique faite avec la combinaison des situations rencontrées dans les fermes. Nos résultats ont montré que l'interaction entre les deux pratiques innovantes n'a pas entraîné d'augmentation significative de la diversité de la faune du sol. Les fonctions microbiennes ainsi que la dynamique du carbone (C) et de l'azote (N) ne semblent pas non plus être affectées par ces pratiques. Il s'avère que les effets bénéfiques de ces pratiques innovantes ne peuvent être envisagés sans prendre en compte la manière dont elles sont mises en œuvre à l'échelle des rotations culturales et des itinéraires techniques. Cela nous a permis de valoriser une seconde action dont l'objectif était de suivre dans les mêmes conditions pédoclimatiques et mêmes itinéraires techniques, l'effet à long terme (quatre ans) de cinq régimes de gestion différents sur les communautés de faune du sol. Les traitements comprenaient des combinaisons de différentes cultures (annuelles, vivaces), de différents taux de fertilisation azotée (ajout d'azote, azote réduit), incorporation ou élimination de résidus de culture et différentes intensités de labour (labour vs. travail superficiel). Les résultats ont montré que la réduction de l'intensité du travail du sol a favorisé la diversité des collemboles et ses groupes fonctionnels grâce à l'amélioration des conditions de l'habitat à travers l'augmentation de la biomasse microbienne de carbone (source trophique). Par ailleurs, les autres composantes de la gestion, soit la « réduction des apports d'azote » et la « restitution / exportation des résidus de culture », n'ont pas eu d'effet sur les collemboles (abondance et richesse), notamment sur ceux vivants dans le sol, qu'ils soient hémi ou euédaphiques. Toutefois, cette étude démontre que la dissemblance dans la composition des assemblages de collemboles augmente avec la différenciation temporelle des pratiques agricoles et le travail du sol est le premier facteur responsable de cette trajectoire. Cette assertion a donné lieu à une troisième action dont l'objectif était de suivre sur une saison de végétation la conversion de la perturbation mécanique résultant du travail du sol sur la résistance et résilience fonctionnelle des assemblages biotiques édaphiques. L'expérimentation intègre trois niveaux de travail du sol : labour profond (état habituel), labour peu profond et non labour (états convertis). Au cours de cette étude, nous avons effectué des échantillonnages réguliers allant de la perturbation mécanique à la récolte. Nos résultats montrent que l'arrêt du travail du sol a entraîné une augmentation de l'abondance, de la diversité et de l'activité des communautés endogées (vers de terre et collemboles) au cours du temps. Ce changement dans le compartiment endogé est lié à l'amélioration de la distribution de, et de l'accessibilité à, la matière organique comme source alimentaire de base, de la structure physique du sol et de la distribution des tailles de pores comme espace de vie. De plus, les organismes du sol semblent répondre différemment quant à l'effet de la perturbation mécanique (Labour profond vs peu profond). La diversité des vers de terre a diminué après réduction du travail du sol alors que les collemboles ont répondu positivement. Ces changements dans les communautés d'organismes du sol se reflètent dans les modifications en termes de groupes fonctionnels. Enfin, nous avons dans un dernier volet testé en conditions contrôlées, l'influence différentielle des groupes fonctionnels de faune (Collemboles) sur différents processus liés au cycle du C et de l'N ainsi que la complémentarité fonctionnelle entre des différentes formes de vie. Les résultats montrent une influence négative des hémiédaphiques sur les communautés microbiennes (abondance, diversité et activité) alors que les épédaphiques et les euédaphiques ont peu ou pas d'effet. De plus, des effets de complémentarité et de compétition ont été constatés entre les formes de vie (groupes fonctionnels).

Les observations découlant de ces travaux de thèse suggèrent un rôle déterminant des communautés biologiques dans les activités liées au fonctionnement de l'écosystème. Ces conclusions ont une résonance tout à fait particulière dans un contexte de mutation de l'agriculture et la proposition de nouvelles pratiques susceptibles de modifier le fonctionnement biologique des sols.

Mots clés : agriculture de conservation, dynamique temporelle, macro – mésofaune, communautés microbiennes, écologie fonctionnelle, matière organique du sol, structure du sol.

## Abstract

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Soil is one of the essential components supporting the functioning of the ecosystem. It is the support of primary production; an habitat for biodiversity, and it fulfills many ecological processes. Human activities, including intensive agricultural practices, have led to impaired soil causing a sharp decline in their biodiversity. In response to these effects, new agricultural practices have been developed to preserve the soils and the ecosystem services they provide. These so-called innovative practices rely mainly on the reduction of tillage, integrated management of crop residues, the installation of permanent plant cover or the introduction of legumes into crop rotations. It is in this context of changes in agricultural practices that this thesis topic lays. This thesis aims to better understand the effects of the adoption of these innovative management practices on (i) the diversity of the macro and mesofauna communities soil and (ii) soil functioning in terms of organic carbon storage (basic food source), soil structure and pore size distribution (living environment). During the different chapters of this work, we highlighted three actions related to innovative agricultural practices combining *in situ* and *ex situ* experimental approaches. The aim of the first action was to study the combined effect of the introduction of legume (faba bean) and the reduction of tillage on the endogenous compartment. To answer this question, we developed an empirical experimental design made with the combination of situations encountered on farms. Our results showed that the interaction between the two innovative practices did not result in a significant increase in the diversity of soil fauna. Microbial functions and the dynamics of carbon (C) and nitrogen (N) also do not seem to be affected by these practices. It turns out that the beneficial effects of these innovative practices cannot be considered without taking into account how they are implemented at the scale of crop rotations and technical itineraries. This allowed us to promote a second action whose objective was to follow, under the same pedoclimatic conditions and the same technical itineraries, the long-term effect (four years) of five different management regimes on the communities of soil fauna. Treatments included combinations of different crops, different rates of nitrogen fertilization, incorporation or removal of crop residues and different plowing intensities. The results showed that the reduction of tillage intensity favored the diversity of Collembola and its functional groups by improving habitat conditions through the increase of microbial carbon biomass (trophic source). In addition, the other components of management, namely the "reduction of nitrogen inputs" and the "restitution / export of crop residues", had no effect on springtails (abundance and wealth), in particular on those living in the soil, whether hemi or euedaphic. However, this study demonstrates that the dissimilarity in the composition of Collembola assemblages increases with the temporal differentiation of agricultural practices, and tillage was the main factor responsible for this trajectory. This assertion gave rise to a third action, aiming to follow over a growing season the conversion of the mechanical disturbance resulting from tillage to the resistance and functional resilience of edaphic biotic assemblages. The experiment incorporates three levels of tillage: deep tillage (normal), shallow tillage and no tillage (converted). During this study, we conducted regular sampling ranging from mechanical disturbance to harvesting. Our results show that the cessation of tillage has led to an increase in the abundance, diversity and activity of endogenous communities (earthworms and Collembola) over time. This change in the soil compartment is related to the improvement of the distribution of, and accessibility to, organic matter as a basic food source, the physical structure of the soil and the distribution of pore sizes as a space for growth. In addition, soil organisms appear to respond differently to the effect of mechanical disturbance (deep vs. shallow tillage). Diversity of earthworms decreased after reduction of tillage while Collembola responded positively. These changes in soil organism communities are reflected at the functional groups level. Finally, we have in a last part tested under controlled conditions, the differential influence of functional groups of fauna (Collembola) on different processes related to the cycle of C and N as well as the functional complementarity between different life forms. The results show a negative influence of hemiapaphic on microbial communities (abundance, diversity and activity) whereas epedaphic and euedaphic have little or no effect. In addition, complementarity and competition effects were found between life forms (functional groups).

The observations from this thesis suggest a significant role for biological communities in activities related to the functioning of the ecosystem. These conclusions have a very particular resonance in a context of change in agriculture and the proposal of new practices likely to modify the biological functioning of soils.

Key words: conservation agriculture, temporal dynamics, macro - mesofauna and microbial communities, functional ecology, soil organic matter, soil structure

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# SOMMAIRE

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<b>Avant-propos.....</b>	<b>i</b>
<b>Résumé .....</b>	<b>ii</b>
<b>Abstract.....</b>	<b>iii</b>
<b>Remerciements.....</b>	<b>iv</b>
<b>INTRODUCTION.....</b>	<b>1</b>
<b>Chapitre 1.    État de l'art .....</b>	<b>2</b>
I.    Cadre de la thèse .....	2
II.   Synthèse bibliographique.....	5
1.   Utilisation des terres : Agriculture intensive .....	6
2.   Vers des agrosystèmes durables.....	7
3.   Modèles d'études : Faune du sol.....	11
III.  Objectifs de la thèse .....	16
IV.  Sites d'études.....	18
<b>RESULTATS ET DISCUSSIONS.....</b>	<b>21</b>
<b>Chapitre 2.    Introduction des légumineuses et réduction du travail du sol.....</b>	<b>23</b>
1.   Introduction .....	24
2.   Materials and methods.....	26
3.   Results.....	30
4.   Discussion.....	41
5.   Conclusion.....	46
<b>Chapitre 3.    Réduction du travail du sol, gestion des résidus de culture, diminution de la fertilisation azotée.....</b>	<b>48</b>
1.   Introduction .....	49
2.   Materials and Methods.....	51
3.   Results.....	55
4.   Discussion.....	64
5.   Conclusion.....	68
<b>Chapitre 4.    Réduction et arrêt de la perturbation mécanique.....</b>	<b>70</b>
1.   Introduction .....	71
2.   Materials and Methods.....	73
3.   Results.....	78
4.   Discussion.....	91
5.   Conclusion.....	96
<b>Chapitre 5.    Relations entre formes de vie des collemboles et communautés microbiennes</b>	<b>98</b>
1.   Introduction .....	99

2. Materials and Methods .....	101
3. Results .....	107
4. Discussion.....	119
5. Conclusion.....	121
<b>CONCLUSION GENERALE ET PERSPECTIVES.....</b>	<b>123</b>
I. Synthèse des résultats .....	125
1. Introduction des légumineuse et réduction du travail du sol (Chapitre 2).....	125
2. Réduction du travail du sol, gestion des résidus de culture, diminution de la fertilisation azotée (Chapitre 3) .....	127
3. Réduction et arrêt de la perturbation mécanique (Chapitre 4).....	127
4. Relations entre les groupes fonctionnels de collemboles et les communautés microbiennes (Chapitre 5).....	128
5. Bilan des travaux.....	129
II. Perspectives .....	131
III. Transfert de connaissances : préconisations quant aux pratiques agricoles novatrices .	133
<b>REFERENCES BIBLIOGRAPHIQUES .....</b>	<b>136</b>
<b>Liste des figures.....</b>	<b>160</b>
<b>Liste des tableaux.....</b>	<b>166</b>
<b>ANNEXES</b>	<b>170</b>









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## **INTRODUCTION**

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## Chapitre 1. État de l'art

### I. Cadre de la thèse

Le sol est une des composantes essentielles au soutien du fonctionnement des écosystèmes terrestres. Il est le support de la production primaire, un habitat pour la diversité biologique et est le siège de nombreux processus écologiques. Les activités anthropiques, et parmi elles, les pratiques agricoles intensives, ont conduit à des déséquilibres au sein du sol causant un fort déclin de leur biodiversité (Giller et al., 1997; Tilman et al., 2002; Tsiafouli et al., 2015). Afin de répondre à ces enjeux globaux et agronomiques, les acteurs du monde agricole développent de nouveaux modes de gestion des agrosystèmes non seulement adaptés socio-économiquement mais aussi tenant compte du maintien et de la durabilité des services écosystémiques et de la préservation de la biodiversité (Brussaard et al., 2007; DeLong et al., 2015a; Tiftonell, 2014). Ainsi, ces systèmes de gestion ont recours à des pratiques culturales telles que la réduction des intrants minéraux et organiques (engrais minéraux, amendements azotés et matière organiques) ou le développement de la fonction « stockage du carbone », via des pratiques culturales adaptées (nouvelles cultures, nouvelles rotations, recyclage des produits organiques, simplification du travail du sol). Les rotations de cultures sont l'une des clés de la réussite du système de production agricole. En effet, l'introduction de plantes ayant des caractéristiques morphologiques, physiologiques ou fonctionnelles différentes, comme l'enracinement ou le retour de matières organiques variable en qualité et quantité, peut permettre d'améliorer la structure, l'aération et la fertilité du sol agricole (D'Annibale et al., 2017; Sileshi and Mafongoya, 2006). Par ailleurs, il n'est pas toujours aisé pour un exploitant de pouvoir allonger sa rotation ou introduire des plantes légumineuses (freins techniques par exemple). Aussi, parmi les pratiques culturales, la réduction du travail du sol occupe une place particulièrement importante. Les effets du travail du sol sont relativement bien documentés, et différentes publications sont parues sur le sujet au cours des dernières années (Figure 1-1a). En général, l'abondance et la diversité des communautés du sol augmentent avec la diminution de l'intensité du travail du sol (Cortet et al., 2002; Dittmer and Schrader, 2000a; El Titi, 2003; Nakamoto et al., 2006; Wardle, 1995). Toutefois, récemment des nuances fortes sont apparues sur l'effet du travail du sol. Il semblerait que la nature du sol, la profondeur et surtout les périodes d'échantillonnages moduleraient très fortement voire inverseraient les réponses observées des organismes aux différents types de travail du sol (Capowiez et al., 2009; Chan, 2001). A titre d'exemple, van Capelle et al. (2012) ont observé dans leur méta-analyse des valeurs d'abondance de collemboles plus élevées dans les systèmes « labour conventionnel »

comparés aux systèmes « non travail du sol ». Cependant, ces auteurs ont trouvé que cela dépendait fortement du type de sol. De plus, Petersen (2002) a montré que l'abondance totale des collemboles était fortement réduite une semaine après les perturbations mécaniques (« labour » et « travail superficiel ») et que l'ampleur de cet effet ne différait pas entre les systèmes de travail du sol. Briones and Schmidt (2017), ont suggéré une réponse positive des populations de vers de terre suite à l'adoption du travail superficiel pendant au moins 10 ans.

Afin de clarifier tous ces aspects, mes travaux de thèse visent à caractériser l'effet de différents types de pratiques innovantes sur les assemblages biotiques du sol, les conséquences sur la qualité et la quantité des stocks de carbone, la structure des sols et la dynamique de l'azote (disponibilité de l'azote pour la plante). Pour ce faire, mes recherches s'articulent autour de trois actions liées à des pratiques agricoles innovantes, combinant des approches expérimentales in et ex situ. L'ensemble des actions de mon projet de thèse a été réalisé en partenariat avec des structures à l'interface entre recherche et application (Chambre d'Agriculture de la Seine Maritime (76) et de l'Eure (27), INRA).

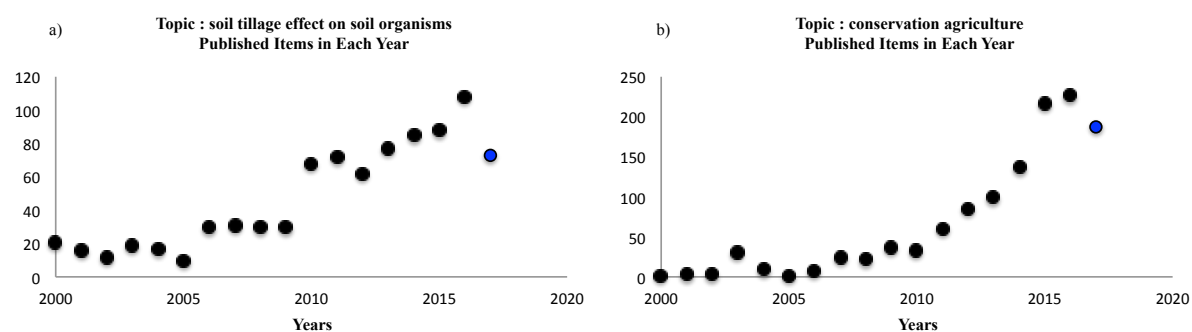


Figure 1-1: Nombre de publications par an relatives à (a) l'effet du travail du sol sur les organismes endogés Topic : « soil tillage effect on soil organisms », (b) agriculture de conservation Topic : « conservation agriculture ». Le point bleu indique l'état pour l'année 2017. (Web of Science, 2017/12/01 ; Timespan = All Years. Databases=SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH, ESCI).

Pour le présent travail, nous avons focalisé notre attention au sein du compartiment endogé sur trois composantes biotiques, à savoir la microflore (bactéries, champignons), la mésofaune (collemboles) et la macrofaune (vers de terre). Les vers de terre et les collemboles, avec des cycles de vie différents, sont respectivement les groupes les plus abondants de macro et de mésofaune dans les systèmes agricoles (Chauvat et al., 2014a; Ponge et al., 2003; van Capelle et al., 2012). De plus, ils sont évidemment importants pour la fertilité des sols agricoles au travers principalement la structuration des sols (Shipitalo et Protz, 1989), la transformation des matières organiques et le recyclage des nutriments par la régulation des communautés

microbiennes (Decaëns et al., 2006; Hopkin, 1997; Jones et al., 1994; Kaneda and Kaneko, 2008; Seastedt, 1984).

### **Organisation du manuscrit**

Le manuscrit comprend une introduction générale répartie en quatre parties, quatre chapitres de résultats et une conclusion générale. Les chapitres de résultats ont été rédigés en anglais sous la forme d'articles scientifiques. Chaque article est précédé par une courte présentation rédigée en français.

## **II. Synthèse bibliographique**

### **Présentation du chapitre 1**

Le cadre conceptuel de cette étude s'appuie sur des fonctions relatives aux sols, les services écosystémiques, l'agriculture intensive, l'agriculture de conservation, les communautés de macro – mésofaune et microbienne, la matière organique du sol et la structure du sol. Dans cette partie, je présente, dans un premier temps, l'action de l'homme par l'utilisation intensive des sols pour subvenir à ses besoins et explique comment cette pratique est responsable de la dégradation des ressources naturelles en mettant un focus sur les sols agricoles. Dans un second temps, je poursuis en introduisant l'agriculture de conservation comme une pratique maintenant la durabilité des ressources naturelles tout en présentant ses avantages et inconvénients. Dans un troisième temps, je présente les organismes étudiés en exposant leurs caractères fonctionnels et indicateurs en lien avec la durabilité de la ressource . Enfin, je finis par présenter les différents sites d'étude utilisés au cours de cette thèse.

## 1. Utilisation des terres : Agriculture intensive

Les modifications de la surface de la Terre sont si importantes que certains prétendent que la totalité de la surface terrestre est altérée par l'action humaine (Meyer and BL Turner, 1994; Redman, 1999). De par sa croissance démographique rapide au cours des derniers siècles, l'Homme a eu un effet majeur sur les écosystèmes terrestres. Cela figure dans les changements de couverture ou d'utilisation des terres/sols qui sont considérés comme des moteurs majeurs des changements globaux exerçant des pressions sur les sols et les services écosystémiques qu'ils fournissent (Smith et al., 2016).

Concernant les sols agricoles, l'impact anthropique le plus marqué au cours du 20e siècle réside dans l'intensification d'utilisation des terres (« révolution verte »). En effet, grâce à la transition démographique et à la révolution industrielle, le monde agricole a pu développer au maximum ses capacités de production en occupant tout l'espace qui lui était offert et en augmentant le rendement de chaque centimètre carré de ses terres (Borlaug, 2002; Conway, 1998; Foley et al., 2005; Pimentel and Pimentel, 2007; Smil, 2000; Tilman et al., 2001). Cela a entraîné une intensification de l'agriculture (encadré 1) à travers la sélection de cultivars de plantes à haut rendement, l'usage de l'irrigation, la généralisation de la mécanisation et l'utilisation massive d'intrants de synthèse (FAO, 2011a).

### **Encadré 1 : définition de l'agriculture intensive**

L'agriculture intensive n'est bien sûr pas seulement affaire de superficie utilisée. Elle se définit comme un système de production agricole caractérisé par l'usage important d'intrants, et cherchant à maximiser la production par rapport aux facteurs de production, qu'il s'agisse de la main d'œuvre, du sol ou des autres moyens de production, tel que le matériel agricole (Bedano et al., 2006; Cheverry, 1998). Elle se caractérise par un ensemble de pratiques, dont notamment l'augmentation des intrants (engrais, pesticides), l'introduction de nouvelles cultures et un recours important à la monoculture, l'évolution du travail du sol et des calendriers de travaux. Classiquement, ces pratiques agricoles ont été créées pour différentes raisons, à titre d'exemple : le travail du sol (parfois appelé labour, culture, creusement). « Acte de perturber le sol par l'utilisation d'un outil alimenté manuellement ou par des animaux ou des tracteurs qui préparent un lit de semence, vise à prévenir la prolifération des mauvaises herbes, des ravageurs et des maladies et donne à la culture les conditions optimales de germination (Gajri et al., 2002)».

Il convient de préciser que cette forme d'optimisation a entraîné des impacts négatifs au niveau environnemental, voire sociétal, tels que l'érosion et la diminution de la matière organique du



sol (perte de fertilité), les émissions des gaz à effet de serre, la pollution des eaux souterraines et la perte de la biodiversité du sol (Holland, 2004; Six et al., 2000; Tilman et al., 2002). Or, au regard de la croissance démographique qui varie en fonction de la disponibilité alimentaire, des études récentes suggèrent que le monde aura besoin de 70 à 100% de nourriture de plus d'ici 2050 (Bank, 2007; FAO, 2009). Un nouveau défi est à venir : comment nourrir neuf milliards d'Hommes avec moins de terres, d'eau et d'énergie ? Ces questions d'ordre environnemental, ainsi que la dépendance de ce modèle agricole à l'énergie fossile sont aujourd'hui des préoccupations majeures pour les sociétés humaines (Conway, 1998; Godfray et al., 2010; Smil, 2000; Tilman et al., 2002).

## **2. Vers des agrosystèmes durables**

Actuellement, la production alimentaire est une préoccupation mondiale dans l'agriculture qui pose des défis importants, mais aussi des possibilités de repenser la gestion des agroécosystèmes (DeLong et al., 2015a; Tiftonell, 2014). Alors que la population humaine continue d'augmenter, la production agricole devrait être réalisée de manière durable, en minimisant les effets environnementaux négatifs et en augmentant les revenus afin d'améliorer les moyens de subsistance (Hobbs, 2007). Il s'agit en d'autres termes de construire des agrosystèmes durables, utilisant des pratiques culturelles, actuellement utilisées en agriculture de conservation (encadré 2), agriculture biologique et agriculture de précision (Altieri, 1983; Kremen and Miles, 2012). Une façon évidente d'atteindre cet objectif de production alimentaire durable est d'utiliser plus efficacement les ressources naturelles nécessaires à l'optimisation de nourriture. Cela inclut l'eau, les sols, l'air, les intrants et les humains.

Au cours des dernières décennies, l'agriculture moderne a attiré l'attention des consommateurs et des décideurs politiques en raison de son appel à la promotion d'une agriculture réduisant l'apport des intrants de synthèse et fondée sur des pratiques écologiques et pour sa préoccupation à la préservation de l'environnement. En 2010, la FAO estimait que plus de 100 millions d'hectares étaient cultivés en agriculture de conservation dans le monde, pour seulement 45 millions au début des années 2000 (FAO, 2010). L'adoption de ces systèmes est donc croissante au niveau mondial et ils sont aujourd'hui présents dans une grande diversité de contextes climatiques (climats tropical, tempéré ou aride). En Europe, le développement de l'agriculture de conservation est bien plus modeste. La tendance y est toutefois en hausse avec 400 000 hectares en 2001 et 630 000 hectares en 2006 pour la France (Scopel et al., 2013). À cet effet, le regard porté par le monde scientifique et le monde agricole sur les sols a changé (Figure 1-1b). Les sols ne sont plus aujourd'hui considérés comme de simples supports de la

production agricole mais comme des entités naturelles à préserver au regard des multiples services qu'ils rendent à l'humanité tels que stockage du carbone, épuration de l'eau, maintien de la biodiversité, régulation du climat (Brevik and Hartemink, 2010; Hellec et al., 2015).

### Encadré 2 : définition de l'agriculture de conservation

L'agriculture de conservation est définie par la FAO (Food and Agriculture Organization of the United Nations) comme une agriculture reposant sur une forte réduction, voire une suppression du travail du sol, une couverture permanente des sols et des successions culturales diversifiées (Brouder and Gomez-Macpherson, 2014; ECAF, 2001; FAO, 2001; García-Torres et al., 2013). Son objectif principal est de conserver, d'améliorer et d'utiliser plus efficacement les ressources naturelles grâce à la gestion intégrée des sols disponibles, de l'eau et des ressources biologiques disponibles, combinés à des intrants externes. Elle contribue à la conservation de l'environnement ainsi qu'à une production agricole améliorée et soutenue, mais aussi au maintien de la viabilité économique et l'amélioration de la qualité de vie (Hobbs, 2007). On peut également l'appeler agriculture de ressources efficaces (FAO, 2009; Lal, 2010). Cela implique la nécessité d'introduire la notion de la « durabilité ». En effet, dans son approche moderne, l'agriculture de conservation remonte aux États-Unis au début des années 1980, indique un mode d'agriculture qui devrait imiter les écosystèmes naturels (Jackson, 1980; Scherr and McNeely, 2007).

### 2.1. Principes des agrosystèmes durables : cas de l'agriculture de conservation

L'agriculture de conservation est basée sur trois grands principes, qui doivent être appliqués simultanément (FAO, 2015; Hobbs, 2007), Figure 1-2.

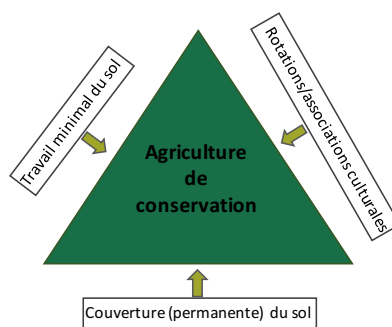


Figure 1-2 : Les principes fondamentaux de l'agriculture de conservation (FAO, 2015).

### 2.1.1. Travail minimal du sol

L'objectif principal est l'arrêt de toute perturbation mécanique apportée au sol. Mais un travail du sol simplifié ou réduit est souvent employé et pratiqué dans les agrosystèmes (Labreuche et al., 2007). Cela implique la diminution de la fréquence mais aussi de la profondeur du travail du sol classiquement appliqué. On retrouve ainsi :

- Le pseudo-labour : autrement appelé sous-solage ou décompactage (15 à 40 cm de profondeur), crée une porosité dans le sol, sans le retourner ni le mélanger.
- Le travail du sol superficiel : de 3 à 15 cm de profondeur avec des outils à disques ou à dents.
- Le semis direct (semis direct sous couvert végétal) : en l'absence de tout travail du sol. Le travail du sol n'est alors réalisé que sur la ligne de semis, à une profondeur faible (<5 cm), et par des semoirs à disques.



Source : <http://www.agriculture.gouv.fr/>

Pseudo-labour



Source : <http://www.agriculture.gouv.fr/>

Travail superficiel



Source : <http://www.agriculture.gouv.fr/>

Semis direct

Ces différentes opérations peuvent être appliquées de manière systématique, ou occasionnelle : labour en alternance avec un semis direct ou avec un travail superficiel.

### 2.1.2. Couverture du sol

Dans le but de protéger la surface des sols afin de maintenir l'humidité et concurrencer les adventices, les sols doivent être couverts en permanence, soit par des résidus de cultures précédentes qui ne sont pas prélevés mais restitués, soit par des plantes de couverture positionnées en inter-culture ou culture précédente (Kassam et al., 2009). Ces couverts peuvent jouer un rôle important dans le fonctionnement du système tel que : recyclage de l'eau et de l'azote, amélioration de la structure du sol, production de biomasse, restauration de la matière organique du sol (Lal, 2013).

### 2.1.3. Rotations/associations culturales

Le but est d'allonger et de diversifier les rotations de cultures afin de ne pas permettre la spécialisation des flores adventices et des ravageurs dans les agrosystèmes. Ainsi, l'alternance

entre cultures d'hiver et de printemps permet de casser les cycles des adventices et de mieux maîtriser leur développement (FAO, 2011b; Friedrich et al., 2012).

D'une manière générale, l'objectif de ces trois principes est de réduire la dégradation des sols et d'améliorer leur fertilité en préservant la matière organique, la faune et la flore des sols. L'intérêt de ces principes est bien documenté et semble faire consensus au sein de la communauté scientifique (Briones and Schmidt, 2017; Hobbs, 2007; Kassam et al., 2010; Lal, 2013, 2010; van Capelle et al., 2012). Si le levier « travail minimal du sol » est le plus emblématique de ces systèmes, il est important de rappeler que ces trois principes doivent être appliqués simultanément, sans quoi les performances peuvent être nettement dégradées. La notion de « système » est ici cruciale. Il ne s'agit pas seulement d'une somme de pratiques mais d'interactions dynamiques entre les composantes du système, qui réclament de nouveaux savoir-faire et compétences de la part de l'agriculteur par rapport au système conventionnel. Ainsi, ce n'est pas tant le levier « travail minimal du sol », pris isolément, qui permet l'amélioration de certaines performances, mais bien la combinaison des trois principes : travail minimal du sol, couverture et rotation (FAO, 2015).

## **2.2. Agriculture de conservation : avantages et inconvénients**

Les systèmes en agriculture de conservation entraînent des améliorations au niveau économique et environnemental. Les améliorations les plus significatives concernent la réduction du temps de labour, entraînant une réduction des émissions de carbone due aux économies de machines et d'énergie (Lahmar, 2010) et la fixation biologique de l'azote (Sileshi and Mafongoya, 2007), augmentant et stabilisant les rendements de culture (Kassam et al., 2010) diminuant ainsi les coûts de production (Lahmar, 2010). En outre, des études antérieures ont montré que l'adoption de l'agriculture de conservation, permettait un taux de séquestration de 100-1000 kg ha<sup>-1</sup> de carbone par an (Lal, 2004), ce qui pourrait protéger les sols contre l'érosion et le compactage (Holland, 2004; Lahmar, 2010) et améliorer la porosité, la température et l'humidité du sol tout en causant moins de dommages sur la faune édaphique (Derpsch et al., 2010b; Hobbs, 2007; Mazvimavi and Twomlow, 2008).

En dépit de ces avantages, l'agriculture de conservation ne constitue ni un idéal ni le modèle unique à promouvoir en tout lieu. Il existe d'autres performances pour lesquelles les résultats sont davantage variables voire controversés. En se focalisant sur la diversité du sol et notamment la faune édaphique, les études disponibles soulignent le manque de données mobilisables et de recul temporel (Capowiez et al., 2009; Chan, 2001; Ivask et al., 2007).

Cependant, les connaissances sont souvent très dépendantes du contexte et donc peu comparables entre elles. De plus, il est particulièrement difficile d'évaluer les systèmes en agriculture de conservation car ceux-ci font l'objet d'une grande flexibilité dans l'application des trois principes (Figure 1-2), d'où une grande diversité des pratiques réelles (Scopel et al., 2013). En ce sens, l'adoption de ces principes est souvent partielle, ce qui accroît encore la variabilité des performances associées. Par exemple, un système sans labour ne permet pas de maîtriser les flores adventices, ce qui nécessite un recours accru à la lutte chimique (Lins et al., 2007). Cette pratique pourrait mener à la contamination et à la persistance chimique dans le sol affectant ainsi ses composantes (Haney et al., 2010).

De nombreuses recherches sont encore nécessaires pour comprendre les interactions entre pratiques agricoles et cycles des différentes ressources naturelles. Si certaines performances font consensus, d'autres donnent encore lieu à des résultats contradictoires et requièrent davantage des perspectives de recherches.

### **3. Modèles d'études : Faune du sol**

Le sol est l'habitat d'une multitude d'organismes interagissant dans le réseau alimentaire. Il constitue la composante des écosystèmes terrestres la plus riche en espèces (Anderson, 1975; André et al., 1994). Ces organismes couvrent plusieurs ordres de grandeur en termes de taille corporelle (Figure 3) et comprennent : la microflore – encadré 3 (bactéries, champignons), la microfaune (taille inférieure à 0,2 mm, nématodes, protozoaires), la mésofaune [largeur du corps allant 0,2 à 2,0 mm, enchytréides, microarthropodes (acariens, collembolés - encadré 4)] et la macrofaune (largeur du corps supérieure à 2 mm, vers de terre - encadré 5, termites, myriapodes, isopodes, arachnides). Même si l'immense diversité taxonomique du sol reste encore largement inconnue (Decaëns et al., 2006), les patrons de structure des communautés d'organismes du sol ainsi que les facteurs qui les régulent sont de mieux en mieux connus aujourd'hui (Bardgett, 2005; De Deyn and Van der Putten, 2005; Decaëns, 2010). La préoccupation du rôle fonctionnel de la biodiversité du sol est quant à elle comparativement plus récente (Brussaard, 1997; Wardle and Giller, 1996). Celle-ci s'inscrit dans le cadre plus général de l'étude des relations entre la biodiversité et le fonctionnement des écosystèmes, qui a constitué une thématique de recherche centrale en écologie ces dernières décennies (Decaëns, 2010; Hooper et al., 2005). Ces études mettent en avant que les caractéristiques fonctionnelles des espèces qui influencent fortement les propriétés de l'écosystème et qu'une plus grande diversité biologique peut permettre un fonctionnement plus efficace de l'écosystème (Loreau et al., 2001).

## ✓ Soil organisms studied in this manuscript

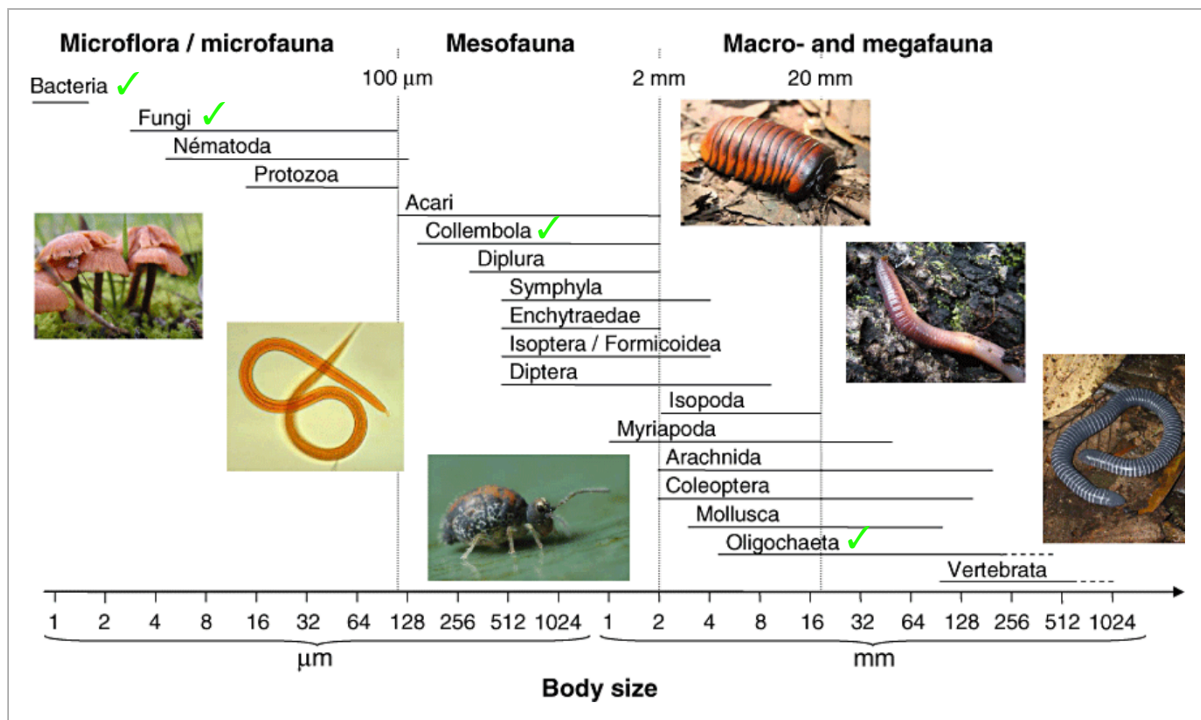


Figure 1-3 : Représentation des principaux groupes taxonomiques d'organismes du sol classé suivant leur taille (Extrait de Decaëns, 2010) d'après Swift and Anderson (1979).

### Encadré 3 : la microfaune - les microorganismes du sol

Ce sont des organismes vivants, invisibles à l'œil nu et appartenant aux règnes procaryotes (*e.g.* Bactéries) et eucaryotes (*e.g.* Fungi). Notre connaissance de la diversité des microorganismes reste largement insuffisante, conduisant ainsi à seulement dresser des estimations de cette diversité (soit plusieurs dizaines de milliers d'espèces différentes dans 100g de sol et d'une biomasse totale de quelques milliers de kilogrammes par hectares (Lavelle and Spain, 2001). Ils jouent un rôle dans les cycles biogéochimiques et donc dans la mise à disposition de nombreux services écosystémiques (Hättenschwiler et al., 2005). La majeure partie des transformations biochimiques de la matière organique est assurée par les microorganismes (Lavelle et al., 2005). Leurs activités sont régulées par les facteurs abiotiques et les interactions avec les autres organismes (Figure 1-4)

En considérant la chaîne alimentaire, les principaux consommateurs sont la microflore, qui est seule capable de décomposer directement les hydrates de carbone complexes dans les débris d'origine végétale et de minéraliser les nutriments contenus dans ces derniers. Les consommateurs secondaires et supérieurs, c'est-à-dire la faune du sol, se nourrissent des

microbes et les uns des autres, et ont une immense importance dans la gestion de ces processus microbiens (Bonkowski et al., 2000; Hanlon and Anderson, 1979; Hooper et al., 2005). Les invertébrés édaphiques impactent la remise à disposition d'éléments nutritifs pour les plantes. Par exemple, des études ont montré que la manipulation de la faune du sol dans un écosystème prairial peut modifier la composition et la diversité des communautés de plantes (De Deyn et al., 2003).

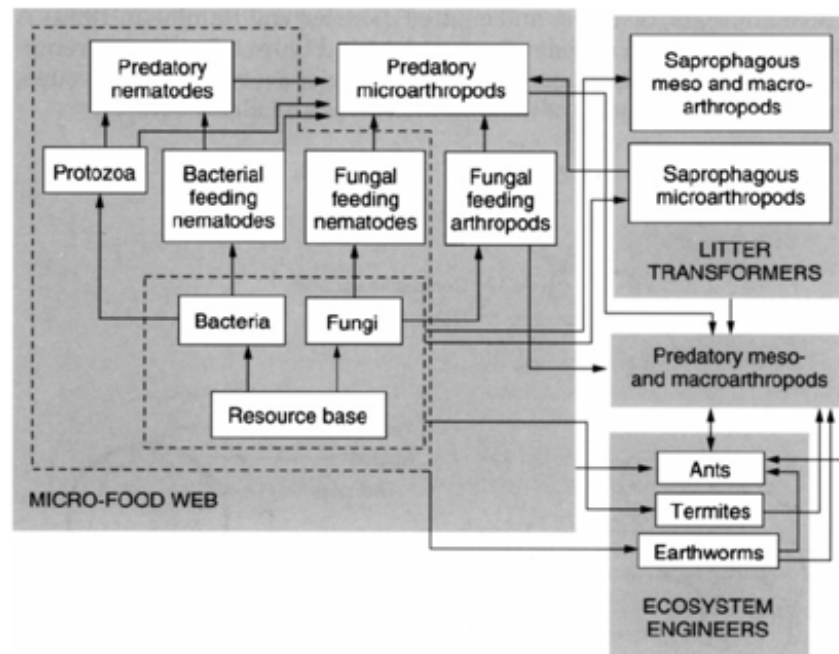


Figure 1-4 : Représentation schématique de la structure des réseaux trophiques du sol : « micro-réseau », « transformateur de litière » et « ingénieur des écosystèmes ». Les flèches indiquent la direction du flux d'énergie (extrait de Lavelle et al., 1995; Wardle, 2002).

#### Encadré 4 : Mésofaune du sol - Organisme modèle : Collemboles

Les collemboles sont les microarthropodes les plus abondants dans les sols avec les oribates (Hopkin, 1997). Ils constituent un groupe très diversifié, connu pour répondre aux changements du couvert végétal et des conditions du sol (Chauvat et al., 2007; Ponge et al., 1993). Ils ont une activité de fragmentation des débris végétaux et, en général, sont reconnus comme fongivores bien que plusieurs études montrent des préférences alimentaires variables suivant les espèces (Chahartaghi et al., 2005; Faber, 1991; Jørgensen et al., 2003; Rusek, 1998). De plus, ils peuvent aussi se nourrir directement sur les parties vivantes des plantes telles que les racines fines (Endlweber et al., 2009). En fonction de leurs densités, les collemboles peuvent réduire ou stimuler l'activité microbienne (Cole et al., 2004). Ainsi, ils affectent la nutrition des plantes en influençant le cycle des éléments nutritifs dans les sols (Filser, 2002).

**Encadré 4 (suite) : Mésofaune du sol - Organisme modèle : Collemboles**

Classiquement, les espèces sont regroupées en trois formes de vie différentes en fonction de leur répartition verticale et de leurs traits morphologiques et physiologiques (Gisin, 1943; Petersen, 2002).



Epédaphique  
*Tomocerus minor* – © S. Hopkin



Hémiédaphique  
*Folsomia quadrioculata*  
© A. Murray



Euédaphique  
*Mesaphorura sp.*  
© A. Murray

**Les Epédaphiques :**

Lieu de vie : litière

Taille : grande ( $\geq 1$  mm, voire  $> 2$  mm)

Ressource trophique : pollen, algue, fungi.

Mobilité : plus élevée que les autres formes de vie, furca très développée

Téguments : colorés, conformations particulières

**Les Hemiédaphiques :**

Lieu de vie : litière et sol

Taille : moyenne ( $\leq 1,5$  mm)

Ressource trophique : variée : algue, lichen, fungi, débris végétaux.

Mobilité : moyenne, furca réduite

Téguments : colorés, souvent unis

**Les Euédaphiques :**

Lieu de vie : sol

Taille : petite ( $\leq 1$  mm)

Ressource trophique : fungi, débris végétaux.

Mobilité : faible, furca vestigiale ou absente

Téguments : non colorés



### Encadré 5 : Macrofaune du sol- organisme modèle : Vers de terre

Les vers de terre sont présents dans la plupart des écosystèmes terrestres non désertiques, et constituent en termes de biomasse une part importante de la faune du sol (Edwards and Bohlen, 1996). Ils assurent différentes fonctions bénéfiques pour les agroécosystèmes sur la répartition des résidus, la structure du sol et la fertilité des sols. Les vers de terre améliorent le flux d'eau et l'infiltration et l'échange de gaz dans le sol en construisant un système de pores macro et en augmentant la stabilité des agrégats de sol (Edwards and Shipitalo, 1998). Ils augmentent l'incorporation et la stabilisation des résidus de carbone dans les agrégats (Bossuyt et al., 2006). En outre, l'alimentation ainsi que l'activité de creusage des vers de terre ont de forts effets sur la microflore du sol (Doube and Brown, 1998) et les processus de décomposition (Devliegher and Verstraete, 1995; Wolters and Schaefer, 1993). Cela conduit à des taux de turnover plus élevés et à une plus grande disponibilité de nutriments dans le sol qui profite à la fertilité des sols et à la croissance des plantes (Scheu, 2003).

Toutes leurs activités varient sensiblement en fonction de l'espèce et de la catégorie écologique considérées (Lee, 1985). Bouché (1977) a ainsi proposé une répartition des espèces de vers de terre selon des critères morphologiques et écologiques. Cette classification écomorphologique est actuellement la plus utilisée et peut se décliner en trois groupes :



Epigé  
*Lumbricus rubellus* (Hoffmeister, 1843)



Endogé  
*Allolobophora chlorotica* (Savigny 1826)



Anécique  
*Lumbricus terrestris* (Linné 1826)

Les espèces **épigées** sont présentes à la surface du sol, dans la litière. Ce sont des espèces de petite taille (1 à 5 cm), généralement nettement pigmentées, et qui ne forment pas de réseau de galeries ou creusent des galeries très superficielles.

Les espèces **endogées** vivent quasi exclusivement dans les horizons organo-minéraux du sol. Ce sont des espèces essentiellement géophages, de taille intermédiaires (de 2 à 20 cm) généralement apigmentées. Elles sont responsables de la formation de galeries horizontales.

Les espèces **anéciques** sont grandes de tailles (10 à 40 cm, voire plus pour certaines espèces géantes). Elles vivent dans le sol, dans lequel elles creusent de profondes galeries verticales, et sont fortement impliquées dans le brassage vertical du sol (la bioturbation) et l'enfouissement de la matière organique fraîche dans les horizons de sol.

### III. Objectifs de la thèse

L'objectif premier de ce travail de thèse vise à explorer les réponses de la faune du sol aux pratiques agricoles innovantes développées en Normandie et en Picardie et d'anticiper les conséquences fonctionnelles de ces changements. Lors de ce travail, je m'intéresserai plus particulièrement à l'effet de l'introduction de légumineuses, la diminution de la fertilisation totale, la réduction du travail du sol, la restitution des résidus de culture, la diversité de la succession culturale dans les rotations agricoles sur (i) la diversité des communautés de la macro- et de la mésofaune du sol et, par l'étude des liens entre faune et composantes microbiennes (ii) sur le fonctionnement du sol en termes de stockage du carbone organique, de disponibilité d'N et de stabilité structurale.

Cet objectif central se décline en sous-objectifs et questions traités au cours des quatre chapitres de résultats de ce travail de thèse (Figure 1-5).

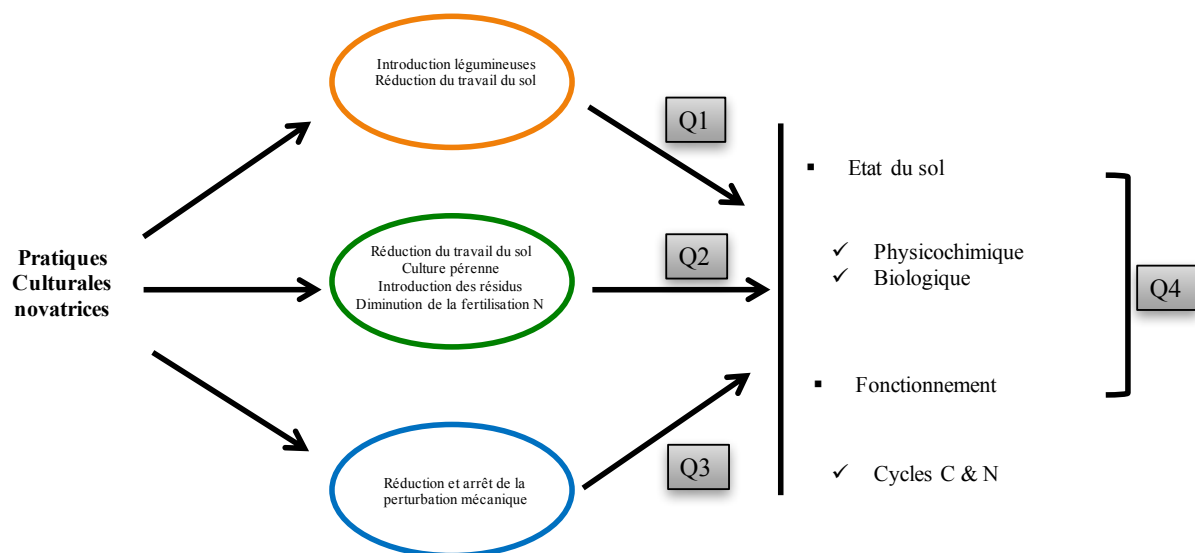


Figure 1-5 : Représentation schématique des différentes pratiques agricoles étudiées en lien avec les chapitres de résultats de la thèse. Q1, Q2, Q3, Q4 indiquent les différentes questions posées respectivement dans les quatre chapitres de résultats.

#### Premier sous-objectif – Chapitre 2

L'objectif de ce chapitre est d'étudier dans les conditions réelles d'exploitation agricole l'effet combiné de l'introduction de légumineuses (féveroles, Faba Bean) et de la réduction du travail du sol sur les assemblages de vers de terre et de collemboles et les fonctions microbiennes. Cette étude se déroule à une échelle spatio-temporelle importante couvrant la Normandie et sur des méthodes d'exploitations en place depuis plus de cinq années. Trois questions (Q1) seront traitées dans ce chapitre :

*Comment le couplage de deux pratiques innovantes favorise-t-il la fonctionnalité des sols agricoles ? Quelle pratique produit le plus d'effet sur la faune du sol ? Observe-t-on une réponse similaire de différents groupes faunistiques aux deux pratiques mises en place ?*

### **Second sous-objectif – Chapitre3**

Le second sous-objectif de ce travail était de suivre dans les mêmes conditions pédoclimatiques (échelle spatiale plus réduite) et les mêmes itinéraires techniques, l'effet à long terme (quatre ans) de cinq régimes de gestion différents sur les communautés de collemboles. Les traitements comprenaient des combinaisons de différentes cultures (annuelles, pérennes), des taux différents de fertilisation azotée (ajout de N, réduction de N), des résidus de culture (incorporation ou élimination de résidus) et différentes intensités de labour (labour profond vs. peu profond). Dans ce chapitre, je traiterai des questions (Q2) suivantes :

*Existe-t-il une dissemblance de structure et de composition des assemblages de collemboles entre les cinq régimes de gestion au cours des quatre années de l'étude (à long terme) ? Si oui, quelle est la modalité de gestion la plus importante (celle imprimant la trajectoire observée) ?*

### **Troisième sous-objectif – Chapitre4**

Le but principal était, sur une échelle spatiotemporelle plus réduite, de suivre sur une saison de végétation l'impact de la conversion de la perturbation mécanique résultant du travail du sol sur les communautés d'organismes du sol (vers de terre et collemboles) et leurs interactions avec certaines propriétés physico-chimiques (pH eau, densité apparente, taille des agrégats et stock de carbone organique) et microbiennes (biomasse microbienne et fongique) du sol.

Nous avons mis en place trois niveaux de travail du sol : labour profond (état habituel), labour peu profond et non labour (états convertis). Ce suivi s'est déroulé à une échelle spatiotemporelle plus réduite, un seul site, une saison de végétation. Cela a permis un suivi dense des changements s'opérant au sein des assemblages faunistiques en réponse aux différents modes de travail du sol. Dans ce chapitre, je traiterai des questions (Q3) suivantes :

*Quel est l'effet de la conversion du travail du sol sur les communautés de vers de terre et de collemboles à court et à moyen terme ? Existe-t-il une résistance et/ou une résilience fonctionnelle de ces communautés ?*

### **Quatrième sous-objectif – Chapitre5**

En complément de ces expérimentations in situ, nous avons réalisé une expérience en microcosmes ciblant les conséquences fonctionnelles des changements d'assemblages de faune

du sol liés aux différentes pratiques agricoles novatrices. Pour cela, nous avons décidé de caractériser dans une approche mécaniste les actions des différentes formes de vie de collemboles (Epédaphique, Hemiédaphique et Euédaphique) sur la composante microbienne du sol (bactéries et champignons). Dans ce chapitre, je traiterai des questions (Q4) suivantes :

*Quelle est l'influence différentielle de chacune des formes de vie sur les communautés de microorganismes ? Existe-t-il une complémentarité fonctionnelle entre les différentes formes de vie ?*

#### **IV. Sites d'études**

Les résultats de ce travail de thèse ont été obtenus en combinant des approches expérimentales in situ et ex situ (Figure 1-6). Pour le chapitre 2, l'étude a été réalisée en 2014 dans le nord-ouest de la France, en région Normandie. Le climat de la région est océanique caractérisé par des précipitations allant de 900 à 1000 mm par an et une température annuelle moyenne de 8 à 12 ° C. Cette étude a été menée grâce à une étroite collaboration avec les conseillers agricoles des Chambres d'Agriculture de la Seine Maritime (76) et de l'Eure (27). Pour le chapitre 3 (in situ), l'étude a été menée sur la plate-forme expérimentale SOERE ACBB (Systèmes d'Observation et d'Expérimentation pour la Recherche en Environnement-Agrosystèmes Cycles Biogéochimiques et Biodiversité), située à Estrées-Mons (Picardie, Nord de la France, 49.873 N, 3.032 E) et gérée par L'INRA (Institut National de la Recherche Agronomique). Le climat est tempéré avec une précipitation moyenne annuelle de 678 mm et une température annuelle moyenne de 10,8 ° C. L'expérience a été établie sur un terrain de 11 ha. Dans le cadre du chapitre 4 (in situ), notre étude s'est portée sur l'une des parcelles annexes de la station expérimentale INRA d'Estrées-Mons (Picardie, Nord de la France). L'expérience a été réalisée sur une superficie de 100 m sur 12 m pendant une saison végétative. Pour finir, l'expérience du chapitre 5 a été menée dans des conditions contrôlées (ex situ, microcosmes). Dans ce chapitre, nous avons utilisé un substrat (sol), provenant d'une zone de pâturage depuis 1968 et gérée par le Lycée Agricole d'Enseignement Général et Technique Agricole d'Yvetot (nord-ouest de la France, 0 ° 45'18.76"E, 49 ° 37 ' 04.00"N). Le climat de de la zone est tempéré océanique, avec une température moyenne annuelle de 10 °C et une précipitation moyenne annuelle de 800 mm.

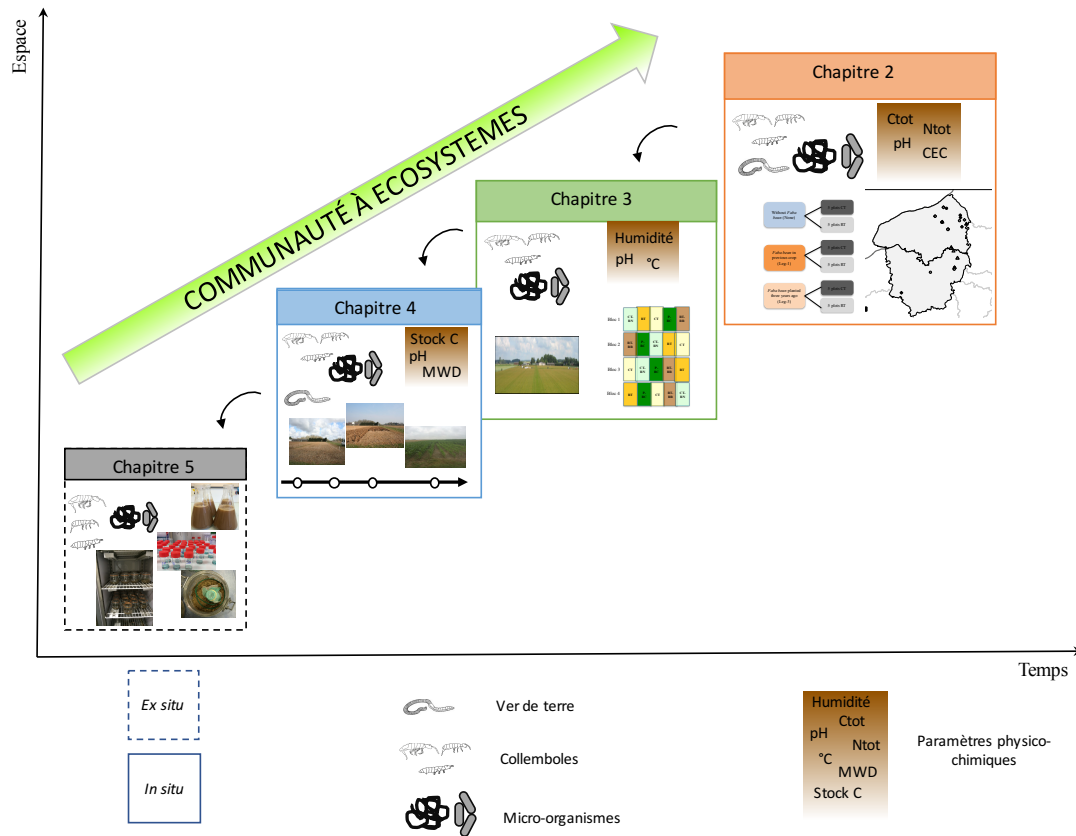


Figure 1-6 : Représentation schématique des différents dispositifs expérimentaux étudiés selon une échelle spatio-temporelle. La taille des carrés est proportionnelle aux échelles de temps et d'espace. Les groupes faunistiques et les paramètres abiotiques étudiés dans chaque chapitre sont figurés.



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## **RESULTATS ET DISCUSSIONS**

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## **Chapitre 2. Introduction des légumineuses et réduction du travail du sol**

### **Présentation du chapitre 2**

Cette étude se déroulant à une échelle spatio-temporelle importante, a été menée au printemps 2014. Deux groupes de faune du sol ainsi que certaines propriétés physicochimiques et microbiennes ont été caractérisées. Les analyses ont été réparties entre les deux laboratoires d'accueil : « Ecodiv » pour la partie faune du sol (Sékou F.M. Couliblay) et « UniLaSalle, Aghyle Unit » pour les analyses physico-chimiques et microbiennes (Dr. Amira Aschi). Dans ce chapitre, nous notons une réponse différente des assemblages de faune du sol suite à l'adoption des deux pratiques agricoles innovantes. Les propriétés physico-chimiques n'ont pas été affectées. Par ailleurs, certaines fonctions microbiennes ont répondu favorablement.

## Soil fauna response to innovative agricultural practices

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*Article en préparation*

### 1. Introduction

The green revolution has successfully increased crop yields by favouring intensive production practices, including genetic crop improvement, the use of massive chemical inputs (e.g., fertilizers and pesticides), and intensive tillage. However, this high input agricultural management has generated many negative environmental impacts, such as soil erosion (loss of organic matter), greenhouse gas emission, groundwater pollution, and biodiversity loss (Tilman et al., 2002). These environmental issues are nowadays of major concerns for human societies, as well as the dependency of this agricultural model on fossil energy. Therefore, modern agriculture must incorporate ecologically intensive farming practices, multifunctional agriculture, or conservation agriculture (Kremen and Miles, 2012). Minimum soil disturbance and implantation of legumes in crop rotation have been recognized as innovative agricultural practices, which can improve soil organic matter and biodiversity (Jangid et al., 2008; van Capelle et al., 2012). Biodiversity belowground, plays a decisive role in ecosystem services such as, among many others, nutrient capture and cycling (Murray et al., 2009; Van Der Heijden et al., 2008), building and control of soil organic matter (SOM) or soil physical structure (Jégou et al., 2001; Wolters, 2000), and vegetation dynamics (De Deyn et al., 2003; Forey et al., 2011; Mitschunas et al., 2006), with synergistic effects on crop production (Eisenhauer et al., 2010).

The changes in agricultural practices can have a direct and indirect impact on living organisms by modifying soil physicochemical and habitat properties (Gil et al., 2011; Lauber et al., 2013). These direct and indirect effects induce changes in the structure and the functions of soil communities leading to significant modifications in carbon and nitrogen dynamics (Burns et al., 2013). The positive effects of conservation agriculture on soil fauna have generally been well documented (Briones and Schmidt, 2017; Coudrain et al., 2016; Dittmer and Schrader, 2000a). However, most of these studies were conducted under controlled field conditions. It is

largely recognized that soil biota and associated functions are determined by a set of physical (e.g. climate), chemical factors, which operate at broader scale than one experimental site (Lavelle and Spain, 2001). If working in experimental sites ensures some homogeneous pedoclimatic context essential to understand more precisely the underlying mechanisms of soil biological and functional responses to agricultural practices; the strict control of field conditions impedes the emergence of clear consensus about practices impacts across broader territories. Moreover, the experimentally studied practices are not always technically easy to implement and economically sustainable enough to be automatically adopted by farmers. Lastly, innovative practices are often tested separately i.e. the comparison of different tillage systems each other or different crops rotation each other while their combined effects on soil functions were poorly documented. Both, resource supply and physical disturbance are considered to be key determinants of biological diversity in aboveground systems (Cole et al., 2008; Lawton and Kinne, 2000). It has been shown that the introduction of nitrogen-fixing plants, such as legumes into agroecosystems, supports the functions and productivity of the ecosystem (Sileshi et al., 2008). Larger amounts of mineral nitrogen are observed in the soil after a pea compared to a cereal harvest; which can be used by the next crop (Nemecek et al., 2008). This could significantly influence microclimatic conditions and increase trophic resources for decomposers (Axelsen and Kristensen, 2000; Kladivko, 2001).

In this study, we try to understand the effects of the potential interaction of two innovative practices (the presence and position of the legume (*Faba Bean*) in crop rotations under two tillage systems) on the diversity and composition of two major groups of soil fauna in agricultural systems (earthworms and Collembola) and on soil functioning. To reach this objective, we developed an empirical experimental design made with the combination of situations encountered in farms through the Normandy Region, France. This has us allowed encompassing the whole variability brought by farmers' practices around the implementation of these two innovative practices. We hope it enabled us to focus on direct and indirect effect of these practices in order to test "under real conditions of farming" the improvement of soil performances by innovative agriculture practices. We expected: (1a) the reduction of tillage intensity (RT) will allow diversification of earthworms and Collembola communities (density, species richness and diversity index); (1b) deep living species to be favored by this reduction of tillage intensity. (2a) Introducing legumes into crop rotations would promote nutrient supply (C, N); microbial functions (DNA and RNA) and assemblages of earthworms and Collembola are expected to increase as well; (2b) by varying the position of the legume (*Faba Bean*) within

the rotation, we were also interested in depicting if this positive effect on soil fauna and associated functions lasted through time; i.e. if *Faba Bean* has an effect going beyond the crop immediately following its breeding. (3) The interactions between the presence of *Faba Bean* and reduced tillage to have a stronger positive effect on the diversity and composition of both earthworms and Collembola than the presence of a single factor; because thanks to a complementary effect of the style, the RT removes a mechanical disturbance and the legumes make it possible to increase the trophic resources of the soil.

## 2. Materials and methods

### 2.1. Study sites and experimental design

The study was carried in 2014 out in the Normandy region (northwest of France) with an oceanic climate characterized by precipitation ranging from 900 to 1000 mm per year and an average annual temperature of 8 to 12° C. In the region, we have selected 30 agricultural sites distributed in 20 farms to reconstitute an empirical experimental design taking into account both the position of the leguminous (*Faba Bean*) in crop rotation and soil tillage intensity (Figure 2-1). The crop rotations consisted *Faba Bean* as previous crop of wheat (Leg-1), *Faba Bean* sown three years before wheat (Leg-3) and rotation without *Faba Bean* and without any leguminous at least during the preceding five years (None).

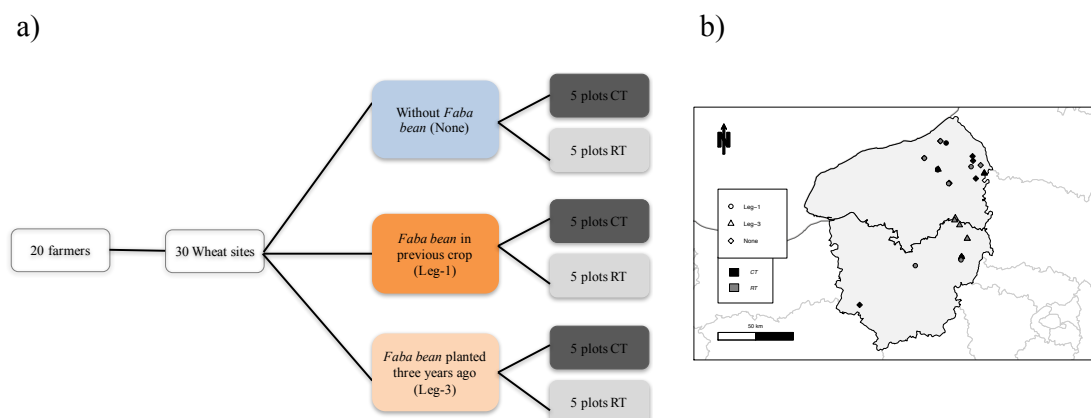


Figure 2-1 : (a) Empirical experimental design studied. CT: Conventional tillage; RT: Reduced tillage; Leg-1: *Faba Bean* as previous crop of wheat; Leg-3: *Faba Bean* sown three years before wheat; None: rotation without *Faba Bean* and without any leguminous at least during the preceding five years, (b) location of plots: (Seine Maritime and Eure).

In each of these rotations, two of the most widespread tillage systems in the region were considered such as conventional tillage with mouldboard ploughing (CT) and reduced tillage using Chisel ploughing (RT). CT involved soil inversion to 25-30 cm depth, while RT involved

mechanical disturbance to less than 8 cm depth, without soil inversion. A total of 6 experimental modalities were studied and each was replicated 5 times (30 agricultural sites, Figure 2-1). All the studied sites were sown with winter wheat during the sampling year in order to homogenize rhizospheric properties.

## **2.2. Soil faunal sampling, extraction and identification**

Soil samples were collected in April 2014 at the start of the vegetation season. The sampling procedure was similar across all sites. Three (3) sampling points were surveyed by plots, constituting 3 pseudo-replicates. These 3 points, spaced 30 m apart, were placed along a transect parallel to the direction of sowing in the central part of the plots.

### **2.2.1. Collembola**

We used soil corers of diameter 5 cm and 10 cm deep. In the laboratory, Collembola were extracted during two weeks using the Berlèse-Tullgren device (Tullgren, 1918) that creates a temperature gradient over soil core, crumbled into a plastic sieve with 2 mm suspended over a collecting vessel containing 70% alcohol. Individuals (Collembola) collected in alcohol were counted and identified following identification keys (Gisin, 1960; Hopkin, 2007). However, some individuals were identified to genera when species identification was not possible. Finally, all species were allocated to one of three different life-forms, i.e. epedaphic, hemiedaphic, Euedaphic (Gisin, 1943). These life forms differ in fundamental ecological properties (including reproduction, vertical distribution, and metabolic activity; cf. Petersen, (2002) and can thus be considered as different functional groups.

### **2.2.2. Earthworms**

One 25 cm × 25 cm × 25 cm monolith were hand sorted for earthworms in each plot. Specimens were fixed in pure alcohol and categorized as juveniles (aclitellates) and adults (clitellates). Adults were identified to species level according to Sims and Gerard, (1999). Juveniles were therefore not taken into account for the estimation of species number but only when calculating density and biomass of earthworms. Thereafter, individuals were classified into various ecological categories (Decaëns et al., 2008) such as anecic and endogeic. No epigeic species were collected for this study

## **2.3. Soil sampling**

Three composite soil samples (combining five cores) were taken from the 0-10 cm depth with a hand auger along the seed line. Each of the 90 samples was passed through a 2 mm sieve and homogenized. Fresh soil was used for biological analyses and air-dried soil was utilized in physicochemical analyses.

### **2.3.1. Chemical and physical characterization**

Soil texture was determined. Five grams of air dried soil were firstly treated by HCl solution to remove soil carbonate then  $H_2O_2$  33% was added to eliminate soil organic matter and finally hexametaphosphate solution was used to break up the soil particles. Reference concentrations were done according to NF X 31-107. Particle size distributions (%) were measured by laser diffraction (Malvern Mastersizer 2000, UK) according to manufacture protocol. Moisture content was recorded after drying at 105°C for 48 h. Cation exchange capacity (CEC) was carried out by the INRA Laboratory of Soil Analysis at Arras according to the extraction method detailed in NF X 31-130 using cobalthexammine trichloride solution. The soil pH<sub>water</sub> was measured in a 1:2.5 soil in water suspension using a glass electrode (NF ISO 10390, 2005). Total carbon (TC) and nitrogen (TN) were analyzed following a dry combustion method using an automatic analyzer (Flash2000 Thermo scientific). Organic carbon (OC) was measured with TOC Analyzer (Shimadzu TOC- SSM 5000), which was conducted on 0.20 mm milled dry soil sub-samples. Permanganate Oxidizable Carbon (eq. Active carbon, POXC) was extracted from 2.5 grams of air-dried soil by quantifying the carbon oxidized by  $MnO_4$  as described by (Culman et al., 2012) using spectrophotometer (Varian Cary 50 Scan) at 550 nm.

### **2.3.2. Measurements of biological indicators**

RNA and DNA were co-extracted from 2 g soil using the Total RNA isolation Kit® and the DNA Elution Accessory Kit® for Soil, respectively (MO BIO-USA). Extracts were stored at -80°C for RNA and -20°C for DNA until use. To remove contaminating DNA from RNA preparation, TURBO DNA free™ kit (Applied Biosystems, France) was used and RNA extracts were further purified with the RNeasy® MinElute Cleanup kit (Qiagen GmbH, Germany) according to the manufacturer's protocol using silica spin columns. Purified nucleic acid extracts were eluted in a final volume of 15 µL with DEPC-treated water and stored at -80°C. The quality of RNA was assessed by Experion™ RNA StdSens Analysis Kit (BIO RAD) according to manufacturer's recommendation. Purified dsDNA and RNA were quantified by fluorimetry. dsDNA quantification was operated by using the Fluorescent DNA quantitation Kit (Hoechst 33258, Biorad) and dsDNA extracts were stored at -20°C (Gangneux et al., 2011).

RNA was quantified using Quant-iT™ RiboGreen® RNA Assay Kit; RNA extracts were stored at -80°C. The cDNA was synthesized from purified RNA using High capacity cDNA reverse transcription kit (Kit Applied Biosystems). Fungal and bacterial communities were estimated on both dsDNA and cDNA by qPCR using universal primer sets designed for each type of microorganism. For total and active fungal communities, 18S rDNA and 18S rRNA gene qPCR amplifications were carried out in a total volume of 25 µL with 1x qPCR Master Mix (SYBR Green I, Applied Biosystem), 0.5 µM of FU18S1 and Nu-SSU-1536 primers (Borneman and Hartin, 2000), 0.5 mg.mL<sup>-1</sup> of BSA (NEB) and 10 ng of total DNA and or cDNA. Standard curves were obtained using serial dilutions of linearized plasmids containing cloned *Fusarium graminearum* 18S rRNA genes (assuming that the *F. graminearum* genome is representative of soil fungi genomes). After an initial denaturation and enzyme activation step of 15 min at 95°C, 40 cycles of PCR were performed in Light Cycler 480 as follows: 40 s at 95°C, 45 s at 64°C and 30 s at 72°C. The qPCR efficiency ranged from 93% to 98%. 16S rDNA and 16S rRNA amplifications were carried out in the same conditions as 18S rDNA and rRNA PCR except for primers [63f 5'-CAGGCCTAACACATGCAAGTC-3' (Marchesi et al., 1998) and BU16S4 5'-CTGCTGCCTCCCGTAGG-3' derived from 341F (Muyzer et al., 1993)] and amplification protocol (40 s at 95°C, 45 s at 64°C and 30 s at 72°C). The 314 bp 16S PCR products exceed the recommendations for SYBR\_Green qPCR analysis. However, the efficiency of the qPCR ranged from 98% to 102%.

#### 2.4. Statistical analysis

We calculated the mean Earthworms and Collembola density, biomass (n = 3) and species richness (n = 3). Density was expressed in number of individuals per square meter. Thereafter, the structure of Earthworms and Collembola communities was described by calculating the diversity index of Shannon (H'). Furthermore, the density, biomass and species richness of each of the functional groups were calculated to perform the different statistical analyses.

We thus aimed at comparing how the tillage (treatment "tillage") and the presence of *Faba Bean* (treatment "leguminous") affect soil fauna and soil functioning. For it, we used Linear Mixed-Effects Models (LMM) with the descriptive variables of Collembola and earthworms (total density; total species richness; diversity index), or environmental parameters as response and the factor "modality" as fixed categorical predictor, the factor "geographical location" as random categorical predictor. Significant differences between means were tested at a 5%

rejection probability level using the Tukey HSD test. Normality and variance homogeneity were tested prior to statistical analyses.

Hypothesis of no difference in assemblage composition between treatments was tested using one-way ANOSIM based on the Bray-Curtis dissimilarity distance configuration (Clarke et al., 2006). To identify the main factors affecting community composition, community dissimilarity among plots was visualized by nonmetric multidimensional scaling (NMDS) computed on Bray-Curtis similarity matrix and 12 environmental variables (Legumineuses, Tillage, pH, CEC, Moisture, TOC, NT, POXC, Fungal DNA, Bacterial DNA, Fungal RNA, Bacterial RNA) were fitted to the ordination plots using the “adonis” function with the vegan package.

The calculations were performed in the R language (Team, n.d.) with the libraries ade4 (Dray and Dufour, 2007), lme4 (Bates et al., 2014), MuMIn (Bartoń, 2013), multcomp (Hothorn et al., 2008), car (Fox and Weisberg, 2010) and vegan (Oksanen et al., 2013).

### 3. Results

#### 3.1. Soil physicochemical properties

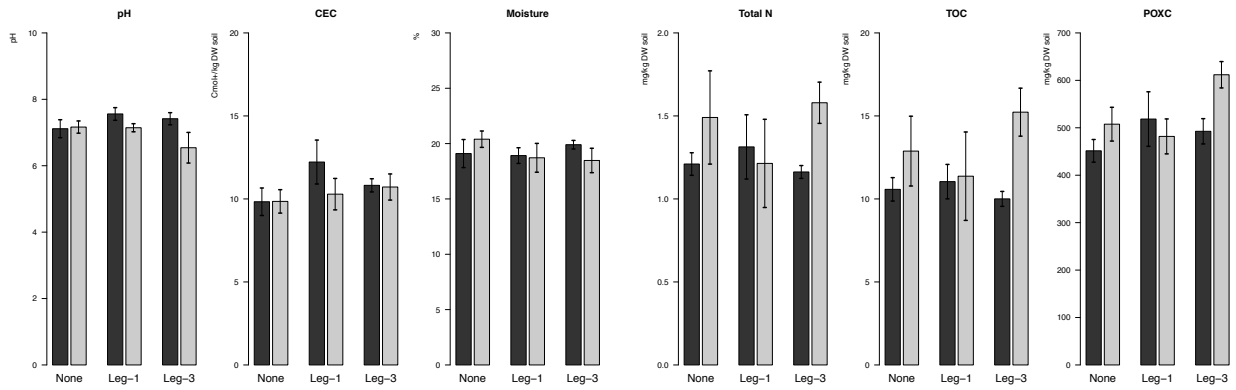
All the parameters we measured (pH, CEC, moisture, proportion of nitrogen, carbon and POXC) were not impacted neither by "tillage", "leguminous", nor by their interaction (Tableau 2-1).

*Tableau 2-1 : Results of Linear Mixed-Effects Models (LMM) of “tillage effect”, “leguminous effect” and “interaction effect” on physicochemical variables (pH, CEC: Cation exchange capacity, moisture, NT: total nitrogen; TOC: total organic carbon; POXC: active carbon). The tests values are given. F: F-value, p: p-value. \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns  $p > 0.05$ . The rejection level was set at  $\alpha = 0.05$ . The location of the significant differences is in Figure 2-2.*

	pH		CEC		Moisture		NT		TOC		POXC	
	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value
Tillage	2.536	0.125 ns	0.913	0.349 ns	0.084	0.775 ns	1.7688	0.196 ns	3.7862	0.064 .	1.8719	0.184 ns
Leg	0.906	0.417 ns	0.982	0.389 ns	0.721	0.497 ns	0.4651	0.634 ns	0.8524	0.439 ns	0.6850	0.514 ns
Tillage x Leg	0.916	0.416 ns	0.758	0.482 ns	0.212	0.811 ns	1.9439	0.165 ns	2.8349	0.079 .	1.7983	0.189 ns

The maximum and minimum pH values were 7.56 and 6.54. The CEC ranged from ca. 9.83 to 12.22  $\text{Cmol}^+ \text{kg}^{-1}$  dry soil. Total organic carbon (TOC) and total nitrogen (total N) content ranged between 8.67 - 12.86- and 1.05 - 1.41  $\text{mg.kg}^{-1}$  dry soil, respectively. POXC ranged from ca. 451.42 to 611.78  $\text{mg.kg}^{-1}$  dry soil (Figure 2-2).





	Tillage		Leg			Tillage x Leg					
	CT	RT	None	Leg-1	Leg-3	CT None	RT None	CT Leg-1	RT Leg-1	CT Leg-3	RT Leg-3
pH	a	a	x	x	x	A	A	A	A	A	A
CEC	a	a	x	x	x	A	A	A	A	A	A
Moisture	a	a	x	x	x	A	A	A	A	A	A
NT	a	a	x	x	x	A	A	A	A	A	A
TOC	a	a	x	x	x	A	A	A	A	A	A
POXC	a	a	x	x	x	A	A	A	A	A	A

Figure 2-2 : pH, CEC: Cation exchange capacity, moisture, NT: total nitrogen; TOC: total organic carbon; POXC: active carbon (means and standard error) according to the different methods studied combining the tillage (CT: conventional tillage-black barplot; RT: reduced tillage-grey barplot) and legume factor (Leg-1: Fabia Bean as previous crop of wheat; Leg-3: Fabia Bean sown three years before wheat; None: rotation without Fabia Bean and without any leguminous at least during the preceding five years.). Different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between “Tillage modalities”. Different minuscule letters (i.e. “x”, “y”) indicated significant differences ( $\alpha = 0.05$ ) between “Leguminous (Leg) modalities”. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between “interactions (Tillage x Leg) modalities”.

### 3.2. Microbial communities

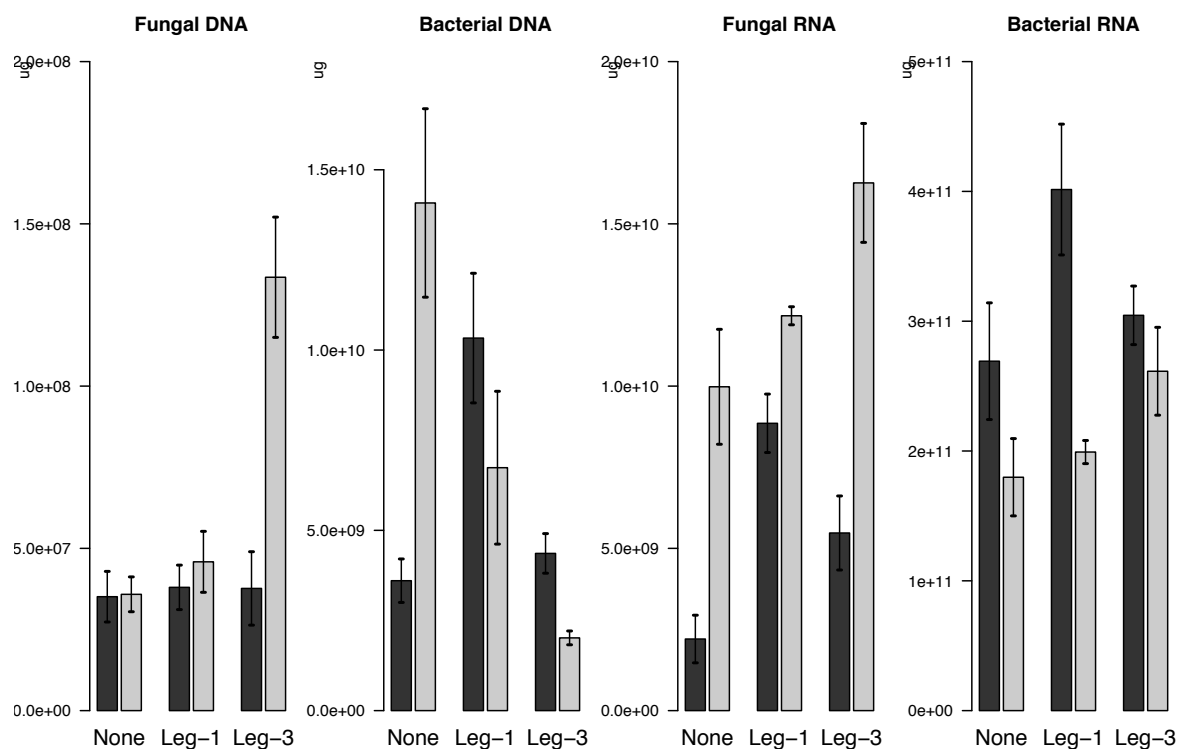
The "leguminous" factor did not affect the fungal DNA, while the factor "tillage" and the interaction of the two factors did (Tableau 2-2).

Tableau 2-2 : Results of Linear Mixed-Effects Models (LMM) of “tillage effect”, “leguminous effect” and “interaction effect” on microbial variables. The tests values are given. F: F-value, p: p-value. The rejection level was set at  $\alpha = 0.05$ . \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns  $p > 0.05$ . The location of the significant differences is in Figure 2-3.

	Fungal DNA		Bacterial DNA		Fungal RNA		Bacterial RNA	
	F	p-value	F	p-value	F	p-value	F	p-value
Tillage	8.735	0.007 **	1.994	0.171 ns	65.15	3.483e-08 ***	15.60	0.0006 ***
Leg	1.972	0.161 ns	3.919	0.0341 *	12.15	0.0002 ***	1.281	0.297 ns
Tillage x Leg	6.587	0.005 **	12.521	0.0003 ***	6.509	0.006 **	1.818	0.189 ns

On average, we recorded more fungal DNA in the RT ( $0.72E+8 \mu\text{g}$ ) than in the CT ( $0.37E+8 \mu\text{g}$ ) when considering the soil tillage factor. The modality RT\_Leg-3 had stronger values compared to all the other modalities (Figure 2-3). Fungal RNA responded significantly to tillage and leguminous treatments, as well as their interaction. Overall, there was 2-fold more fungal RNA in RT compared to CT ( $128.0E+8 \mu\text{g}$  vs.  $55.1E+8 \mu\text{g}$ ). Presence of leguminous within the

rotation (either Leg-1 or Leg-3) led to significantly higher values of Fungal RNA (108.7E+8-  $\mu\text{g}$  and 105.1E+8  $\mu\text{g}$  vs. 60.92 E+8- $\mu\text{g}$ ). The interaction of these two treatments (tillage and leguminous) showed that in each leguminous system (None, Leg-1, Leg-3), RT exhibited higher values of fungal RNA compared to those of CT (Figure 2-3).



	Tillage		Leg			Tillage x Leg					
	CT	RT	None	Leg-1	Leg-3	CT_None	RT_None	CT_Leg-1	RT_Leg-1	CT_Leg-3	RT_Leg-3
<b>DNA</b>											
Fungal	b	a	x	x	x	B	B	B	B	B	A
Bacterial	a	a	x	x	y	C	A	B	BC	C	D
<b>RNA</b>											
Fungal	b	a	y	x	x	E	BC	C	B	D	A
Bacterial	a	b	x	x	x	A	A	A	A	A	A

Figure 2-3 : Fungal DNA, bacterial DNA; fungal RNA and bacterial RNA (means and standard error) according to the different methods studied combining the tillage (CT: conventional tillage-black barplot; RT: reduced tillage-grey barplot) and legume factor (Leg-1: Faba Bean as previous crop of wheat; Leg-3: Faba Bean sown three years before wheat; None: rotation without Faba Bean and without any leguminous at least during the preceding five years.). Different minuscule letters (i.e. "a", "b") indicated significant differences ( $\alpha = 0.05$ ) between "Tillage modalities". Different minuscule letters (i.e. "x", "y") indicated significant differences ( $\alpha = 0.05$ ) between "Leguminous (Leg) modalities". Different capital letters (i.e. "A", "B") showed significant differences ( $\alpha = 0.05$ ) between "interactions (Tillage x Leg) modalities".

In opposite, the "tillage" factor did not affect bacterial DNA, but the "leguminous" factor and the interaction of the two factors did (Tableau 2-2). Globally, we recorded more bacterial DNA in None and Leg-1 compared to Leg-3 (88.41E+8  $\mu\text{g}$  and 85.34E+8  $\mu\text{g}$  vs. 31.88E+8-  $\mu\text{g}$ ). In addition, the interaction of these two factors showed that firstly in None, the RT system had

stronger bacterial DNA values compared to those of CT (140.8E+8- vs. 36.03E+8- µg) and the opposite was observed in Leg-3 where the RT had lower values compared to CT (20.17E+8- vs. 43.60E+8- µg). And secondly, among all the modalities studied, RT\_None had higher values of bacterial DNA and while RT\_Leg-3 was lower (Figure 2-3). In the case of bacterial RNA, only the soil tillage factor influenced this parameter. On average, there was 1.5 times more fungal RNA in the CT compared to RT (3251E+8- vs. 2135E+8-µg).

### 3.3. Soil fauna

#### 3.3.1. Earthworms

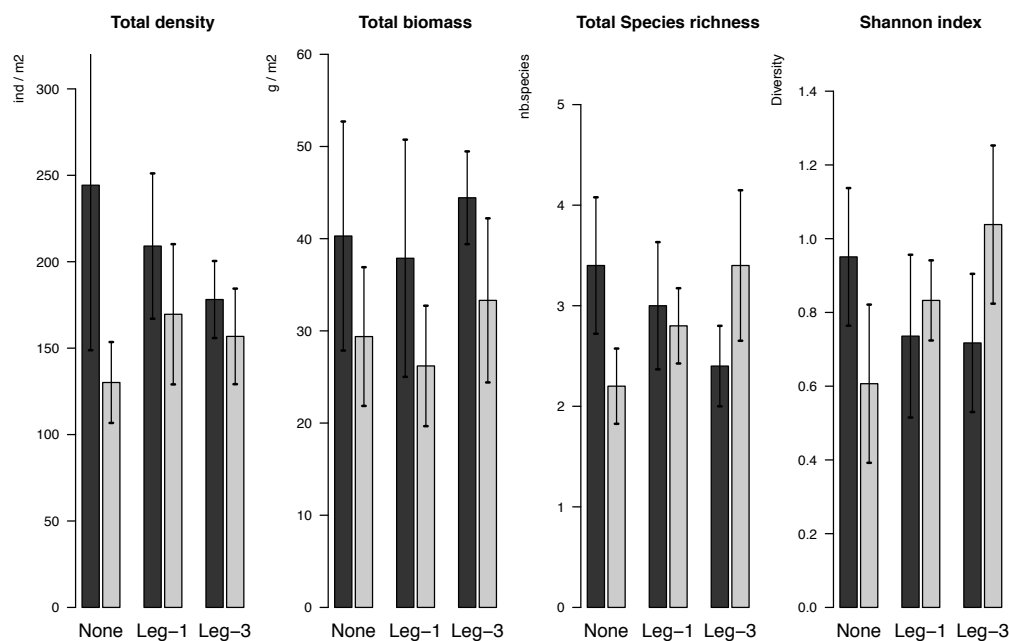
More than 75% of earthworms were juveniles, so we included them in the density and biomass calculations, but not for the diversity indices (species richness, Shannon index).

The position of the leguminous (*Faba Bean*) in crop rotation combined with tillage systems (conventional or reduced tillage) had no significant effect on total density, biomass, species richness and Shannon index of earthworms (Tableau 2-3).

*Tableau 2-3 : Results of Linear Mixed-Effects Models (LMM) of “tillage effect”, “leguminous effect” and “interaction effect” on total density, biomass, species richness and Shannon index of earthworms. The tests values are given. F: F-value, p: p-value. The rejection level was set at  $\alpha = 0.05$ . \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns  $p > 0.05$ . The location of the significant differences is in Figure 2-4.*

	Total density		Total biomass		Total richness		Total Shannon	
	F	p-value	F	p-value	F	p-value	F	p-value
Tillage	2.412	ns	2.031	ns	0.376	ns	0.014	ns
Leg	0.266	ns	0.225	ns	0.302	ns	0.101	ns
Tillage x Leg	0.351	ns	0.001	ns	1.108	ns	0.978	ns

For all the modalities studied, the density and biomass ranged from  $130 \pm 23.4$  to  $244 \pm 95.5$  individuals  $m^{-2}$  at  $26.2 \pm 6.53$  and  $44.4 \pm 5.03$  g  $m^{-2}$ , respectively, the species richness ranged from  $2.20 \pm 0.37$  to  $3.4 \pm 0.67$  species at  $0.61 \pm 0.21$  and  $1.04 \pm 0.21$ , respectively (Figure 2-4).



	Tillage		Leg			Tillage x Leg					
	CT	RT	None	Leg-1	Leg-3	CT_None	RT_None	CT_Leg-1	RT_Leg-1	CT_Leg-3	RT_Leg-3
Total density	a	a	x	x	x	A	A	A	A	A	A
Total biomass	a	a	x	x	x	A	A	A	A	A	A
Total richness	a	a	x	x	x	A	A	A	A	A	A
Shannon index	a	a	x	x	x	A	A	A	A	A	A

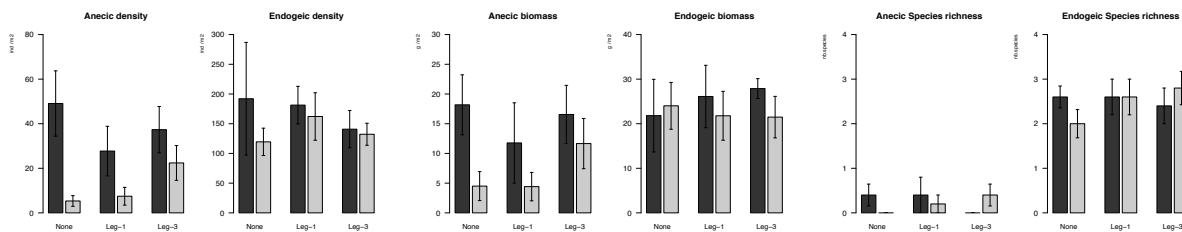
Figure 2-4 : Total density, biomass, species richness and Shannon index of earthworms (means and standard error) according to the different methods studied combining the tillage (CT: conventional tillage-black barplot; RT: reduced tillage-grey barplot) and legume factor (Leg-1: Faba Bean as previous crop of wheat; Leg-3: Faba Bean sown three years before wheat; None: rotation without Faba Bean and without any leguminous at least during the preceding five years.). Different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between “Tillage modalities”. Different minuscule letters (i.e. “x”, “y”) indicated significant differences ( $\alpha = 0.05$ ) between “Leguminous (Leg) modalities”. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between “interactions (Tillage x Leg) modalities”.

Considering the ecological categories, the density and biomass of anecic earthworms responded significantly to the treatment "tillage" but neither to treatment "Leguminous" nor to the interaction of these two treatments (Tableau 2-4).

On average, anecic density were three times higher in CT (38 individuals  $m^{-2}$ ) than in the RT treatments (12 individuals  $m^{-2}$ ). The anecic biomass displayed the same pattern, being significantly higher in CT compared to RT (16 vs. 7  $g m^{-2}$ ). In opposite none of the endogeic earthworms parameters (density, biomass, and specific richness) significantly differed between the different modalities tested (Figure 2-5).

Tableau 2-4 : Results of Linear Mixed-Effects Models (LMM) of “tillage effect”, “leguminous effect” and “interaction effect” on total density, biomass, species richness of functional groups of earthworms. An: Anecic, En: Endogeic. The tests values are given. F: F-value, p: p-value. The rejection level was set at  $\alpha = 0.05$ . \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns  $p > 0.05$ . The location of the significant differences is in Figure 2-5..

	An		En	
	F	p	F	p
<b>Density</b>				
Tillage	12.65	0.002 **	0.875	0.359 ns
Leg	0.994	0.385 ns	0.352	0.707 ns
Tillage x Leg	0.922	0.414 ns	0.186	0.832 ns
<b>Biomass</b>				
Tillage	6.736	0.016*	0.223	0.641 ns
Leg	0.763	0.478 ns	0.138	0.872 ns
Tillage x Leg	0.191	0.827 ns	0.204	0.817 ns
<b>Species richness</b>				
Tillage	0.435	0.516 ns	0.174	0.681 ns
Leg	0.522	0.600 ns	0.118	0.889 ns
Tillage x Leg	0.804	0.459 ns	0.663	0.526 ns



	Tillage		Leg			Tillage x Leg					
	CT	RT	None	Leg-1	Leg-3	CT None	RT None	CT Leg-1	RT Leg-1	CT Leg-3	RT Leg-3
<b>Density</b>											
An	a	b	x	x	x	A	A	A	A	A	A
En	a	a	x	x	x	A	A	A	A	A	A
<b>Biomass</b>											
An	a	b	x	x	x	A	A	A	A	A	A
En	a	a	x	x	x	A	A	A	A	A	A
<b>Richness</b>											
An	a	a	x	x	x	A	A	A	A	A	A
En	a	a	x	x	x	A	A	A	A	A	A

Figure 2-5 : Figure 5: Density, biomass and species richness of functional groups of earthworms (means and standard error) according to the different methods studied combining the tillage (CT: conventional tillage-black barplot; RT: reduced tillage-grey barplot) and legume factor (Leg-1: Faba Bean as previous crop of wheat; Leg-3: Faba Bean sown three years before wheat; None: rotation without a Faba Bean and without any leguminous at least during the preceding five years.). Different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between “Tillage modalities”. Different minuscule letters (i.e. “x”, “y”) indicated significant differences ( $\alpha = 0.05$ ) between “Leguminous (Leg) modalities”. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between “interactions (Tillage x Leg) modalities”.

NMDS ordination (Figure 2-6) showed no differentiation between the modalities studied. This indicates that all modalities were similar in species composition (ANOSIM  $r_2 = 0.036$ , p-value = 0.249).

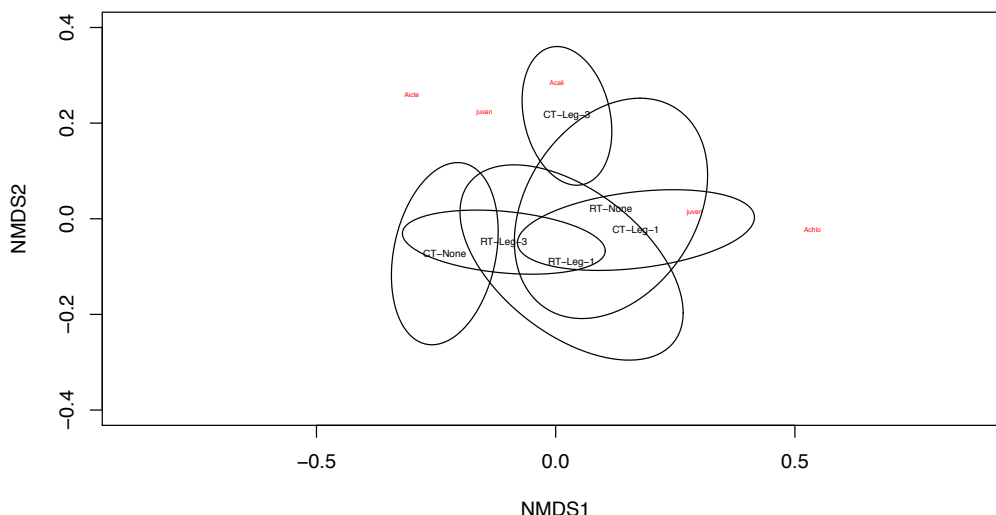


Figure 2-6 : Non-metric multidimensional scaling (NMDS) plot based on Bray-Curtis dissimilarity indices derived from abundance of earthworms species recorded in six different modalities. CT-None: conventional tillage - rotation without Faba Bean and without any leguminous at least during the preceding five years.; CT-Leg-1: conventional tillage - Faba Bean as previous crop of wheat; CT-Leg-3 : conventional tillage - Faba Bean sown three years before wheat; RT-None : reduced tillage - rotation without Faba Bean and without any leguminous at least during the preceding five years.; RT-Leg-1: reduced tillage - Faba Bean as previous crop of wheat; RT-Leg-3 : reduced tillage - Faba Bean sown three years before wheat.

Among the parameters used ("leguminous " and "tillage" factors, physicochemical and microbial variables), only the "tillage" factor and CEC were significantly related to the composition of the community earthworms between the plots (Figure 2-7).

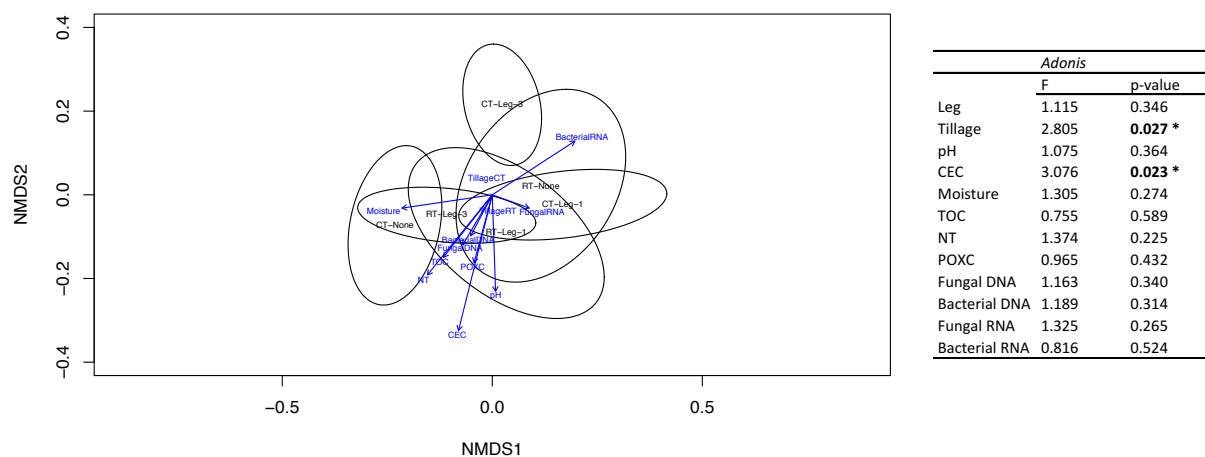


Figure 2-7 : Earthworms community compositions of the plots displayed using NMDS. Stress of the ordination is 0.18. Significant variables ( $P < 0.05$ ) are shown by arrows whose length is proportional to the strength of the correlation, and they are shown in bold in the table.

The composition of the earthworm communities was not related to the geographical position ( $r^2 = 0.00057$ ,  $p$ -value = 0.618) (Figure 2-8).

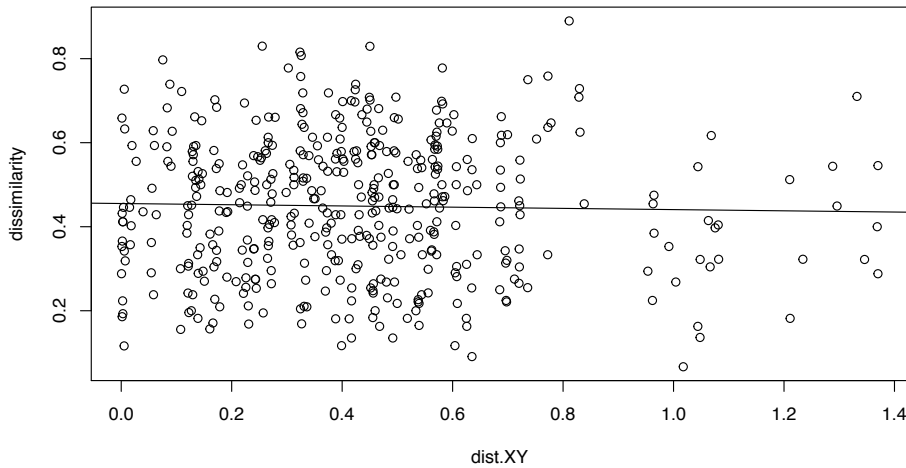


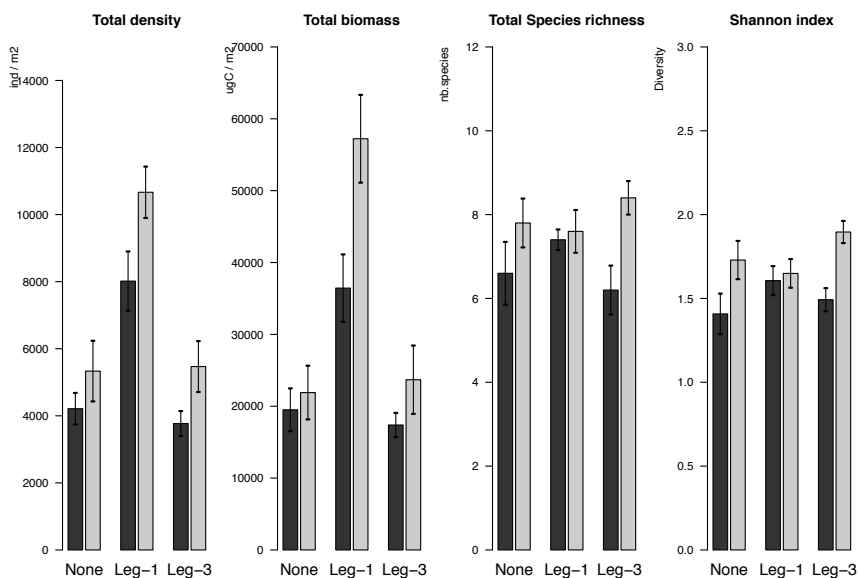
Figure 2-8 : Relationship between earthworm assemblages (based on bray Curtis distance) and geographical distances (based on Euclidian distance).

### 3.3.2. Collembola

Tableau 2-5 : Results of Linear Mixed-Effects Models (LMM) of “tillage effect”, “leguminous effect” and “interaction effect” on total density, biomass, species richness and Shannon index of Collembola. The tests values are given. F: F-value, p: p-value. The rejection level was set at  $\alpha = 0.05$ . \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns  $p > 0.05$ . The location of the significant differences is in Figure 2-9.

	Total density		Total biomass		Total richness		Total Shannon	
	F	p	F	p	F	p	F	p
Tillage	7.490	0.012 *	4.12	0.0493 *	10.22	0.001 **	14.39	0.0009 ***
Leg	23.18	2.823e-06 ***	19.39	1.082e-05 ***	0.703	0.382 ns	1.760	0.194 ns
Tillage x Leg	0.110	0.896 ns	0.671	0.523 ns	3.756	0.019 *	3.307	0.0494 *

Both total density and biomass of Collembola were influenced by "tillage" and "leguminous" treatments. However, no significant interactions between those factors were revealed (Tableau 2-5). Total density and biomass were higher in RT compared to CT (7156 individuals  $m^{-2}$  and 34.27  $mgC\ m^{-2}$  vs. 5333 individuals  $m^{-2}$  and 24.44  $mgC\ m^{-2}$ , respectively). Also, density and biomass were higher in Leg-1 (18683 individuals  $m^{-2}$  and 93.66  $mgC\ m^{-2}$ ) than in None (9545 individuals  $m^{-2}$  and 41.41  $mgC\ m^{-2}$ ) and Leg-3 (9239 individuals  $m^{-2}$  and 41.08  $mgC\ m^{-2}$ ). The total species richness and Shannon index were not affected by the leguminous factor, but both were significantly influenced by tillage systems and the interaction of the two factors (Tableau 2-5). On average, the highest values of these two parameters were found in RT, being significantly different from those found in CT. Significant interactions between the two factors resulted in higher values of specific richness and Shannon index in the RT-Leg-3 modality compared to the CT-Leg-3 and CT-None modalities (Figure 2-9). Considering the life forms, the specific richness of each of them was not influenced by the different modality studied but the abundances and biomasses were (Tableau 2-6, Figure 2-10).



	Tillage		Leg			Tillage x Leg					
	CT	RT	None	Leg-1	Leg-3	CT None	RT None	CT Leg-1	RT Leg-1	CT Leg-3	RT Leg-3
Total density	b	a	y	x	y	A	A	A	A	A	A
Total biomass	b	a	y	x	y	A	A	A	A	A	A
Total richness	b	a	x	x	x	B	AB	AB	AB	B	A
Shannon index	b	a	x	x	x	B	AB	AB	AB	B	A

Figure 2-9 : Total density, biomass, species richness and Shannon index of Collembola (means and standard error) according to the different methods studied combining the tillage (CT: conventional tillage-black barplot; RT: reduced tillage-grey barplot) and legume factor (Leg-1: Faba Bean as previous crop of wheat; Leg-3: Faba Bean sown three years before wheat; None: rotation without Faba Bean and without any leguminous at least during the preceding five years.). Different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between “Tillage modalities”. Different minuscule letters (i.e. “x”, “y”) indicated significant differences ( $\alpha = 0.05$ ) between “Leguminous (Leg) modalities”. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between “interactions (Tillage x Leg) modalities”.

Tableau 2-6 : Results of Linear Mixed-Effects Models (LMM) of “tillage effect”, “leguminous effect” and “interaction effect” on total density, biomass, species richness of functional groups of Collembola. Ep: Epedaphic; He: Hemiedaphic; Eu: Euedaphic. The tests values are given. F: F-value, p: p-value. The rejection level was set at  $\alpha = 0.05$ . \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns  $p > 0.05$ . The location of the significant differences is in Figure 2-10.

	Ep		He		Eu	
	F	p	F	p	F	p
<b>Density</b>						
Tillage	29.53	1.518e-05 ***	0.784	0.385 ns	4.1430	0.053 .
Leg	33.74	1.279e-07 ***	7.214	0.004 **	2.8807	0.076 .
Tillage x Leg	3.94	0.03639 *	1.699	0.209 ns	6.2274	0.008 **
<b>Biomass</b>						
Tillage	12.55	0.002 **	0.892	0.355 ns	6.154	0.021 *
Leg	27.76	6.654e-07 ***	6.632	0.0053 **	7.554	0.003 **
Tillage x Leg	3.074	0.0452 *	1.262	0.305 ns	6.052	0.009 **
<b>Species richness</b>						
Tillage	2.044	0.166 ns	4.338	0.05841.	1.891	0.182 ns
Leg	0.345	0.712 ns	0.153	0.859 ns	0.376	0.691 ns
Tillage x Leg	0.679	0.517 ns	1.217	0.318 ns	1.888	0.174 ns



For epedaphic, both density and biomass were influenced by "tillage", "leguminous" and their interaction. We recorded a higher density and biomass of epedaphic in the RT than in the CT and more in Leg-1 than in Leg-3 and None (Tableau 2-6, Figure 2-10). Furthermore, the interaction of these two factors revealed that density and biomass of epedaphic did not differ between RT and CT when a leguminous was previously introduced in the rotation three years ago (Leg-3). For hemiedaphic, density and biomass were influenced only by the position of the *Faba Bean*, the other factors showed no effect (Tableau 2-6, Figure 2-10). Density was higher in Leg-1 (5571 individuals m<sup>-2</sup>) than in Leg-3 (1529 individuals m<sup>-2</sup>) and None (3295 individuals m<sup>-2</sup>) and a higher biomass was found in Leg-1 (18403 g m<sup>-2</sup>) compared to in Leg-3 (45.95 mgC m<sup>-2</sup>), none had intermediate biomass values (11.31 mgC m<sup>-2</sup>). For euedaphic, density and biomass were only influenced by the interaction of leguminous and soil tillage (Tableau 2-6, Figure 2-10), being significantly higher in RT compared to CT only when a leguminous was grown (Leg-1 or Leg-3).

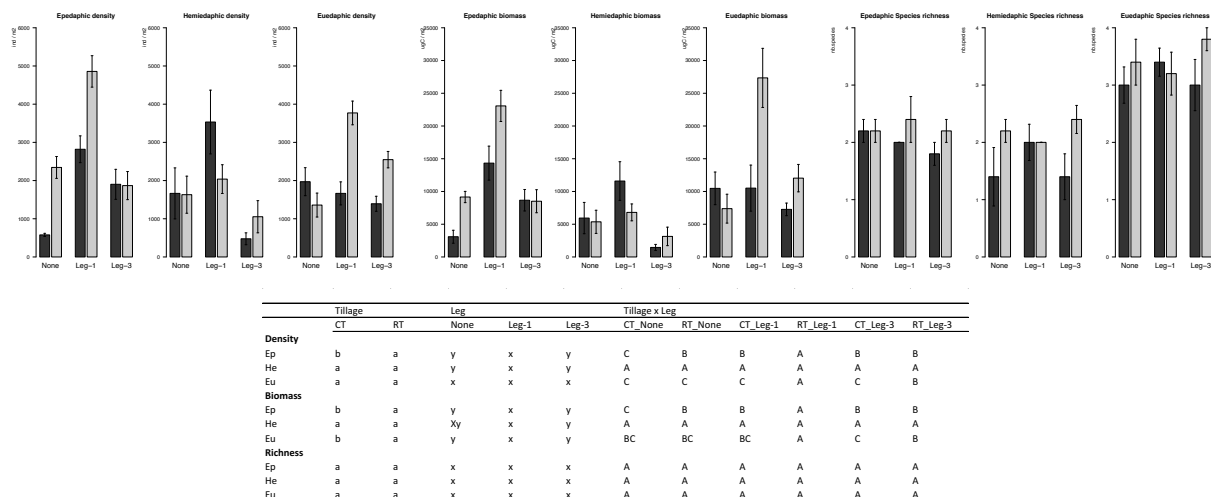


Figure 2-10 : Density, biomass and species richness of functional groups of Collembola (means and standard error) according to the different methods studied combining the tillage (CT: conventional tillage-black barplot; RT: reduced tillage-grey barplot) and legume factor (Leg-1: Faba Bean as previous crop of wheat; Leg-3: Faba Bean sown three years before wheat; None: rotation without Faba Bean and without any leguminous at least during the preceding five years.). Different minuscule letters (i.e. "a", "b") indicated significant differences ( $\alpha = 0.05$ ) between "Tillage modalities". Different minuscule letters (i.e. "x", "y") indicated significant differences ( $\alpha = 0.05$ ) between "Leguminous (Leg) modalities". Different capital letters (i.e. "A", "B") showed significant differences ( $\alpha = 0.05$ ) between "interactions (Tillage x Leg) modalities".

Assemblages of Collembola strongly differed between modalities as revealed by the overall ANOSIM ( $r^2 = 0.394$ ,  $p\text{-value} = 0.001^{***}$ ). CT-None and RT-Leg-1 were different from all other modalities tested (Tableau 2-7). This is clearly visible in the NMDS ordination (Figure 2-11). *Megalothorax minimus*, *Mesaphorura* sp and *Parisotoma notabilis* strongly dominated

in CT-None, whereas *Stenacidia violacea*, *Lepidocyrtus violaceus* and *Protaphorura armata* were stronger in RT\_Leg-1. CT\_None modality was very variable in its composition of species. Moreover, we noted a differentiation in the modalities presenting the system CT with CT-Leg- 1 and CT-Leg-3 that were closer than CT-None.

Tableau 2-7 : Results of ANOSIM analyses between Collembola assemblages within six different modalities. p-values after correction of Bonferroni are given. CT-None: conventional tillage - rotation without Faba Bean and without any leguminous at least during the preceding five years.; CT-Leg-1: conventional tillage - Faba Bean as previous crop of wheat; CT-Leg-3 : conventional tillage - Faba Bean sown three years before wheat; RT-None : reduced tillage - rotation without Faba Bean and without any leguminous at least during the preceding five years.; RT-Leg-1: reduced tillage - Faba Bean as previous crop of wheat; RT-Leg-3 : reduced tillage - Faba Bean sown three years before wheat.

	CT-None	CT-Leg-1	CT-Leg-3	RT-None	RT-Leg-1	RT-Leg-3
CT-None						
CT-Leg-1	<b>0.0094</b>					
CT-Leg-3	<b>0.0074</b>	<b>0.0176</b>				
RT-None	<b>0.0073</b>	0.1051	0.3081			
RT-Leg-1	<b>0.0075</b>	<b>0.0166</b>	<b>0.007</b>	<b>0.008</b>		
RT-Leg-3	<b>0.009</b>	<b>0.0144</b>	0.6288	0.089	<b>0.0091</b>	-

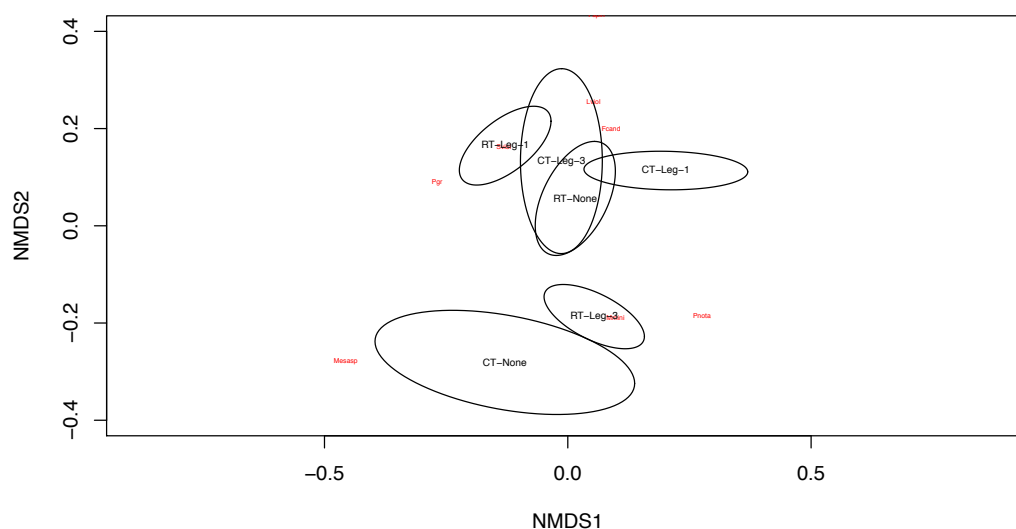


Figure 2-11 : Non-metric multidimensional scaling (NMDS) plot based on Bray-Curtis dissimilarity indices derived from abundance of Collembola species recorded in six different modalities. CT-None: conventional tillage - rotation without Faba Bean and without any leguminous at least during the preceding five years.; CT-Leg-1: conventional tillage –Faba Bean as previous crop of wheat; CT-Leg-3 : conventional tillage - Faba Bean sown three years before wheat; RT-None : reduced tillage - rotation without Faba Bean and without any leguminous at least during the preceding five years.; RT-Leg-1: reduced tillage - Faba Bean as previous crop of wheat; RT-Leg-3 : reduced tillage - Faba Bean sown three years before wheat.

Among the parameters used the "leguminous" factor, the CEC, pH and bacterial DNA were significantly related to the composition of the Collembola community (Figure 2-12).

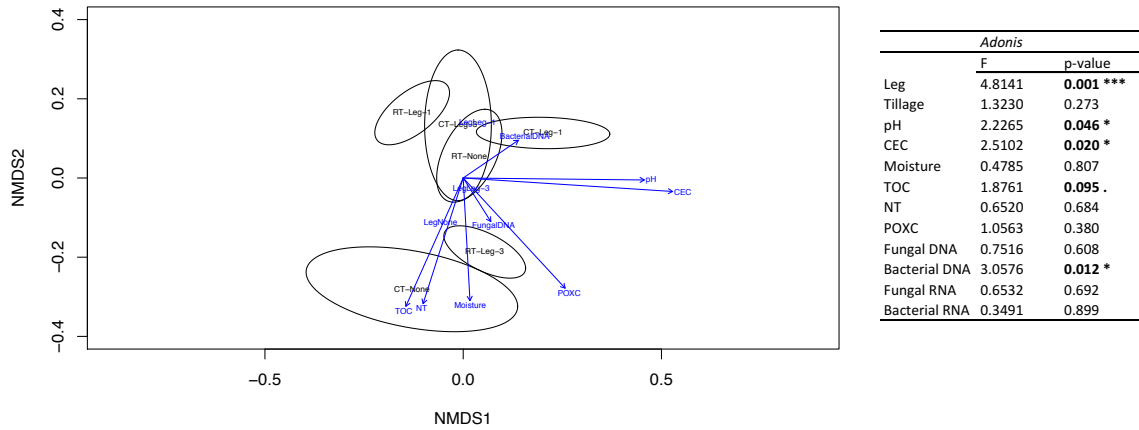


Figure 2-12 : Collembola community compositions of the plots displayed using NMDS. Stress of the ordination is 0.19. Significant variables ( $P < 0.05$ ) are shown by arrows whose length is proportional to the strength of the correlation, and they are shown in bold in the table

There was a very low, but statistically significant, correlative link (1.88%) between the composition of the Collembola communities and the geographical distance ( $r^2 = 0.018$ , p-value = 0.00244 \*\*\*) (Figure 2-13).

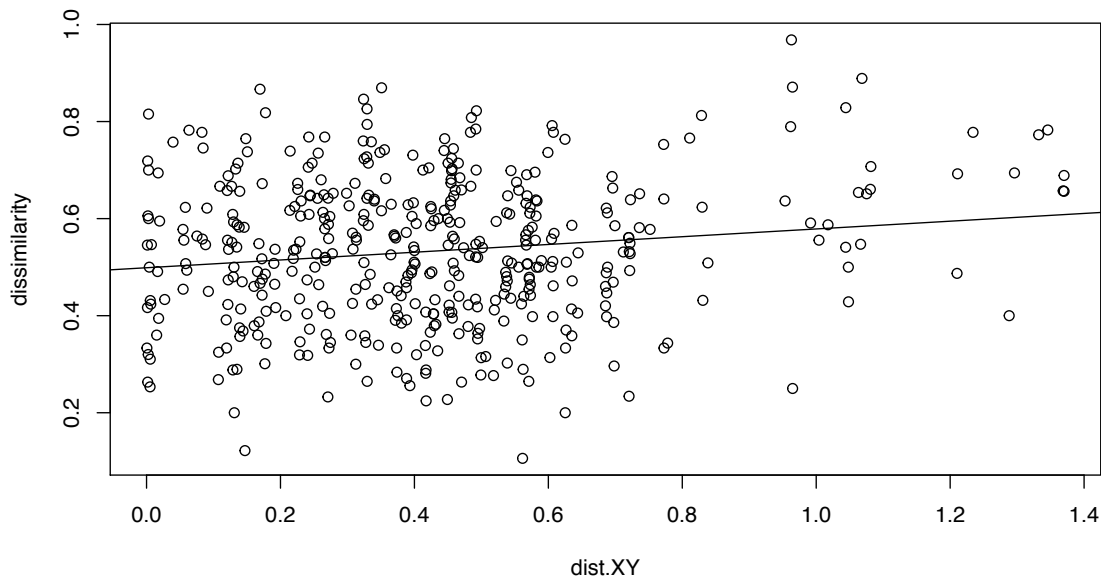


Figure 2-13 : Relationship between Collembola assemblages (based on Bray-Curtis distance) and geographical distances (based on Euclidean distance).

#### 4. Discussion

In this study, we followed the potential interaction of two innovative practices (the presence and position of the legume (*Faba Bean*) in crop rotations and the application of reduced tillage) used in farms in Normandy (France). We wanted to know if the shift towards innovative cultivation practices (from conventional to reduced tillage with the incorporation of legume in

the crop rotation) would benefit earthworms and Collembola assemblages in the short or medium term.

The density, biomass, and species richness of both earthworms and Collembola collected in all plots agree with published data from similar systems within Europe (Briones and Schmidt, 2017; Petersen, 2002; van Capelle et al., 2012).

#### **4.1. Tillage effect**

Our results showed that the global community of earthworms (total density, biomass, species richness and Shannon index) did not show any effect in relation to the different modalities tested. In the literature, previous studies have often shown a negative impact of conventional tillage on earthworms, either directly by wounding them, or indirectly by exposing them to harsh environmental conditions, the destruction of their biogenic structures (pores and tunnels) and burial of their food sources, which could lead to mortality effects (Briones and Schmidt, 2017). As a result, the adoption of conservation tillage should minimize these effects. According to the results of Holland, (2004); Pelosi et al., (2009) the number of earthworm species and species diversity was increased in systems with reduced tillage intensity. This was not our case, since we did not detect any differences between the contrasted tillage systems, thereby not validating our first hypothesis for the case of "earthworms". Furthermore, in terms of functional groups (ecological categories), our results showed that anecic earthworms were reactive to tillage systems. The density and biomass of this group were higher in the conventional tillage compared to the reduced tillage. This is in contradiction with the results of Chan (2001), and in disagreement with our expectations, but in agreement with the results of Edwards and Lofty, (1969). Indeed, considering the behaviour of anecic earthworms, in soil they have a higher displacement capacity and migrate vertically in the first layers of soil (0-10 cm; Bouché, (1977)). Knowing that the reduced tillage is performed by means of a rotating disk over the first ten cm of the soil, thus affecting the large species living in the soil with direct effects such as injuries, mortality and exposure to predators (Briones and Schmidt, 2017; van Capelle et al., 2012). At the same time, the adoption of conservation tillage does not automatically translate into an optimal population of worms in terms of abundance and diversity. Briones and Schmidt, (2017) have shown in their meta-analysis a very strong positive response of earthworm populations to RT operations when the soil had been under RT for a long time (>10 years). In our study, the RT was introduced very recently (<10 years) and may have not allowed for a positive response of earthworms. On the other hand, like the global community of earthworms, the endogeic showed no significant difference whatever the factor tested. In this study, we

harvested only few species of earthworms (mainly juveniles indeed). This low taxonomic richness may reveal the presence of few resistant species specialized to these agricultural systems. This can be seen in the NMDS results which shows a high community similarity between the different modalities tested. The composition of the earthworm communities was not related to the geographical position indicating no influence of the composition of earthworm communities in the heterogeneity of this study (Figure 2-8).

Unlike earthworms, Collembola assemblages differed between the cultivation practices we surveyed. Both the densities and biomass of Collembola have been higher in conservation systems compared to conventional ones (RT vs. CT, respectively). This is in agreement with the results of the previous studies (Petersen, 2002; Wardle, 1995) and supports our first hypothesis. This fits with the common assumption that conservation agricultural practices have a positive effect on Collembola communities (Cortet et al., 2002; Dittmer and Schrader, 2000b; Petersen, 2002; Winter et al., 1990a). Within soil fauna, Collembola are considered to be a fast responsive group (r-strategist) to environmental changes (Butcher et al., 1971; Chauvat et al., 2003; Dunger, 1975; Kaczmarek, 1975; Klironomos and Kendrick, 1995; Ponge, 1983). According to Wardle, (1995), Collembola are usually slightly stimulated when shifting from conventional toward no-tillage management, probably due to a stress-release.

Regarding the life forms, the density and biomass of ep- and euedaphic Collembola responded positively to reduced tillage. As for hemi-edaphic (density, biomass as well as species richness), RT and CT showed no significant difference. However, their relative abundance dropped by 13 points when reducing tillage (i.e. from CT to RT, Table 8), but this was due to a single species, *Parisotoma notabilis* with a relative abundance decreasing from 20.2% to 10.3% in CT and RT, respectively (cf. Appendix A-Table A1).

Indeed, the reduction of tillage has especially favored the two most distinct forms of life. We observed a slight increase in the relative abundance of euedaphic Collembola from 31.4 to 35.8 in CT and RT, respectively (Table 8); this was due to an increase of *Protaphorura armata* in the RT treatments. This is consistent with our hypothesis 1b, although we have observed a slight stimulation of euedaphic collembolan (deep living species). For epedaphic collembolan, relative abundance strongly increased between CT and RT (i.e. from 33.1% to 42.3%, respectively, Table 8). Relative abundances of all epedaphic Collembola species (*Etmobrya lanuginosa*, *Lepidocyrtus violaceus*, *Stenacidia violacea*) were promoted during the reduction of tillage. This could be due to the improvement of the microhabitat conditions with the availability of the residues of the preceding culture attracting them (Chauvat et al., 2007; Ponge

et al., 1993). This is not the case for conventional tillage, since its effect is often accompanied by the burial of residues, so accessibility to epedaphic species could be compromised. These results are in agreement with the evolutionary model of reproduction strategies "r" and "k" proposed by Marc Arthur and Wilson in 1967, the epedaphic collembolan have a high reproduction rate, therefore of "r" strategy. They are good colonizers of a disturbed environment, but live on the surface of the soil and, as a result, are more at risk (New, 2005). This is why we noticed their decrease in CT compared to RT.

The absence of effect upon hemiedaphic collembolans may be related to their intermediate characteristics (rk-strategist) between the two life forms (ep- and eu-edaphic), so some can be favored and others not. In the end, nothing moves for the hemiedaphic Collembola.

#### 4.2. Leguminous effect

Contrary to our hypothesis, introducing Leguminous (*Faba Bean*) into crop rotations had no effect on nutrient content (C, N) during our study. This is in disagreement with the common assumption that the introduction of nitrogen-fixing plants, such as legumes, leads to significant amounts of mineral nitrogen (Brockwell et al., 1995; D'Annibale et al., 2017; Nemecek et al., 2008; Sileshi et al., 2008; Sileshi and Mafongoya, 2006). We could explain this, through the variability brought by farmers' practices around the implementation of this innovative practice as well as the technical itineraries. Coupled with the geographic variability that could translate soil type and micro-climatic conditions, we could not reveal an overarching effect of this leguminous practice on nutrients cycle.

However, considering associated functions like microbial ones, fungal RNA responded favourably to introduction of leguminous. This is in agreement with the literature stating that the introduction of nitrogen-fixing plants into agroecosystems, supports the functions and productivity of the ecosystem (Sileshi et al., 2008). For example, this practices was shown to significantly influence microclimatic conditions with stimulation in the amount of microbes and so; increasing trophic resources for decomposers (Axelsen and Kristensen, 2000; Kladvko, 2001). At the same time, our results showed that the density and biomass (total, ep-and hemi-edaphic) Collembola were favored in the presence of legumes, especially when applied before cultivation. Collembola are known to respond to changes in vegetation cover and soil conditions (Chauvat et al., 2007; Ponge et al., 1993). According to our results NMDS, the presence of leguminous was the main factor explaining the differentiation of communities of Collembola

across sites. Other factors such as pH, CEC and bacterial DNA also explained shift in the composition of the Collembola assemblages between the treatments.

Interestingly, the more we move away from the legume presence (Leg-3 in our case), the more the positive impact on Collembola assemblages. Accordingly, microbial functions such as bacterial DNA and fungal RNA also decreased three after application of legumes (Leg-3, Figure 2-3). Obviously, the leguminous improved environmental (biotic and abiotic) conditions for Collembola, and thereby promote them but only at a very short term. The overall increase in Collembola assemblages in Leg-1 was mainly related to an increase in r-strategist Collembola. The improvement of microclimatic conditions (especially in soil surface following the application of legumes) and of food sources tends to increase their abundance and biomass in contrary to deep living soil species (k-strategist) that did not respond to the presence of leguminous. The introduction of legumes promoted epe- and hemiedaphic Collembola in the very short term (Leg-1). The relative abundances of *Lepidocyrtus violaceus* (epedaphic), *Parisotoma notabilis* and *Folsomia spinosa* (hemiedaphic) were increased (cf. Appendix A-Table A2).

In contrary, the introduction of legumes into crop rotations had no effect on earthworm density, diversity and composition. These findings are misunderstood in the literature, and different studies show a positive effect on earthworms. For example, Milcu et al., (2008) showed that an increase in earthworms (density and biomass) was mainly due to the increased incidence of legumes with increasing diversity. These authors reported that increased earthworm density allows accelerating the decomposition of nitrogen-rich legume litter, and this was more pronounced at higher plant diversity. In our case, since we did not detect any effects on total nitrogen (as described above), this could be explained by the lack of effect of earthworm assemblages.

#### **4.3. Interaction effect between legume introducing and reduced tillage.**

Interactions between the presence of the leguminous and reduced tillage did not affect the earthworm assemblages. However, this hypothesis has been validated for Collembola. Indeed, our results showed that overall diversity increased in RT\_Leg-3 modality compared to the other modalities studied. This increase in diversity was reflected at the functional level because the density and biomass of Collembola euedaphic were high when RT was crossed with Leg-3. This was due to the increase in the relative abundance of two euedaphic species such as *Protaphorura armata* and *Megalothorax minimus* (cf. Appendix A-Table A3). This suggests that

the use of *Faba Bean* (leguminous) in crop rotations associated with a decrease in tillage depth for 3 years could entail the stabilization of certain microclimatic conditions such as habitats and resources (root exudation). Our results on DNA and fungal RNA support this assertion, showing higher values in the RT\_Leg-3 modality compared to other modalities. This positive effect of the combination of the two innovative factors (reduced tillage x Leg-3) on microbial functions (in particular fungal) can explain the marked increase in the density and biomass of euedaphic Collembola because they are rather controlled by trophic resources (Henneron et al., 2016; Schneider and Maraun, 2009), than by top-down pressure. Moreover, regardless of the position of the legume in crop rotation x to the reduction of tillage, the density and biomass of euedaphic Collembola showed higher values. This shows that the combination of the two innovative practices has a marked effect on k-strategist Collembola, which persists over time.

In a general way, apart from all the factors studied, the interaction of the two innovative practices "RT" x "Leg" (especially RT\_Leg-1) greatly stimulated the total abundance of Collembola compared to a single factor response (RT or Leg). This allowed us to validate our last hypothesis.

## 5. Conclusion

This study under real conditions of farming showed that the earthworm and Collembola assemblages did not respond similarly to the application of innovative practices. The Collembola were stimulated while the earthworms showed no response. This confirms the rapid response of Collembolans to environmental change. The interactions between *Faba Bean* presence and reduced tillage were more positive on Collembola assemblages than the precognition of one of the two factors. This demonstrates the advantage of applying together the two innovative practices, the RT removes a mechanical disturbance and the legumes increase the trophic resources of the soil. By varying the position of the bean in the rotation, this positive effect lasted in time and especially the euedaphic Collembola were favored. Finally, in view of our empirical approach, it turns out that certain beneficial effects of these innovative practices cannot be considered without taking into account how they are implemented at the scale of crop rotations and technical itineraries.

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## **Chapitre 3. Réduction du travail du sol, gestion des résidus de culture, diminution de la fertilisation azotée**

### **Présentation du chapitre 3**

Cette étude s'effectuant à une échelle spatiale plus réduite, s'est menée dans le cadre du projet ANR - SOFIA (Agence Nationale de la Recherche - SOil Functional diversity as an Indicator of sustainable management of Agroecosystems). Ce projet a permis à différentes équipes travaillant sur le sol de suivre à long-terme l'impact des stratégies de gestion des cultures arables. Nous avons focalisé notre attention au sein du compartiment endogé sur une partie de la mésofaune, plus précisément les collemboles. Les propriétés physico-chimiques et microbiennes utilisées, ont été fournies par UMR614 FARE, Reims (Pr. Sylvie Recous). L'étude a fait sortir trois points forts à savoir :

- La réduction du travail du sol a entraîné une augmentation générale du nombre de collemboles
- La réduction du travail du sol a favorisé la diversité des collemboles et des groupes fonctionnels.
- La restitution des résidus de culture n'a eu aucun effet sur les espèces vivant dans le sol

## Effect of different crop management practices on soil Collembola assemblages: a 4-year follow-up.

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### 1. Introduction

Conservation agriculture aims at developing sustainable agricultural systems that pursue crop production while greatly mitigating their negative environmental impacts (Bommarco et al., 2013; Hobbs, 2007). To do so, agronomical practices must integrate ecological processes in order to rely more efficiently on agroecosystem self-regulation (Altieri, 1999; Wezel et al., 2014). Sustainable systems are generally based on decreasing soil disturbance by reducing tillage intensity, decreasing N fertilisation, and increasing restitution of crop residues to restore soil organic matter content (Michels et al., 1995; Scheunemann et al., 2015b).

One of the major processes taking place in soil and linked to plant production is the decomposition of organic matter and subsequent nutrient cycling performed by soil organisms (de Graaff et al., 2015; Kibblewhite et al., 2008; Van Der Heijden et al., 2008). Within agrosystems, beside soil microbial communities, Collembola is one of the most abundant groups of organisms. They have been shown to significantly influence belowground processes such as organic matter decomposition rate, N mineralisation, soil respiration or leaching of dissolved organic carbon (Filser, 2002) and were shown in turn to impact plant performance (Forey et al., 2015). Most of these effects are indirect, i.e. acting via alterations in microbial activities (Moore et al., 1988; Verhoef and Brussaard, 1990; Visser, 1985) and by transporting fungal propagules (Lussenhop, 1992; Seastedt, 1984). In turn, the Collembola critically depend on microbial communities fuelled by plant litter and root exudates (Moore et al., 2003; Schneider and Maraun, 2009). Due to their notable contribution in shaping soil microbial

communities, Collembola are considered to play an important role in biological control of fungal plant pathogens (Klironomos and Kendrick, 1995; Lartey et al., 1994; Wolfarth et al., 2013). Collembola species are usually aggregated in three different life forms (epedaphic, hemiedaphic, and euedaphic) that closely relate to both dispersal ability and various functional attributes such as reproduction, mobility, and metabolic activity (Gisin, 1943) and therefore to biodemographic strategies. These life forms can be assimilated to functional groups. Aggregation to life forms or functional groups is a convenient way to detect changes in components of soil biota with broadly similar ecologies (Chauvat et al., 2003).

In general, positive effects of new conservation agricultural practices on Collembola communities have been observed (Cortet et al., 2002; Dittmer and Schrader, 2000b; Petersen, 2002; Winter et al., 1990b) but may depend on the soil depth considered (See Petersen, 2002). According to a compilation of the results of 106 studies done by Wardle, (1995), Collembola are usually slightly stimulated when shifting from conventional toward no-tillage management, probably due to a stress-release. Furthermore, the restitution of crop residues (organic matter), was shown to significantly influence microclimatic conditions and increase trophic resources for decomposers (Axelsen and Kristensen, 2000; Kladviko, 2001), including Collembola, but see (Ngosong et al., 2009). However, several studies revealed contradictory patterns with either no or negative effect of conservation practices on soil Collembola compared to conventional management (Cole et al., 2008; Holland, 2004; Postma-Blaauw et al., 2010; Scheunemann et al., 2015b; Tsiafouli et al., 2015; van Capelle et al., 2012).

Only few studies have so far focused on the dynamics of the different Collembola functional groups according to changes in agricultural practices. This approach could refine our understanding of Collembola responses to environmental changes (Chauvat et al., 2014a) and the subsequent consequences on ecological processes (Petersen, 2002). Furthermore, studies generally compared single agricultural practices, e.g. tillage type, N fertilisation rate or residues management. The effect of combining these different practices has little been addressed. Both, resource supply and physical disturbance are considered to be key determinants of biological diversity in aboveground systems (Cole et al., 2008; Lawton and Kinne, 2000).

In the present study, we monitored Collembola assemblages over four years in response to different practices varying according to crop rotations (annual vs perennial), the rate of N fertilization (low vs high), tillage (deep vs reduced), and crop residues management (restitution vs removal). The main objective of this study was to follow the differentiation of Collembola assemblages between agricultural practices over time. We hypothesized that (1a) decreasing

soil mechanical disturbance will increase abundance and richness of the whole Collembola assemblage, (1b) deep living species to be favored by a reduction of tillage intensity. (2a) Reducing trophic resources through exportation of crop residues (i.e. removal) or lower N fertilization negatively impact Collembola assemblages; (2b) soil living species will mainly suffer from reducing the amount of organic matter and N entering the system. (3) Dissimilarity in Collembola assemblages composition increases with time-differentiation of agricultural practices.

## 2. Materials and Methods

### 2.1. Site description

The study was conducted on the experimental platform SOERE-ACBB (Systèmes d'Observation et d'Expérimentation pour la Recherche en Environnement-Agrosystèmes Cycles Biogéochimiques et Biodiversité), located at Estrées-Mons (Northern France; 49.873 N, 3.032 E) and managed by the INRA (Institut National de la Recherche Agronomique). Soil is a typical LUVISOL (clay =  $187 \pm 31$  g kg<sup>-1</sup>, silt =  $744 \pm 34$  g kg<sup>-1</sup>, sand =  $69 \pm 21$  g kg<sup>-1</sup>, pH in water =  $8.20 \pm 0.10$ , organic C =  $10.40 \pm 0.80$  g kg<sup>-1</sup>, and total N =  $1.04 \pm 0.05$  g kg<sup>-1</sup>), climate is temperate with an annual average rainfall of 678 mm and an average annual temperature of 10.8 °C. The site characteristics were fully described by Coudrain et al. (2016).

### 2.2. Experimental design

The experiment was established on a 11 ha field and initiated by setting up a six-year rotation composed of spring pea (*Pisum sativum*, L.), winter wheat (*Triticum aestivum*, L.), rapeseed (*Brassica napus*, L.), spring barley (*Hordeum vulgare*, L.), maize (*Zea mays*, L.), winter wheat. A specific treatment was dedicated to switchgrass (*Panicum virgatum*, L.), a perennial crop used as bioenergy crop. The design consisted of 4 randomized blocks of 6 plots (24 plots in total, each plot was 85 m long and 48 m wide). Prior to the setting of the experiment (y+0), all the plots were managed under conventional tillage (CT, see below). In spring 2010, 6 different treatments/practices were established according to different crop rotations (annual and bioenergy crop rotations), rate of N fertilization (reference rate vs. one third of reference rate), crop residue management (returned vs. removed), soil tillage (full-inversion ploughing vs. reduced tillage) (Table1). Only five treatments (20 plots, cf. Appendix B-Figure B1) were investigated in the present study: CT (conventional tillage); CT-RN (conventional tillage and

reduced N fertilization); RT (reduced tillage); RT-RR (reduced tillage and crop residues removal); P-BC (perennial and bioenergy crop). For detailed information see to Tableau 3-1.

The mean amount of C returned through aerial residues was estimated to range between 1.6 and 3.2 t C ha<sup>-1</sup> yr<sup>-1</sup> in the exported vs. the returned crop residue treatments, respectively. Over the full rotation, the mean fertilization rate (reference) was 134 kg N ha<sup>-1</sup> yr<sup>-1</sup> except for the treatment RN that received only 43 kg N ha<sup>-1</sup> yr<sup>-1</sup>.

*Tableau 3-1 : Description of the 5 investigated treatments of the SOERE ACBB located in Estrées-Mons, France, according to three main practices: soil tillage, crop residue management, and N fertilization rate.*

Code	Treatment	Soil tillage Depth in cm	Crop residue management	N Fertilisation rate (kgN ha <sup>-1</sup> yr <sup>-1</sup> )
CT	Conventional tillage	Annual ploughing 25	Returned (mouldboard ploughing)	134
CT-RN	Conventional tillage and reduced nitrogen	Annual ploughing 25	Returned (mouldboard ploughing)	43
RT	Reduced tillage	Shallow tillage 8	Returned (Disk ploughing)	134
RT-RR	Reduced tillage and residue removal	Shallow tillage 8	Exported (Hay baler)	134
P-BC	Perennial and bioenergy crop	Ploughing before culture 25	Exported (Hay baler)	134

### 2.3. Sampling, extraction and identification of Collembola

Soil samples were collected in March 2010 (y+0) before the set-up of the experiment, then in March 2012 (y+2), 2013 (y+3), and 2014 (y+4) at the start of the vegetation season. In each of the 20 experimental plots, 3 soil samples (at the Northeast, Central, Southwest of each plot) were collected (60 sampling points in total) by means of soil corers (diameter 5 cm). A single core included the organic layer and the top 5 cm of the mineral horizon. We focused on the topsoil (0-5cm) as more than 90% of the Collembola are to be found within this layer in this experimental site (Coulibaly & Chauvat unpubl.). In the laboratory, Collembola were extracted during two weeks using the Berlese-Tullgren device (Tullgren, 1918) that creates a temperature gradient over soil core, crumbled into a plastic sieve with 2 mm suspended over a collecting vessel containing 70% alcohol. Individuals (Collembola) collected in alcohol were counted and identified following identification keys (Gisin, 1960; Hopkin, 2007). However, some individuals were identified to genera when species identification was not possible. Finally, all species were allocated to one of three different life-forms, i.e. epedaphic, hemiedaphic, euedaphic (Gisin, 1943). These life-forms differ in fundamental ecological properties (including reproduction, vertical distribution, and metabolic activity; cf. Petersen, (2002) and can thus be considered as different functional groups.

## 2.4. Soil chemical properties and microbial communities

Initial soil physico-chemical parameters and their spatial variability were measured in January 2010 in the upper layer (0–20 cm). Details concerning methods and protocols are available in Coudrain et al., (2016). At each of the 60 sampling points in y+2, y+3, and y+4, five comparative soil cores were taken, then pooled to obtain one sample per plot for each year. Soil samples were placed in plastic containers, stored in cool boxes at 4 °C and transported to the laboratory for microbial or chemical analyses. In the laboratory, soil samples were sieved at 2mm and stored at 4°C during few days, until further analyses.

Total organic carbon concentration (TOC) was measured for each sieved soil sample using an elemental analyser (NA 1500, Carlo Erba, Milan, Italy). Microbial biomass carbon (MBC or C<sub>biom</sub>) was determined using the fumigation-extraction method described by Vance et al., (1987). The extraction of dissolved organic C (DOC) from soil samples either fumigated with chloroform or not, was performed with 40 mL of K<sub>2</sub>SO<sub>4</sub> 0.03 M (soil-solution 1:4, agitation 30 min, 20°C) and the concentration of DOC in extracts was analysed with a C-analyser (1010, O.I. analytical, Globalspec, NY, USA). The amount of C in microbial biomass was calculated as the difference in DOC contents between fumigated and unfumigated samples, with a correction factor KEC of 0.38 (Vance et al., 1987). C mineralization was measured in standardized conditions using C-CO<sub>2</sub> emitted from soils during a 72 h-incubation at 15°C and was used as a proxy of soil heterotrophic microbial activity. To do so, moist soil samples (42 g equivalent dry soil at 18.6 g H<sub>2</sub>O 100g<sup>-1</sup> soil) were placed in jars containing a beaker with water and a vial with 0.25 M NaOH solution to trap the CO<sub>2</sub> produced. The concentration of CO<sub>2</sub> trapped in the NaOH solution was measured by continuous flow colorimetry (Chaussod et al., 1986) using an autoanalyser (TRAACS 2000, Bran and Luebbe, Norderstedt, Germany). Soil pH<sub>H2O</sub> was measured with soil diluted with demineralized water (1:2.5 w/w). Finally, standard sensors were used to continuously monitor soil temperature (TEMP) and humidity (HUM) over the project period.

## 2.5. Statistical analyses

For each plot and each year (y+0 to y+4), we calculated the mean Collembola density (n=3) and species richness (n=3). Density was expressed in number of individuals per square meter. Thereafter, the structure of Collembola communities was described by calculating the diversity index of Shannon (H') and the Evenness (J') Index. Furthermore, the density and species

richness of each of the three functional groups were calculated to perform the different statistical analyses.

We were interested in differentiation of Collembola assemblages between treatments over time. Therefore, statistical analyses focused on the data collected for each date separately (y+0, y+2, y+3, y+4), because interannual variation within a single treatment was beyond the scope of our study. We, nevertheless, also performed analyses to quantify changes between years for a single treatment.

To investigate the effect of agricultural practices on Collembola communities, soil abiotic and microbial parameters, we used Linear Mixed-Effects Models (LMM) with the descriptive variables of Collembola communities (total density; total species richness, density and species richness of each life form and the community diversity indices), or environmental parameters as response and the factor “treatments” (CT, CT-RN, P-BC, RT and RT-RR) as fixed categorical predictor, the factor “experimental blocks” (B1, B2, B3 and B4) as random categorical predictor. Significant differences between means were tested at a 5% rejection probability level using the Tukey HSD test. Normality and variance homogeneity were tested prior to statistical analyses.

Hypothesis of no difference in assemblage composition between treatments was tested using one-way ANOSIM based on the Bray-Curtis dissimilarity distance configuration (Clarke et al., 2006). If two groups of sampling units (treatments) are really different in their species composition, then compositional dissimilarities between the groups ought to be greater than those within the groups. ANOSIM was performed with 10000 permutations and Bonferroni’s correction was applied a posteriori. In case of significant results, SIMPER analysis based on the Bray-Curtis dissimilarity distance was run to determine the species that contribute most in differentiating the two groups tested by ANOSIM. Finally, in order to visualize the pattern of species composition over all experimental treatments we used Non-metric multidimensional scaling (NMDS) computed on Bray-Curtis similarity matrix using yearly average values for each treatment.

We finally performed a Redundancy Analysis (RDA) to depict relationships between Collembola community variables as response matrix (Y) and environmental variables as explanatory matrix (X). The response matrix consisted of total density of Collembola, total species richness, density and richness of each of the three life forms. Data were transformed prior analysis to follow the normal distribution based on Gaussian or Normal distribution (data normed weighted averages). Explanatory matrix contained microbial biomass carbon (Cbiom),



metabolic activity (CO<sub>2</sub>), soil water content (HUM), Soil temperature (TEMP), and pHwater. With redundancy analysis, the components extracted from X are such that they are as much as possible correlated with the variables of Y and vice versa.

ANOSIM, SIMPER and NMDS analyses were performed with the free PAST 3.14 software. Univariate statistical analyses and RDA were performed using R software (Team, n.d.) with the libraries ade4 (Dray and Dufour, 2007), lme4 (Bates et al., 2014), MuMIn (Bartoń, 2013), multcomp (Hothorn et al., 2008), car (Fox and Weisberg, 2010) and vegan (Oksanen et al., 2013).

### 3. Results

#### 3.1. Community structure indices

At the onset of the experimental setup (before the introduction of agronomic treatments) (y+0), we recorded on average over all plots  $4.60 \pm 0.99$  species and  $1585 \pm 757$  individuals m<sup>-2</sup>. The Shannon and the Evenness indices at site level (i.e all plots) were  $1.30 \pm 0.31$  and  $0.84 \pm 0.08$ , respectively.

##### 3.1.1. Time effect within each treatment

Abundances and species richness in RT-RR differed significantly from y+2 till y+4, with in both cases higher values in y+4 (Tableau 3-2).

*Tableau 3-2 : Results of Linear Mixed-Effects Models (LMM) of the effect of year (y+2, y+3 and y+4) on total density, species richness of Collembola assemblages for each agricultural treatment (CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal). The tests values are given. Chisq : Chi-squared, p : p-value, R<sup>2</sup> : variance explained by both fixed and random factors. Degree of freedom = 4. The rejection level was set at  $\alpha = 0.05$ . \*\*\*p<0.001, \*\*p<0.01, \*p<0.05, ns p>0.05.*

	LMM outputs		
	Chisq	p	R <sup>2</sup> (%)
CT			
Total density	15.0	***	67.7
Total species richness	5.25	ns	32.3
CT-RN			
Total density	21.5	***	71.9
Total species richness	17.3	***	68.0
RT			
Total density	5.15	ns	35.5
Total species richness	8.91	**	63.9
RT-RR			
Total density	4.59	ns	29.5
Total species richness	9.75	**	65.7
P-BC			
Total density	55.7	***	83.5
Total species richness	11.1	**	50.2

Abundances recorded in RT did not differ significantly from y+2 till y+4, but species richness did, with higher values in y+2 and y+4. In conventional tillage treatments (CT and CT-RN), the factor "time" significantly impacted the species richness with lower values in y+3 compared to y+2 in CT, and also lower values in y+3 compared to y+2 and y+4 in CT-RN. Accordingly, the abundance in y+3 in CT-RN was significantly lower than in the other years. In CT, no difference was found regarding abundance of Collembola between the last two years. Both abundance and species richness of Collembola in the treatment P-BC were significantly impacted by the factor time with a consistent pattern of higher values in y+4 compared to the other years (Tableau 3-2 and Figure 3-1).

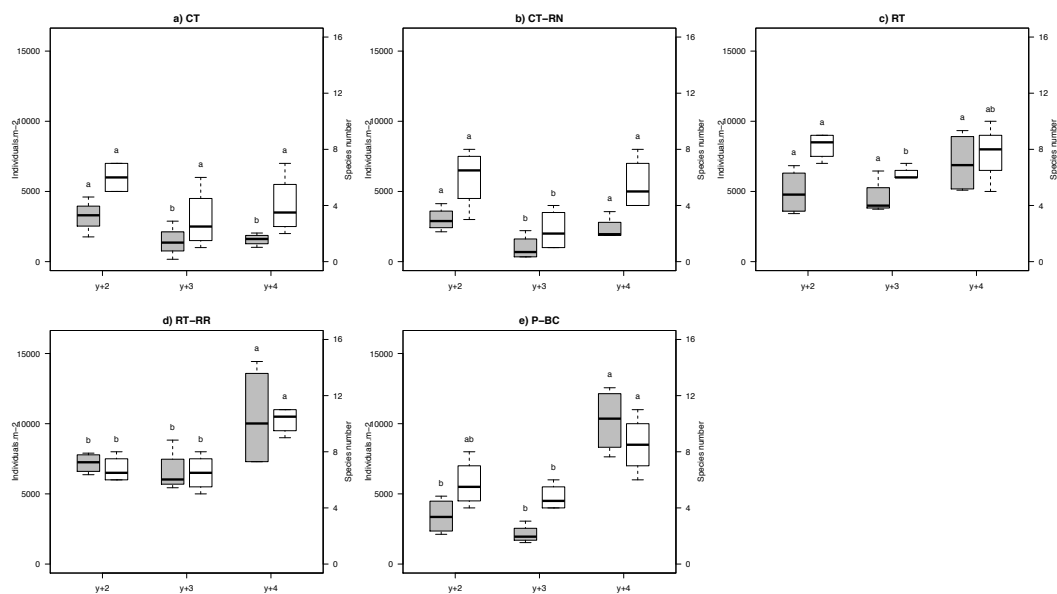


Figure 3-1 : Total density (grey boxplots) and species richness (white boxplots) of Collembola assemblages between years (y+2: 2012, y+3: 2013 and y+4: 2014) for five different agricultural treatments (North of France). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced. P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Different letters for a single parameter indicate significant Turkey's HSD differences between treatments at  $\alpha=0.05\%$ .

### 3.1.2. Treatment effect within each year

After 2 years (y+2), only the total density differed significantly between treatments (Tableau 3-3), with about 2-fold higher values in RT-RR than in CT (7193 and 3243 individuals  $m^{-2}$ , respectively). The three other treatments showed intermediate values (Figure 3-2 a). After 3 years (y+3), all community indices were influenced by experimental treatments (Tableau 3-3). The Collembola density ranged from ca 1440 to 6580 individuals  $m^{-2}$  (in CT and RT-RR, respectively). On average, 3-fold more individuals were collected in RT and RT-RR than in

CT, CT-RN and P-BC (5563 and 1515 individuals m<sup>-2</sup>; (Figure 3-2 b). The total species richness and the Shannon index displayed the same pattern, being significantly higher in RT and RT-RR compared to CT and CT-RN. P-BC showed an intermediate richness value (Figure 3-2 b and Figure 3-3 b). The evenness was significantly higher in CT-RN (0.97 ± 0.06) compared to RT-RR (0.75 ± 0.11), the other treatments being intermediate (Figure 3-3 b). After 4 years (y+4), all indices, except the evenness, significantly differed between treatments (Tableau 3-3). The density ranged from 1952 to 9242 individuals m<sup>-2</sup> (in CT and CT-RN vs. RT-RR and P-BC; Figure 3-2 b). Species richness and Shannon index likely responded to the treatments, with maximum values in RT-RR and minimum values in CT, the other treatments exhibiting intermediate values (Figure 3-2 c and Figure 3-3 c).

*Tableau 3-3 : Results of Linear Mixed-Effects Models (LMM) of the effect of treatment on total density, species richness, Shannon index and evenness of Collembola assemblages sampled at three different sampling dates (y+2, y+3 and y+4). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. The tests values are given. Chisq : Chi-squared, p : p-value, R<sup>2</sup> : variance explained by both fixed and random factors. Degree of freedom = 4. The rejection level was set at  $\alpha = 0.05$ . \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns  $p > 0.05$ .*

	LMM outputs		
	Chisq	p	R <sup>2</sup> (%)
y+2			
Total density	36.0	***	65.4
Total species richness	7.77	ns	29.0
Shannon (H')	3.76	ns	16.5
Evenness (J')	4.71	ns	19.7
y+3			
Total density	69.7	***	78.6
Total species richness	29.6	***	60.9
Shannon (H')	20.5	***	54.5
Evenness (J')	10.8	*	36.3
y+4			
Total density	71.7	***	80.0
Total species richness	27.4	***	59.0
Shannon (H')	11.4	*	37.5
Evenness (J')	6.63	ns	25.9

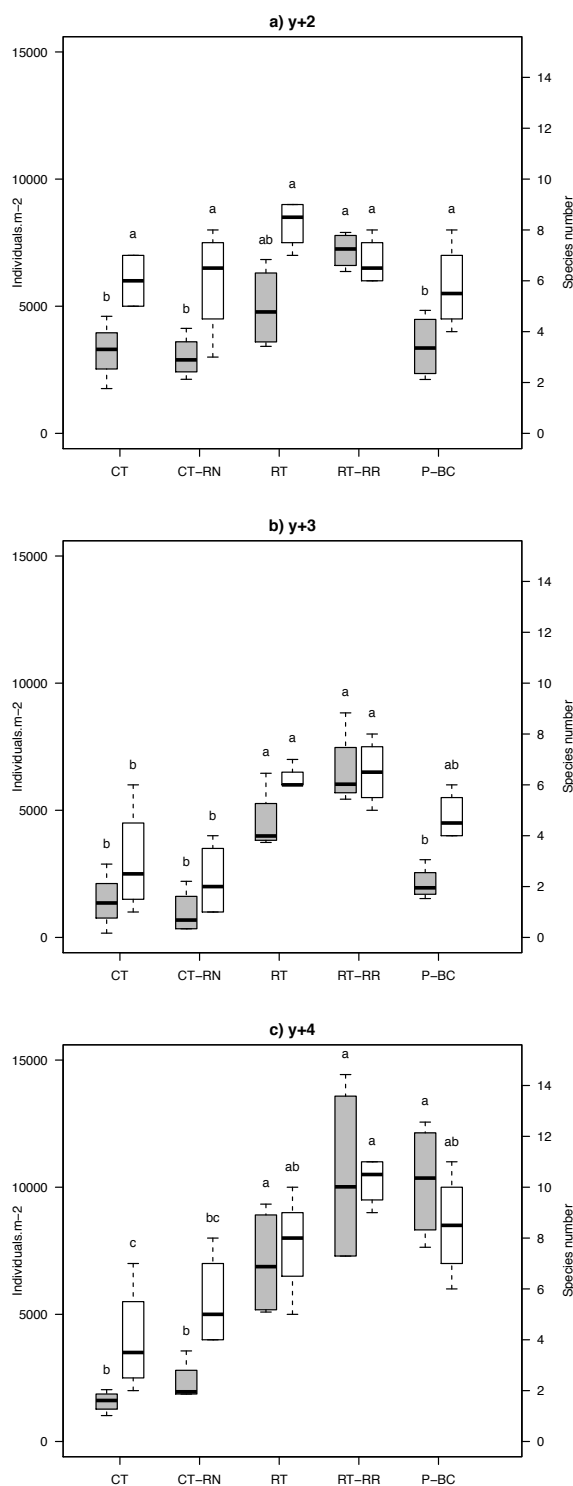


Figure 3-2 : Total density (grey boxplots) and species richness (white boxplots) of Collembola assemblages of five different agricultural treatments (North of France) over a 4-year period (2a: y+2: 2012. 2b: y+3: 2013 and 2c: y+4: 2014). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Different letters for a single parameter indicate significant Turkey's HSD differences between treatments at  $\alpha=0.05\%$ .

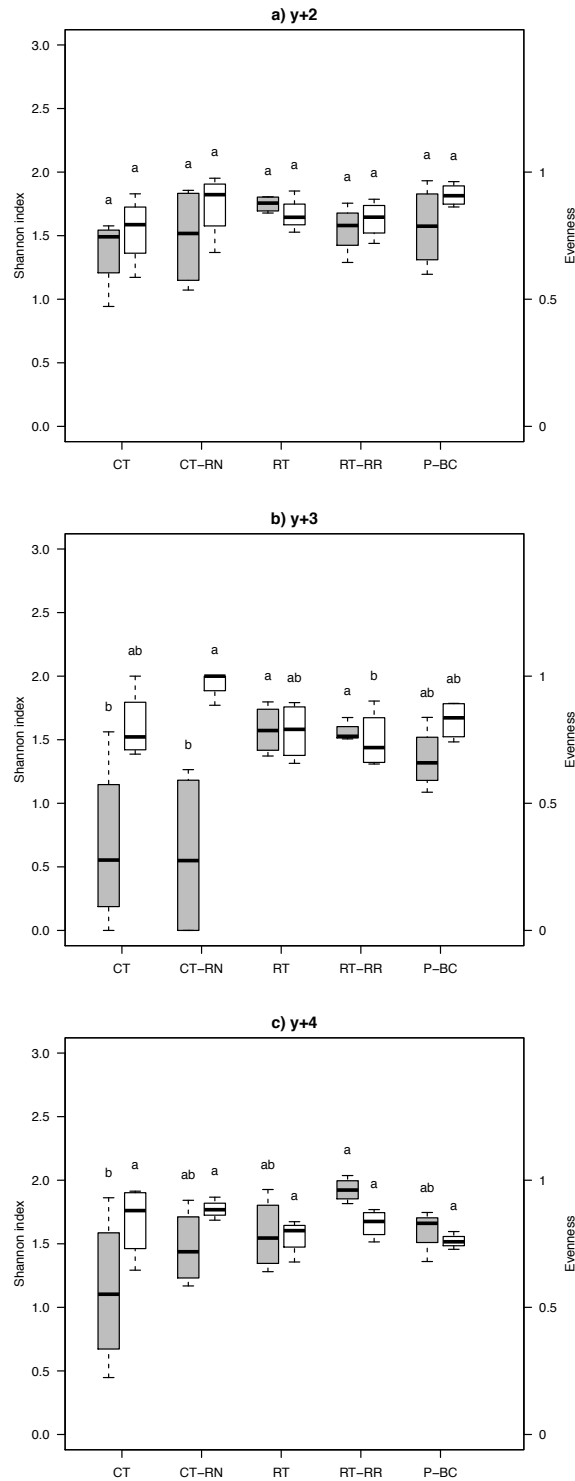


Figure 3-3 : Shannon index (grey boxplots) and Evenness (white boxplots) of Collembola assemblages of five different agricultural treatments (North of France) followed over 4 years (3a: y+2: 2012. 3b: y+3: 2013 and 3c: y+4: 2014). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Different letters for a single parameter indicate significant Turkey's HSD differences between treatments at  $\alpha=0.05\%$ .

### 3.2. Community composition

NMDS ordination of the experimental treatments over the different years (y+2, y+3, y+4) revealed a clear temporal differentiation between CT and CT-RN on one side and both RT and RT-RR on the other side of the first axis. P-BC became at y+4 quite isolated according to the second axis. Dissimilarities between treatments increased over time as distances between them in the NMDS increased (Figure 3-4).

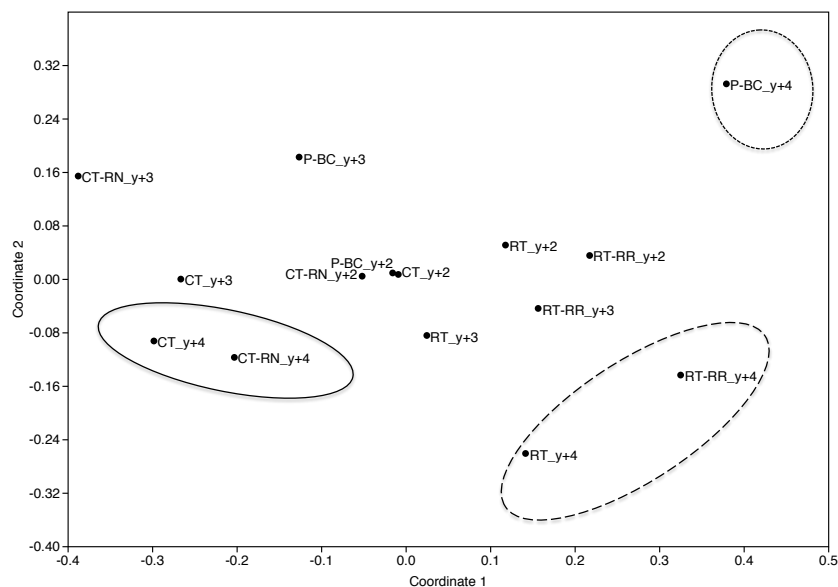


Figure 3-4 : Non-metric multidimensional scaling (NMDS) plot based on Bray-Curtis dissimilarity indices derived from abundance of collembolan species recorded in five different agricultural practices (North of France) across a 4-year period (y+2: 2012, y+3: 2013 and y+4: 2014). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal.

ANOSIM analyses showed significant differences in species composition after 3 and 4 years but not after 2 years (Tableau 3-4).

Tableau 3-4 : Results of ANOSIM analyses between collembolan assemblages within five different agricultural treatments (North of France) after 3 (y+3) and 4 years (y+4) following experimental set-up. CT: Conventional tillage; CT-RN: Conventional tillage and nitrogen reduced. P-BC: Perennial and Bioenergy Crop. RT: Reduced tillage; RT-RR: Reduced tillage and crop residues removal. P-value and R-values (within brackets) are given. For clarity, significant results are in bold.

	CT	CT-RN	RT	RT-RR	P-BC
y+3					
CT		0.42 (0.02)	0.12 (0.13)	<b>0.03 (0.29)</b>	0.17 (0.18)
CT-RN			<b>0.03 (0.55)</b>	<b>0.03 (0.61)</b>	0.15 (0.14)
RT				0.34 (0.02)	<b>0.03 (0.70)</b>
RT-RR					<b>0.02 (0.84)</b>
P-BC					
y+4					
CT		0.77 (0.14)	<b>0.03 (0.81)</b>	<b>0.03 (0.87)</b>	<b>0.03 (0.97)</b>
CT-RN			<b>0.02 (0.59)</b>	<b>0.03 (0.65)</b>	<b>0.03 (0.89)</b>
RT				<b>0.03 (0.50)</b>	<b>0.03 (0.99)</b>
RT-RR					<b>0.03 (0.84)</b>
P-BC					

After 3 years, composition differed in RT-RR from CT, CT-RN and P-BC, and the latter two differed from RT. This pattern was mainly due to the contribution of two species. *Parisotoma notabilis* dominated in CT and RT while *Protaphorura armata* was dominant in CT-RN and RT-RR (cf. Appendix B - Table B1). After 4 years, differences between assemblages were stronger, and only assemblages under conventional tillage (CT and CT-RN) did not differ from each other. A different set of species contributed to assemblages' dissimilarity. For instance, *Mesaphorura sp.* and *Sminthurinus elegans* mostly contributed to discriminate P-BC from treatments under conventional tillage. *Megalothorax minimus* differentiated RT, CT and CT-RN. Finally, *Parisotoma notabilis* and *Isotoma anglicana* participated to discriminate RT-RR from CT-RN, CT and RT (cf. Appendix B - Table B2).

### 3.3. Functional groups

After 2 years, only euedaphic density showed significant differences between treatments (Tableau 3-5), with twice as many individuals found in RT-RR than in CT and CT-RN (3214 and 1223 individuals m<sup>-2</sup>, respectively). The other treatments presented intermediate values (Figure 3-5).

After 3 years, the density of each of the three functional groups was significantly influenced by the treatments (Tableau 3-5). On average, epedaphic density was almost 38 times higher in RT and RT-RR (average values of 3217 individuals m<sup>-2</sup>) than in other treatments (average values of 85 individuals m<sup>-2</sup>). Similarly, hemiedaphic Collembola were approximately 3.8 times more abundant in RT and RT-RR (average values of 1655 individuals m<sup>-2</sup>) than in CT, CT-RN and P-BC (average values of 439 individuals m<sup>-2</sup>). Euedaphic density also ranged from minimum values in CT and CT-RN (average values of 638 individuals m<sup>-2</sup>) to a maximum in RT-RR (3400 individuals m<sup>-2</sup>). In parallel to the density, the number of epedaphic species in RT-RR was 5.5 times higher than in CT, CT-RN and P-BC. RT had an intermediate value. The number of euedaphic species in RT was 2.4 times greater than in CT-RN. The 3 other treatments had intermediate values (Figure 3-5).

After 4 years, both the density and species richness of each of the three functional groups were significantly influenced by experimental treatments (Tableau 3-5). On average, epedaphic density in RT-RR and P-BC were about 10 times higher than in CT (1677 vs. 170 individuals m<sup>-2</sup>), CT had the lower epedaphic species richness compared to all other treatments. Hemiedaphic density ranged from 700 to 3170 individuals m<sup>-2</sup> (average values of CT and CT-RN vs RT, RT-RR and P-BC), in parallel, the number of hemiedaphic species in RT-RR was

2.3 times higher than in CT and CT-RN. RT and P-BC exhibiting intermediate values. Finally, euedaphic density displayed the same pattern as the hemiedaphic with significantly more individuals and species in P-BC, RT and RT-RR than in CT and CT-RN (Figure 3-5).

Tableau 3-5 : Results of Linear Mixed-Effects Models (LMM) of the effect of the factor treatment on the density and species richness of the three functional groups after 2 (y+2), 3 (y+3) and 4 years (y+4). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Chisq: Chi-square value. p : p-value. R2: variance explained by both fixed and random factors. Degree of freedom = 4. The rejection level was set at  $\alpha = 0.05$ . \*\*\* $p < 0.001$ . \*\* $p < 0.01$ . \* $p < 0.05$ . ns  $p > 0.05$ .

LMM outputs			
	Chisq	p	R <sup>2</sup> (%)
<b>y+2</b>			
<b>Density</b>			
Epedaphic	3.66	ns	16.2
Hemiedaphic	8.56	ns	31.1
Euedaphic	20.0	***	53.7
<b>Species richness</b>			
Epedaphic	1.59	ns	7.72
Hemiedaphic	6.86	ns	26.5
Euedaphic	6.61	ns	36.4
<b>y+3</b>			
<b>Density</b>			
Epedaphic	21.0	***	52.5
Hemiedaphic	26.3	***	59.9
Euedaphic	15.2	**	46.1
<b>Species richness</b>			
Epedaphic	30.3	***	61.5
Hemiedaphic	8.87	ns	56.4
Euedaphic	11.3	*	44.4
<b>y+4</b>			
<b>Density</b>			
Epedaphic	19.8	***	51.0
Hemiedaphic	50.8	***	72.8
Euedaphic	44.5	***	74.4
<b>Species richness</b>			
Epedaphic	15.4	**	44.7
Hemiedaphic	17.4	**	47.7
Euedaphic	17.9	**	48.5

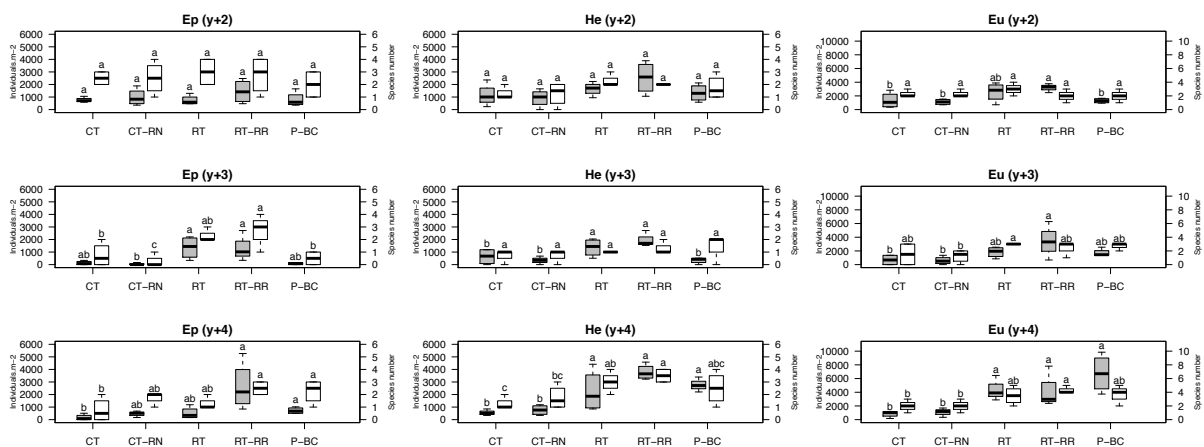


Figure 3-5: Density (grey boxplots) and species richness (white boxplots) of the three Collembola functional groups recorded in five different agricultural treatments across a 4-year period (y+2, y+3 and y+4). Ep: Epedaphic, He: Hemiedaphic, Eu: Euedaphic. CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Different letters within a single parameter denote significant differences between treatments at  $\alpha=0.05\%$  (Turkey's HSD).



### 3.4. Environmental parameters

From y+2 to y+4, microbial biomass (Cbiom) and activity of the microflora (CO<sub>2</sub>) significantly differed between treatments (Appendix B-Table B4), with maximum values in P-BC and minimum values in CT and CT-RN. Soil moisture (Hum) and pHwater showed significant differences only after 3 years. Lower soil moisture values were found in CT-RN compared to other treatments (CT exhibiting intermediate value) and at the same time, pH values were higher in CT-RN than in CT, the other treatments being intermediate. Soil temperature was significantly influenced by the treatments at y+2 and y+4, with always minimum values in P-BC. At y+3, one month prior to our sampling, the average soil temperature did not differ between the treatments and was of 3.78°C considering all treatments together.

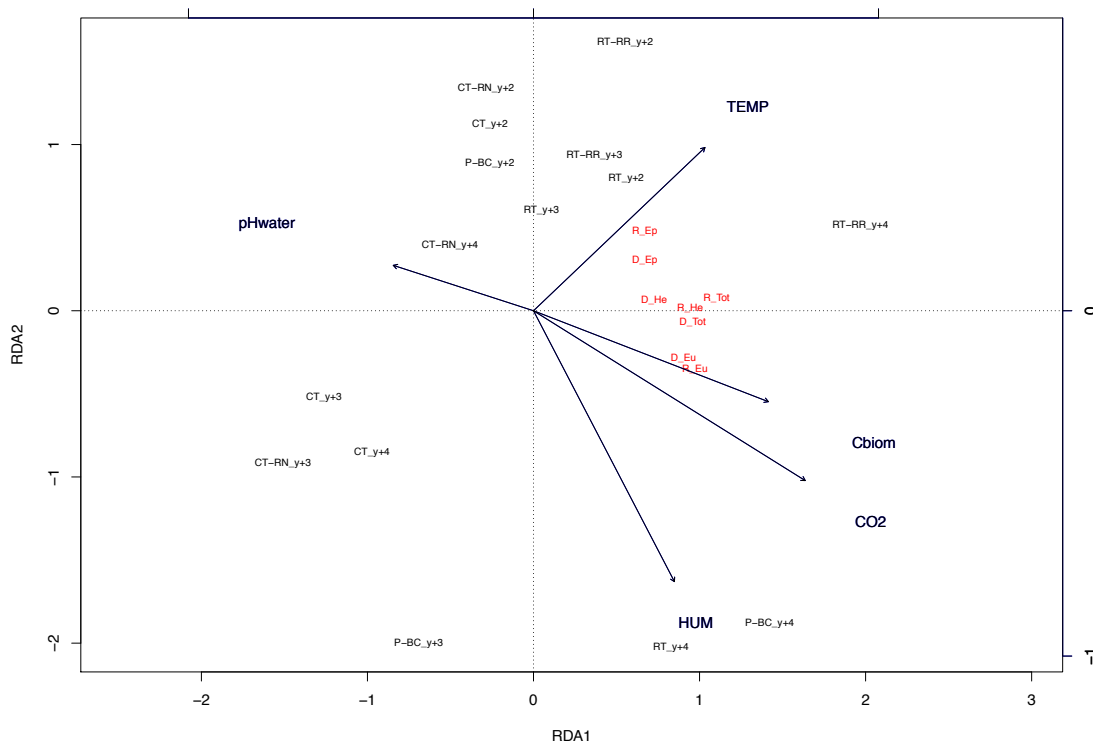


Figure 3-6 : Redundancy analysis (RDA) based on Total density of Collembola ( $D_{tot}$ ), total species richness ( $R_{tot}$ ), density and richness of each of the three life forms ( $D_{Ep}$ ,  $D_{He}$ ,  $D_{Eu}$ ,  $R_{Ep}$ ,  $R_{He}$ ,  $R_{Eu}$ ), microbial C biomass (Cbiom), microbial activity (CO<sub>2</sub>), soil moisture (HUM), soil temperature (TEMP) and soil pH (pHwater). All variables were measured in five different agricultural treatments (north of France) 2 to 4 years (y+2: 2012, y+3: 2013 and y+4: 2014) after experimental set-up. CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal.

The proportion of the total variance in the RDA (Figure 3-6), which is explained by all environmental parameters, is 67%. The first axis accounted for 60% of variance and the second only for a further 5%. Basically, treatments under conventional tillage were separated from the treatments under reduced tillage along the first axis, with the latter correlating to high values of

all collembolan parameters. Abundance and richness of euedaphic species were related to higher values of soil humidity (HUM), microbial C biomass (Cbiom) and microbial activity (CO<sub>2</sub>), while high values of abundance and richness of epedaphic Collembola were correlated to higher values of soil temperature (TEMP).

#### **4. Discussion**

We followed 5 different crop practices commonly used in Western Europe. Since all the studied plots were previously for at least 15 years managed under conventional tillage (CT), this offered us the opportunity to evaluate if shifting from CT towards less intensive management may produce changes in soil Collembola assemblages by minimizing disturbances due to soil tillage in particular. Furthermore, we could over a 4-year-period follow the differentiation of the Collembola assemblages within and between the treatments.

Overall, the mean density and species richness of soil Collembola found in our study (ranging from 168 to 14430 individuals m<sup>-2</sup> and from 1 to 11 species, respectively) are in the range of other European studies focusing on agricultural land (Bosch-Serra et al., 2014; Chauvat et al., 2014a; Petersen, 2002; Scheunemann et al., 2015a; van Capelle et al., 2012). Low values of abundance and species richness were noticeable after 3 years (y+3) in almost all treatments. This may be due to a severe winter in 2013 with soil (5cm depth) mean temperature, within the sampling site, during the month before sampling of around 3°C compared to average temperatures of 7 and 8°C in comparative period of 2012 and 2014, respectively. It is well known that among abiotic factors, temperature has a direct effect on activity, fecundity and mortality of collembolans (Christiansen, 1964; Eaton et al., 2004). Under field conditions, the correlation between collembolans and temperature is usually hard to establish or is only weakly confirmed. But for example, Wolters, (1998) and Bedano et al., (2006), found that Collembola density was negatively correlated with soil and/or air temperature.

##### **4.1. Soil mechanical disturbance**

Our results showed a general increase in collembolan density and species richness with reduction of tillage intensity which is in accordance with a number of previous studies (Brennan et al., 2006; Petersen, 2002; Wardle, 1995) and confirms our first hypothesis. But this is in contradiction to the findings of van Capelle et al., (2012), who recently in a meta-analysis on German data found no difference in abundance of Collembola between conventional tillage and reduced tillage and even a higher number of Collembola in convention tillage compared to no-tillage systems. However, they found this pattern to be strongly dependent of soil type. For

example, in silty soils, as in our study, they rather found reduced tillage to foster Collembola abundance (+47%) compared to conventional tillage. In our study, we recorded a much higher stimulation of Collembola individual numbers between CT and RT after 4 years (+400%). This agrees well with a general view that soil biota are usually inhibited by cultivation. In their meta-analysis, van Capelle et al., (2012) showed that total earthworm abundance, biomass, and species diversity were increased significantly in tillage systems with lower tillage intensity. Nakamoto et al., (2006) found the same results on the numbers of nematodes, but Didden et al., (1994) indicate that enchytraeids are unaffected by tillage due to their small body size and their great reproductive rates. Generally, larger organisms are more sensitive to tillage practices than smaller ones (Wardle, 1995). Within soil fauna, Collembola are considered to be a fast responsive group (r-strategist) to environmental changes (Butcher et al., 1971; Chauvat et al., 2003; Dunger, 1975; Kaczmarek, 1975; Klironomos and Kendrick, 1995; Ponge, 1983).

In our case, according to the NMDS and the RDA results (Figure 3-4 and Figure 3-6), tillage type (conventional vs. reduced) is the first factor driving the fate of collembolan assemblages in terms of species composition and relative abundance. Indeed we observed in y+4 a very clear separation between three clusters (Figure 3-4), each one with a different dominating species, one made of the two CT treatments dominated by *P. notabilis*, a second one made of the two RT treatments dominated by *M. minimus*, and the third one with the P-BC alone with *Mesaphorura sp.* *M. minimus* and *Mesaphorura sp.* are the main species contributing for composition dissimilarities between the treatments. Both species are rather small and live deep in the soil. Their respective abundance increased over time in reduced tillage (RT) or in perennial crop (P-BC or no tillage) treatments compared to the treatments under conventional tillage. Probably, reducing physical disturbance in deep soil layers alleviates constraints on them and allow population growth over time. They also may benefit from a more stable resource supply (fungal mycelium) in those treatments with a lower mechanical disturbance.

The dissimilarity in species composition between tillage conventional and reduced tillage treatments was not visible at a functional level. Surprisingly the proportion (relative abundance) of the three collembolan functional groups did not really differ between conventional (CT and CT-RN) and reduced tillage (RT and RT-RR) treatments after y+4 (see Appendix B-Table B3). This is partly in contradiction with the findings of Sabatini et al., (1997), but rather in accordance with the meta-analysis of van Capelle et al., (2012) concluding that all three functional groups were equally promoted under reduced tillage in silty soils.

#### 4.2. Management of crop residues and N fertilization

Contrary to our hypothesis, the other components of management, either "nitrogen input reduction" and " restitution/exportation of crop residues " did not favour soil living Collembola, either hemiedaphic or euedaphic.

For crop residues management, no difference in density or species richness was found between RT-RR and RT for both hemi- and euedaphic during the study (y+2 at y+4, Figure 3-5). However, relative abundance of euedaphic Collembola species in y+4 dropped by 22 points when removing the crop residues (i.e from RT to RT-RR, Appendix B-Table B3), but this was due to a single species, *M. minimus* with a relative abundance decreasing from 41.6% to 14.2% in RT and RT-RR, respectively (cf. Appendix B-Table B3). In a recent study, Scheunemann et al., (2015a) found that in arable soil, shoot residues only form an additional resource of minor importance to soil fauna compared to the predominant importance of root-derived resources, suggesting that removal of shoot residues should not strongly impact Collembola. On the other hand, the restitution of residues, specifically the superficially burying into the soil of residues using disk ploughing, causes an additional mechanical disturbance that may impact Collembola assemblages especially soil living species. Our results support this assertion with the relative abundance of three dominant soil living species, namely *P. notabilis*, *Mesaphorura sp.*, *P. armata*, that decreased in RT compared to RT-RR from y+3 to y+4 (see Appendix B-Table B3). Furthermore, Brennan et al., (2006) found the addition of crop residues to also decrease the abundance of two euedaphic Collembola species: *Mesaphorura krausbaueri*, *Supraphorura furcifera*, and one hemiedaphic species: *Friesea truncata*. They suggest that the presence of crop residues on the soil surface may lead to an increase in predatory arthropods, as found by Scheunemann (2015b) for Gamasid mites, and therefore a higher top-down regulation on soil Collembola. We believe that both mechanical disturbances linked to burying of crop residues and an increase in top-down regulation, counterbalance the well-known positive effect of beneficial resources provided by crop residues to decomposers (Cochran et al., 1994; Hall and Hedlund, 1999).

Also our results (Figure 3-5) showed that density and diversity parameters did not differ significantly between the perennial crop (P-BC with exportation of crop residues) and both reduced tillage treatments RT (with restitution of crop residues) and RT-RR (with exportation of crop residues). However, at the functional level, P-BC showed relative abundances of functional groups much more similar to those observed in RT than those in RT-RR, especially for epedaphic and euedaphic Collembola. Perennial habitats, even with exportation of residues

likely provide resources that are unavailable in annual crops between harvesting and planting, such as root turnover and exudation (Bianchi et al., 2006). Our RDA results support this assertion, by showing a correlation between euedaphic Collembola abundance and richness and microbial biomass (Cbiom). The positive effect of energy crops on the microbial biomass (Appendix B4-Table B4) may explain the marked increase of euedaphic species as they are known to be rather bottom-up controlled by trophic resources (Henneron et al., 2016; Schneider and Maraun, 2009).

For N fertilization, our results showed no impact of reducing N mineral input on both density and species richness of Collembola (CT vs. CT-RN, Please refer to Figure 3-2). Under field conditions, correlations between Collembola and total N are usually weak (Filser, 2002). But we could have anticipated a change in basal microbial groups following N reduction that would have scaled-up till Collembola. This is apparently not the case, since even microbial biomass (Cbiom) and activity of the microflora were low in these treatments (Appendix B-Table B4). Our results are comparable to those of Ngosong et al., (2009), who indicate that Collembola density was not influenced by N fertilisation rate. Villenave et al., (2010) found that mineral nitrogen fertilization had little impact on free-living nematodes and that only plant-feeding nematodes increased mostly with increased mineral fertilization, the other groups of nematodes showed no difference. Potter et al., (1985) indicated a highly significant linear decrease in earthworm density and biomass as annual rates of N fertilization increased. These authors found that mites were unaffected by N fertilization. While few studies have considered consequences of lowering N application on soil biota, current evidence indicates only a weak effect at a short-term at least.

### **4.3. Differentiation with time**

In our study, two years after the start of the experiment, surprisingly few differences were noticeable between the treatments. Keeping in mind that all plots were under conventional tillage prior to our experiment, it seems that at least two to three years were necessary for Collembola species to colonize plots that were converted into different management. As suggested by several authors (Auclerc et al., 2009; Ims et al., 2004), colonization rate may strongly depend on surrounding landscape. Differences in assemblages across treatments increased afterwards with time as we hypothesized. Finally, four years seemed not enough to obtain stabilized assemblages across the treatments, as differentiation between the treatments seems still on its way. It is highly probable looking at the results of the NMDS (Fig. 4) that collembolan assemblages will continue to diverge in the next years according to the different

treatments. Time seems, therefore, an important aspect when considering the response of Collembola to agricultural practices. Time may, together with the soil type (van Capelle et al., 2012) and the surrounding landscape (Auclerc et al., 2009; Ims et al., 2004) explained the discrepancies found in the literature about the response of Collembola to different tillage intensities. Focusing on ecomorphological groups allowed us to show that functional groups responded differently to the agricultural management, contributing unequally to the differentiation over time. For instance, the euedaphic species still increased after four years in the more conservative treatment (P-BC). Finally, we demonstrated that the species richness of epedaphic Collembola rapidly and strongly changed already after 2 years, which was not the case for euedaphic ones. This is in line with the better abilities of epedaphic species to disperse and colonize (Chauvat et al., 2014b).

## 5. Conclusion

This study over several years under field conditions showed that Collembola assemblages were more sensitive to tillage intensity than to either residue management or N fertilization. This demonstrates the impact of mechanical disturbance on the dynamics of collembolan assemblages. Differentiation of Collembola assemblages between cropping systems increased with time and may not reach a maximum even after 4 years. Thus, long-term studies are essential in assessing temporal responses of soil biota to cropping systems, especially according to the natural backdrop of temporal variation (Wardle et al., 1999). Finally, our functional approach showed complex responses of soil Collembola to agricultural practices and therefore pleads in favour of improving our knowledge of relationships between soil biota and functions performed.

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## Chapitre 4. Réduction et arrêt de la perturbation mécanique

### Présentation du chapitre

Les conclusions du précédent chapitre, nous ont permis de suivre sur une échelle spatiotemporelle plus réduite, 1 seul site, 1 saison de végétation, l'effet de la conversion du travail du sol sur le compartiment endogé. L'étude a été effectuée en partenariat avec INRA (Institut National de la Recherche Agronomique) d'Estrées-Mons (Picardie, France). Les paramètres biotiques et abiotiques présentés dans ce chapitre ont été analysés au sein du laboratoire « Ecodiv ». Seules les données climatiques ont été fournies par l'INRA.

L'étude a fait sortir que :

- L'arrêt du travail du sol a entraîné une augmentation générale de la taille des populations de vers de terre et de collemboles
- Les différences entre les trois niveaux de travail du sol sont principalement attribuables à la date d'échantillonnage.
- À court terme, les collemboles résistent mieux à la perturbation mécanique du sol que les vers de terre.



## **Short-term dynamic of soil properties and soil fauna under contrasting tillage systems**

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### **1. Introduction**

Human activities, among them, land use and soil management are major drivers exerting pressures on soils and ecosystem services they provide (Smith et al., 2016). In agrosystems, although conventional tillage (CT) is an effective practice in repressing annual weeds and facilitating precise seeding (Ehlers and Claupein, 1994); its application is often accompanied by the destruction of the habitat of edaphic organisms, thereby eliminating natural homeostatic mechanisms and preventing agro-ecosystem self-regulation (Altieri, 1991; Holland, 2004; Six et al., 2000; Tsiafouli et al., 2015). Thus, a main goal in soil research is to rethink agroecosystems to achieve sustainable and profitable methods that improve livelihoods of farmers and the best possible utilization of naturally occurring soil processes (DeLong et al., 2015b; Petersen, 2002; Tittonell, 2014; Wezel et al., 2014). To do so, it has been suggested that agrosystems should imitate natural ecosystems (Jackson, 1980; Scherr and McNeely, 2007), through the application of three fundamental principles of Conservation Agriculture (CA): "minimal mechanical soil disturbance, permanent soil cover and crop rotations" (Brouder and Gomez-Macpherson, 2014; ECAF, 2001; FAO, 2010; García-Torres et al., 2013; Hobbs, 2007; Knowler and Bradshaw, 2007; Valbuena et al., 2012). Indeed, the main goal of CA, ranges from reducing the ploughing depth (reduced or superficial tillage, RT) while retaining crop residues on or near the soil surface, to direct seeding without any soil tillage (no-till, NT), whose the only soil disturbance being caused by seeding and during harvest (Kassam et al., 2009).

Furthermore, conversion from CT to RT and/or NT was considered to be one of the potentially efficient strategies, especially in terms of reduction of tillage time, leading to reduced carbon emissions due to savings in machinery and energy use (Lahmar, 2010), favouring biological nitrogen fixation (Huggins and Reganold, 2008), raising and stabilizing yields (Kassam et al., 2010) and lowering production costs (Lahmar, 2010). In addition, previous studies highlighted that the adoption of CA especially NT, allowed a rate of C sequestration of 100–1000 kg ha<sup>-1</sup> per year (Lal, 2004), which could protect soils from erosion and compaction (Holland, 2004; Lahmar, 2010) and improve soil porosity, temperature and humidity while causing minimum damage to edaphic fauna (Derpsch et al., 2010a; Hobbs, 2007; Stewart, 2007). As soil biota and the processes they drive have large direct and indirect effects on crop growth, soil- and residue-born pests, nutrient cycling and water transfer, the conservation of their diversity has become a key component of a strategy towards agricultural sustainability (Swift et al., 2004). To develop cropping practices that ensure an optimal use and protection of soil biodiversity, allows to predict the impacts of tillage systems on organisms and to understand the links between ecosystem processes and services (Brussaard et al., 2007; Roger-Estrade et al., 2010). The principal differences between tillage systems involve the depth of tillage (as just described), frequency of the tillage operations (per annum or per seasons) and manipulation of weed levels (Wardle, 1995). Accordingly, properties and habitat conditions in soil, which partly drive biodiversity below ground, differ as well. Abundance, diversity and activity of soil biota, in this context, are hypothesized to be mainly affected by distribution of organic matter as basic food source, soil structure and pore size distribution as available living and moving space, air and water movement as environmental milieu, and indirectly via changed interactions within the soil food web (Wardle, 1995). The adoption of less intensive soil cultivation practices is expected to increase soil biota and their contributions to ecosystem functioning (Briones and Schmidt, 2017; van Capelle et al., 2012).

However, the adoption of more sustainable managed systems does not always result in an increase in soil fauna abundance and diversity (Berner et al., 2008; Chan, 2001; van Capelle et al., 2012). This conflicting picture might be the result of failing to examine the effects of tillage intensity under a broader scheme including the levels of tillage. But also, the lack of study during a growing season, since the number (secondary tillage/surface tillage after mouldboard tillage) and frequency of the tillage operations (per annum or per seasons) are also known to influence soil organisms (Capowiez et al., 2009; Ivask et al., 2007) as well as variations of climatic factors (e.g. temperature, rainfall) during a vegetative season (Bertrand et al., 2015;

Chan, 2001). Furthermore, some studies on the impact of tillage on soil processes have shown that the different parameters such as soil fauna, dynamic of soil organic matter (SOM), soil structure respond differently to the tillage system from the time of till to crop growth (Bedano et al., 2006; Petersen, 2002). This approach could plead in favour of improving our knowledge of relationships between soil biota and functions performed.

In the present study, we monitored earthworms and Collembola assemblages over a growing season in response to different practices varying in tillage intensity (CT, RT and NT) on a field that has been under CT for at least 15 years. Earthworms and Collembola, with different life-cycles, are the most abundant groups of macro and mesofauna, respectively, in agricultural systems (Chauvat et al., 2014a; van Capelle et al., 2012). They are obviously important for the fertility of agricultural soils through mainly soil structuring, the transformation of organic matter and the recycling of nutrients by the regulation of microbial communities (Filser, 2002; Hopkin, 1997; Kaneda and Kaneko, 2008; Lee, 1985; Petersen, 2000; Seastedt, 1984). Our main objective was to study dynamic of these two groups of soil organisms and their interactions with some soil physico-chemical (pH water, bulk density, aggregates size and soil organic carbon stock) and microbial properties (microbial and fungal biomass and their potential C mineralizing activity) when shifting from conventional tillage towards less intensive management (reduced-tillage and no-tillage). We hypothesized that (1a) the reduction and especially the stopping of the mechanical perturbation lead overall to an increase in the density, the specific richness and the diversity of Collembola and earthworms; (1b) earthworms will be favoured by the improvement of the physical structure of the soil; whereas Collembola will be oriented by access to food resources. (2a) Differences between tillage systems are dependent on the sampling date due to the role of external driving factors like climate or vegetation growing; (2b) Collembola and earthworms communities become more resilient before harvest in each of the three tillage levels.

## 2. Materials and Methods

### 2.1. Site description

We used a field set-up held on the INRA experimental station of Estrées-Mons (North of France). Soil is a “LUVISOL typique” according to the “Référentiel pédologique 2008” (Baize and Girard, 2009) and is equivalent to LUVISOL in the World Reference Base (FAO, 2006). Initial soil physico-chemical parameters measured on the depth of 0-20 cm indicate: clay =  $187 \pm 31 \text{ g.kg}^{-1}$ , silt =  $744 \pm 34 \text{ g.kg}^{-1}$ , sand =  $69 \pm 21 \text{ g.kg}^{-1}$ , pH in water =  $8.20 \pm 0.10$ , organic C

=  $10.40 \pm 0.80 \text{ g.kg}^{-1}$ , and total N =  $1.04 \pm 0.05 \text{ g.kg}^{-1}$ . Climate is temperate with an annual average rainfall of 678 mm and an average annual temperature of  $10.8 \text{ }^{\circ}\text{C}$ .

The experiment was established on an area of 100 by 12 m, which was under conventional tillage (mouldboard ploughing, depth = 25cm) with crop rotation for several decades. In spring 2014, instead of a single conventional tillage on this plot, we introduced three levels of tillage: conventional tillage (CT) with the soil inverted up to 25 cm depth by mouldboard ploughing, reduced tillage (RT) - i.e. shallow tillage - limited to the first 8 cm of soil depth using disk ploughing and no-tillage (NT) without any mechanical disturbance. Each system (level) was replicated 4 times randomly (12 sub-plots in total, each sub-plot is 9 m long and 6 m wide, Figure 4-1). The sub-plots were separated by 6 m wide buffer strips (Figure 4-1). During the experiment, two tillage operations were performed on the sub-plots CT and RT one at the end of March after the winter and one in mid-May corresponding to the surface disturbance (seedbed of maize; *Zea mays*, L.). The seedbed establishment corresponds to a reduced tillage. NT was sown manually without any soil mechanical preparation. Glyphosate was applied to all sub-plots (NT including) just prior to sowing (3 days before the seed beds) to remove weeds. Standard sensors were used to continuously monitor rainfall and soil temperature over the study period (Figure 4-2).

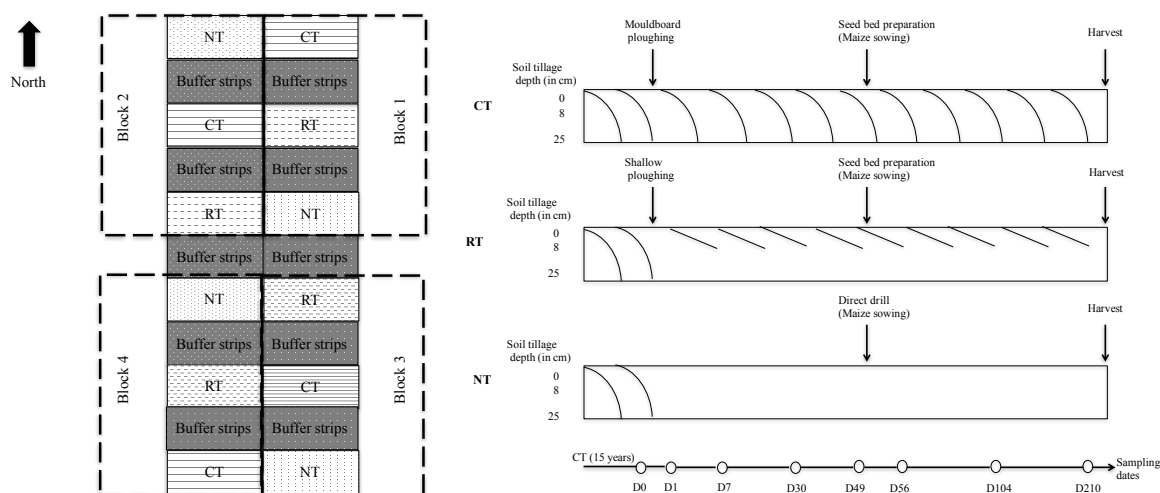


Figure 4-1: Design of the experiment set-up and samplings schedule. 12 sub-plots in total, each sub-plot is 9 m long and 6 m wide; CT = Conventional Tillage, RT = Reduced Tillage, NT = No Tillage. Samplings: 0: 1 day before Tillage, 1: 1 day after Tillage (aT), 2: 7 days aT, 3: 30 days aT, 4: 49 days aT, 5: 56 days aT, 6: 104 days aT, 7: 210 days aT.

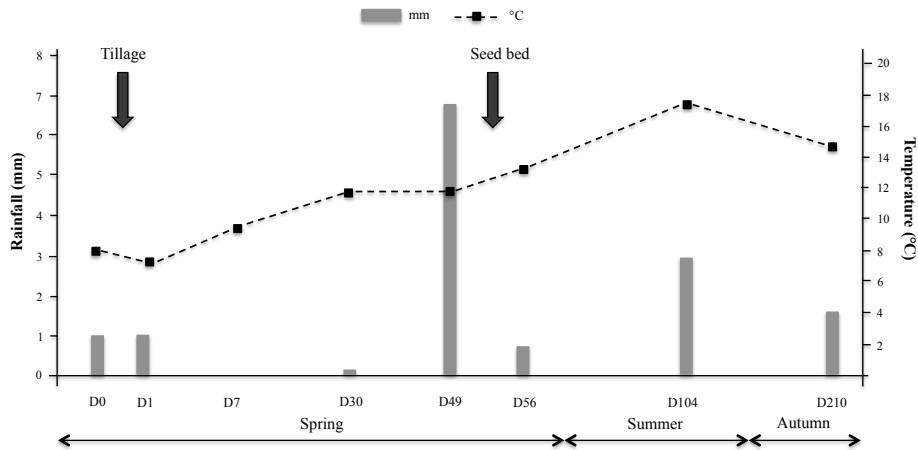


Figure 4-2 : Ombrothermic diagram of Cumulative mean temperature and total rainfall values on 7 days before each sampling date on the experimental site, SOERE ACBB, Estrées-Mons, Picardie, France. D0 is the start of the experiment (la date) and D210 (Date) is the end of the experiment 210 days after D0.

## 2.2. Soil fauna samplings, extraction and identification

Samplings were performed on a regular basis according to the first tillage operation: 1 day before, and respectively 1, 7, 30, 49, 56, 104 ; 210 days after (Figure 1).

### 2.2.1. Collembola

For each of the twelve (12) plots and each sampling date, two soil samples were collected by means of soil corers (diameter: 5 cm). A single core included the organic layer and the top 10 cm of the mineral horizon. In the laboratory, Collembola were extracted during two weeks using the Berlese-Tullgren device (Tullgren, 1918), that creates a temperature gradient over soil cores, crumbled into a plastic sieve with 2 mm suspended over a collecting vessel containing 70% alcohol. Individuals (Collembola) collected in alcohol were counted and identified following identification keys (Gisin, 1960; Hopkin, 2007). However, some individuals were identified to genera when species identification was not possible.

### 2.2.2. Earthworms

One 25 cm × 25 cm × 25 cm monolith was hand sorted for earth- worms in each plot and for each sampling date. Specimens were fixed in pure alcohol and categorized as juveniles (acitellates) and adults (clitellates). Adults were identified to species level according to Sims and Gerard (1999). Juveniles were therefore not taken into account for the estimation of species number but only when calculating total earthworm density. Densities were expressed individuals m<sup>-2</sup>.

### 2.3. Soil physico-chemical properties

As for fauna, soil samplings were performed on a regular basis according to the first tillage operation: 1 day before, and respectively 1, 7, 30, 49, 56, 104; 210 days after (Figure 1). Soil pHwater was measured with soil (sieved at 2 mm) diluted with demineralized water (NF ISO 10390). Bulk density (BD) was determined by taking two undisturbed soil cores from each sub-plot from 0- to 5-; 5- to 10; 10- to 20-; 20- to 30-cm depths. We took the cores by using a metal cylinder 100 cm<sup>3</sup>. The cylinders were sealed and transported to the laboratory. Thereafter, the collected soil sample weighed, and then dried at 105°C until the weight of the soil remained constant, a period of approximately 24 h. BD is equal to the dry mass of soil (g) contained in the metal cylinder divided by the volume of the cylinder (cm<sup>3</sup>) (Guo and Gifford, 2002). BD is expressed in g cm<sup>-3</sup>, which is numerically equal to BD expressed in SI unit Mg m<sup>-3</sup>.

Total Carbon (TC) was measured from dry samples and crush by gas chromatography with Thermo scientific Flash 2000 CHN S / O analyzer. We then measured the Soil Organic Carbon (SOC) by making the correction of the TC by the mineral carbon (CaCO<sub>3</sub>). Subsequently; we were able to calculate SOC stocks according to the following formula (Mann 1986): SOC stock (kgC.m<sup>-2</sup>) = SOC (kgC.kg of soil) x BD (kg of soil.m<sup>-3</sup>) x D (m); where D is soil sampling depth. The SOC stock was measured on the depth of 0- to 0.05-m.

For the size distribution of aggregates, we have collected a soil monolith of 8 cm minimum in each sub-plot. The collected monoliths (10 cm depth) were transported and stored in plastic boxes (Labovida; width = 17cm, height = 10 cm) closed and handled carefully to avoid destroying the soil structure. In the laboratory, the samples were passed through an 8 mm mesh and dried in ambient air for one week. Subsequently, we used a dry sieving method according to Robertson et al. (1999). This consists of taking 50 g of dry soil pre-sieved to 8 mm and placing in an automatic sieving machine RETSCH AS 200 digit comprising various sieve sizes (5 mm, 2 mm, 0.250 mm, 0.05 mm and a bottom of sieve). For each sample, the machine was calibrated in continuous vibration with amplitude of 2 mm and duration of 5 min. We then recovered five aggregates fractions of different sizes, namely aggregates greater than 5 mm, those between 5 and 2 mm, 2 and 0.25 mm, 0.25 and 0.05 mm, and clays and silt less than 0.05 mm. All fractions were dried in an oven at 60 ° C. for 24 h and their weights were noted thereafter. At the same time, we measured the residual moisture by taking 10 g of the starting soil (8 mm) and we passed it in an oven at 105 ° C. for 24 hours. We calculated the size of the Macro-Aggregates (MAG) by summing the aggregates > 0.250 mm (see appendix C). Finally,

Mean Weight Diameter (MWD) was calculated from the size distribution (Van Bavel, 1950).  
 $(MWD = \sum (\varnothing \text{ mean between 2 sieves} \times [\% \text{ weight of particles retained on sieve}]) / 100.$

#### **2.4. Microbial and fungal biomass and potential C mineralization**

At each of the 12 sampling points for each date, two comparative soil cores were taken to a depth of 10 cm and then pooled to obtain one sample per plot. Soil samples were placed in plastic containers, stored in cool boxes at 4 °C and transported to the laboratory for microbial analyses. In the laboratory, soil samples were sieved at 2mm.

The microbial biomass carbon (MBC) was estimated by chloroform fumigation-extraction technique (Jenkinson and Powlson, 1976). Before and after fumigation, 20 g of soil was shaken for 1 h in a solution of K<sub>2</sub>SO<sub>4</sub> at 0.05M then filtered at 0.45 µg and analysed for dissolved organic C on Shimatzu-TOC-5050A.

Ergosterol concentration, used as a proxy for fungal biomass, was determined according to the method of Gong et al. (2001). Briefly, 4 g of moist soil was added to a vial (20 ml) containing 4 g of acid washed glass beads and 6 ml of methanol. The vial was stirred on an orbital shaker for 1h at 320 rpm. After shaking, the soil mixture was allowed to sediment for 15 min. An aliquot of 1.5 ml of supernatant was centrifuged for 10 min at 11000 rpm at 5°C. The supernatant was filtered (0.2 µm) and injected for the HPLC analysis, using UV detection at 282 nm.

Potential C mineralization was recorded by incubation of 50 g of soil under controlled conditions (28°C and 80% of field capacity-WHC) for a 7 days period in hermetic pots. CO<sub>2</sub> released was captured by NaOH (0.2 M) and measured by conductivity meter. CO<sub>2</sub> was used as a proxy of soil heterotrophic microbial activity. The results will be expressed in mg C-CO<sub>2</sub> kg<sup>-1</sup> d<sup>-1</sup>.

#### **2.5. Statistical analysis**

Firstly, statistical analyses focused on the data collected for each date separately (D0 to D210), in order to compare the experimental treatments over time (treatment effect). Secondly, we performed analyses to quantify changes between sampling dates for a single treatment (sampling day effect). To investigate the effect of tillage practices on soil fauna, soil abiotic and microbial parameters, we used Linear Mixed-Effects Models (LMM) with the descriptive variables of Collembola and earthworms (total density, total species richness, diversity index), or environmental parameters as response and the factor “treatments” (CT, RT and NT) as fixed

categorical predictor, the factor “experimental blocks” (B1, B2, B3 and B4) as random categorical predictor. Significant differences between means were tested at a 5% rejection probability level using the Tukey HSD test. Normality and variance homogeneity were tested prior to statistical analyses.

We finally performed a Redundancy Analysis (RDA) to visualize relationships between soil fauna community variables (total density and species richness of Collembola and earthworms) as response matrix (Y) and abiotic and microbial variables as explanatory matrix (X). RDA (Legendre and Legendre, 2012; Rao, 1964) is an extension of multiple regressions that allows one to explain (in the same sense as in regression analysis) the variation of a multivariate response data table using explanatory variables. A linear function of time allowed us to model the variation in soil fauna community among sampling dates in circle of correlation. We have thus analysed separately the three treatments, to see the individual effect of system. RDA were computed on log-transformed data,  $y' = \log(y+1)$ .

The calculations were performed in the R language (Team, n.d.) with the libraries ade4 (Dray and Dufour, 2007), lme4 (Bates et al., 2014), MuMIn (Bartoń, 2013), multcomp (Hothorn et al., 2008), car (Fox and Weisberg, 2010) and vegan (Oksanen et al., 2013). Redundancy analyses were computed with the rdaTest package available on <http://adn.biol.umontreal.ca/~numerica/ecology/Rcode>.

### 3. Results

#### 3.1. Soil fauna

*Tableau 4-1: Results of Linear Mixed-Effects Models (LMM) of “the effect of treatment for each sampling date” and “the effect of sampling day for each treatment” on total density, species richness and Shannon index of Collembola and earthworm. D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage. CT: Conventional tillage, RT: Reduced tillage and NT: No tillage. The tests values are given. F: F-value, p: p-value, R2: variance explained by both fixed and random factors. The rejection level was set at  $\alpha = 0.05$ . \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns  $p > 0.05$ . The location of the significant differences is in Figure 4-3, Figure 4-4, Figure 4-5, Figure 4-6, Figure 4-7 and Figure 4-8.*

	Tillage effect																	
	Collembola						Earthworm						Earthworm					
	Density			Species richness			Shannon index			Density			Species richness			Shannon index		
	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)
D0	0.04	ns	26.8	0.27	ns	24.8	0.39	ns	0.66	0.12	ns	12.2	0.14	ns	2.42	0.16	ns	2.85
D1	2.51	ns	31.4	1.10	ns	16.7	0.65	ns	27.1	5.29	*	49.0	8.6	*	61.0	14.1	**	71.9
D7	4.78	ns	50.2	1.53	ns	47.9	1.09	ns	26.3	123	***	95.7	36.7	***	86.7	15.1	**	73.2
D30	2.34	ns	33.0	3.89	ns	54.5	3.84	ns	62.5	32.4	***	85.5	9.00	*	62.1	8.59	*	62.1
D49	6.59	*	54.5	3.89	ns	54.5	4.34	ns	67.7	22.5	**	80.4	19.5	**	78.6	17.4	**	77.7
D56	25.9	***	82.5	34.2	***	86.5	13.8	**	73.6	18.4	**	77.0	14.33	**	76.6	6.95	*	62.8
D104	6.32	*	55.9	6.77	*	55.2	10.3	**	65.2	39.8	**	87.8	4.20	ns	63.8	2.08	ns	60.7
D210	1.73	ns	24.0	0.65	ns	10.6	0.79	ns	12.6	55.1	***	91.3	4.50	ns	48.5	3.99	ns	43.3
	Sampling day effect																	
	Collembola						Earthworm						Earthworm					
	Density			Species richness			Shannon index			Density			Species richness			Shannon index		
	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)
CT	11.7	***	72.5	4.40	***	49.8	3.12	*	41.3	33.4	***	89.0	17.8	***	80.7	9.82	***	68.9
RT	7.34	***	62.4	4.07	**	55.1	2.48	*	51.9	38.0	***	89.6	18.1	***	80.4	8.51	***	65.8
NT	2.77	*	45.8	2.47	*	37.4	1.84	*	35.5	22.4	***	84.0	19.6	***	81.7	13.4	***	75.9



### 3.1.1. Collembola

Total density, total species richness and Shannon index (community indices) of Collembola varied significantly over time in each of the three experimental treatments (sampling day effect, Tableau 4-1). In CT, these community indices have higher values before tillage (D0), D30 and D210 and lower values at D56 (seed bed) and D104 (germination). All community indices of Collembola in RT treatment showed higher values at D0; D30; D49 than other sampling days; D210 exhibiting intermediate values. For NT treatment, lowest values were found at D7 and D104 (total density) and only at D104 (total species richness and Shannon index; (Figure 4-3, Figure 4-4 and Figure 4-5).

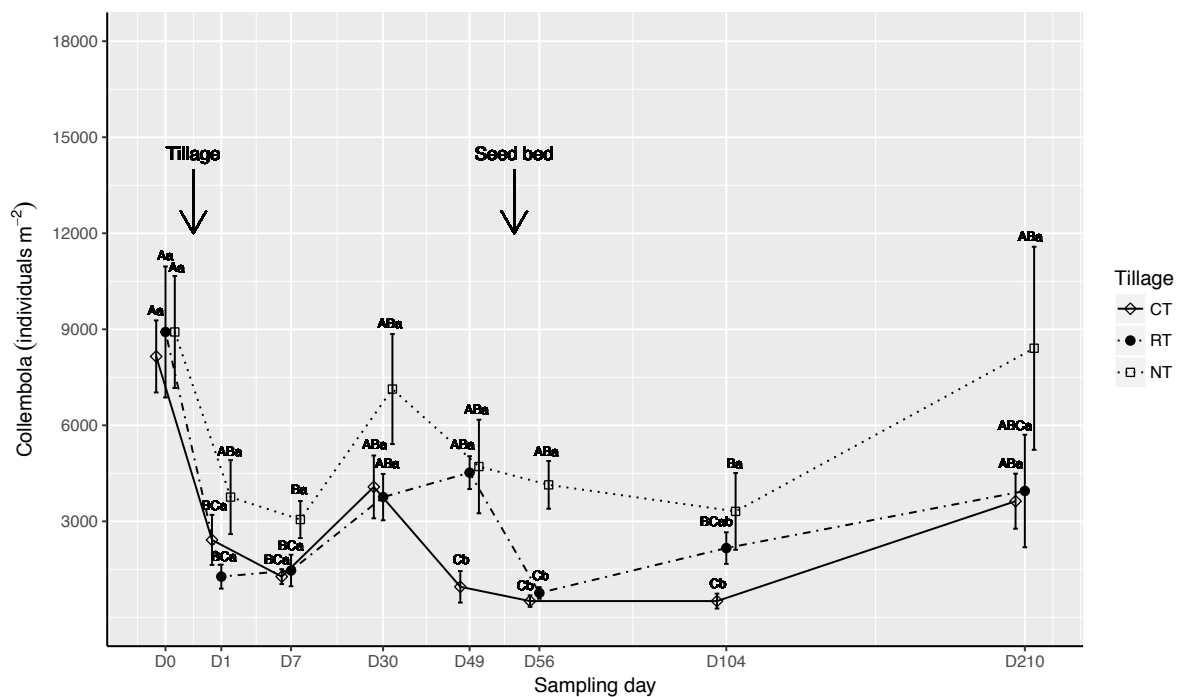


Figure 4-3 : Total density of Collembola assemblages (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment.

Total density was highest in NT, but differences with the other treatments were statistically significant only on specific sampling times such as D49, D56, D104 (treatment effect, Tableau 4-1). At D49, on average, 4-fold more individuals were collected in NT and RT than in CT (4618 and 955 individuals m<sup>-2</sup>; Figure 4-3). After seedbed (D56), the total density was about 6-fold higher in NT compared CT and RT (4140 and 637 individuals m<sup>-2</sup>; Figure 4-3). At D104,

total density ranged from ca 510 to 3312 individuals  $m^{-2}$  (in CT and NT, respectively), RT showed intermediate values (Figure 4-3).

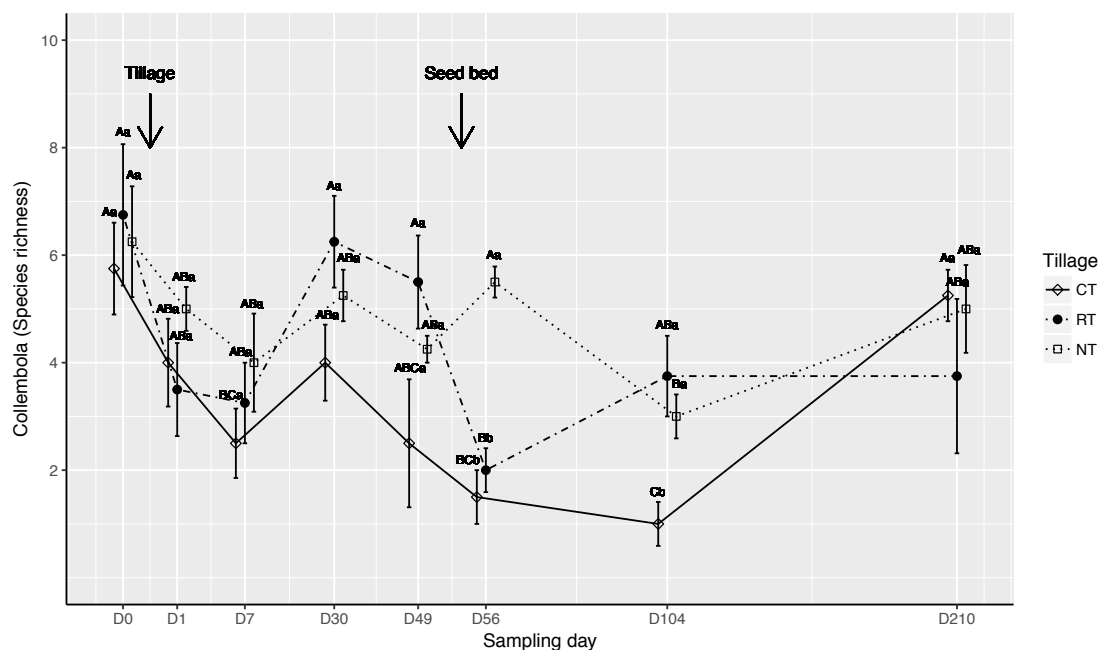


Figure 4-4 : Total species richness of Collembola assemblages (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment.

Total species richness and Shannon index displayed the same pattern, but only D56 and D104 showed significant differences (treatment effect, Tableau 4-1). At D56, just after seedbed, the Collembola species richness and Shannon index were significantly higher in NT compared to CT and RT. At D104, a different pattern was observed with significantly higher species richness and Shannon index in RT and NT than in CT (Figure 4-4 and Figure 4-5).

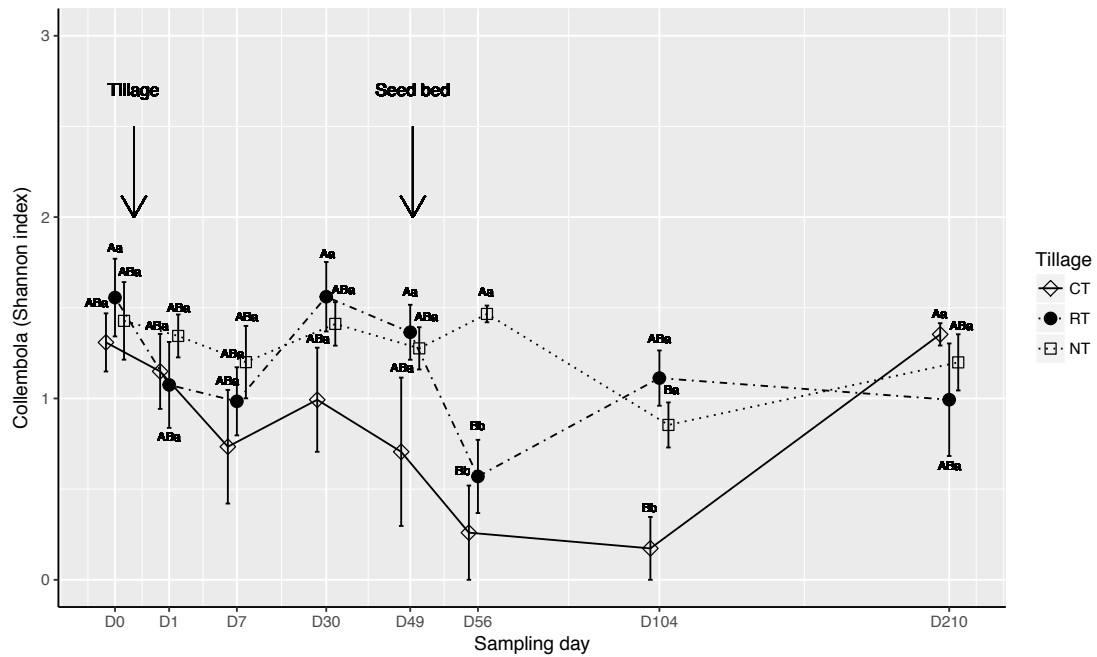


Figure 4-5 : Shannon index of Collembola assemblages (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment.

### 3.1.2. Earthworms

The factor “time” significantly impacted all community indices (total density, total species richness and Shannon index) of Earthworms in each of the three treatments (sampling day effect, Tableau 4-1). For CT and RT, only D0 showed higher values total density. The values decreased progressively over time, with lower values observed at D56 in CT and D210 in RT (Figure 4-6). Total species richness and Shannon index displayed the same pattern, being significantly lower at D49 and D56 in CT and D56 and D210 in RT (Figure 4-7 and Figure 4-8). For NT, total density was higher at D0 and D7, lower values recorded from D56 to D210 (Fig.6). Total species richness and Shannon index in NT showed higher values at D0; D1 and D7; and after decreased progressively over time, with lower values observed at D210 (Figure 4-7 and Figure 4-8).

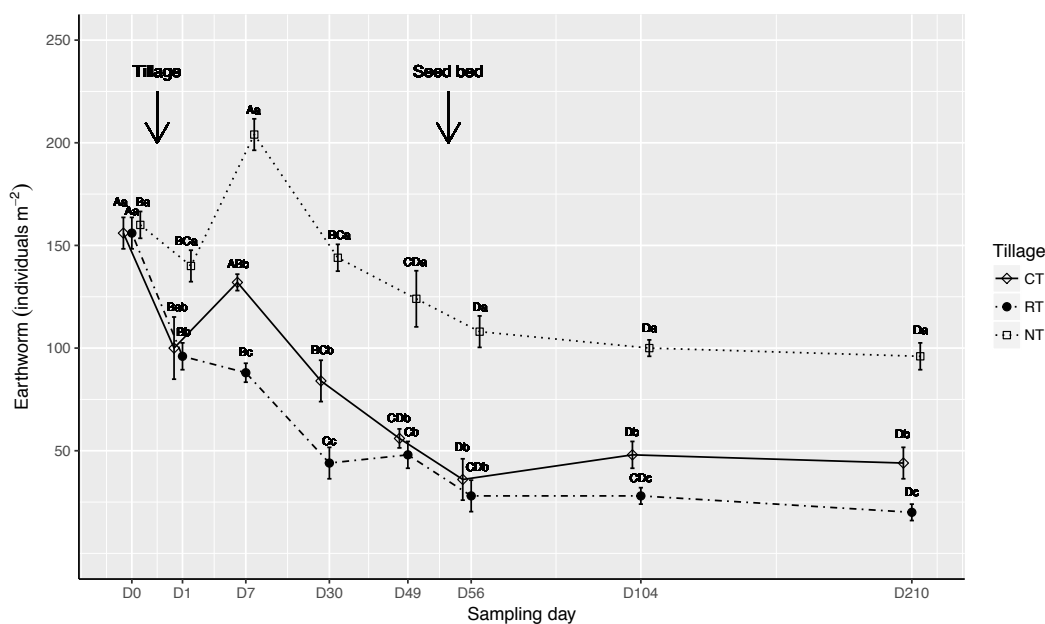


Figure 4-6 : Total density of earthworm (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment.

The total density of earthworms differed significantly between treatments at all sampling dates after tillage (from D1 to D210, treatment effect, Tableau 4-1). During the study, the highest densities of earthworms were recorded in NT treatment compared to CT and RT (Figure 4-6). Also, we note that the density was significantly lower in RT than in CT on some dates such as D7 (88 vs. 132 individuals m<sup>-2</sup>); D30 (44 vs. 84 individuals m<sup>-2</sup>); D104 (28 vs. 48 individuals m<sup>-2</sup>) and D210 (20 vs. 44 individuals m<sup>-2</sup>). The total species richness and Shannon index of earthworms was influenced by experimental treatments from D1 till D56 (Tableau 4-1), with higher values in NT compared to CT and RT (Figure 4-7 and Figure 4-8).

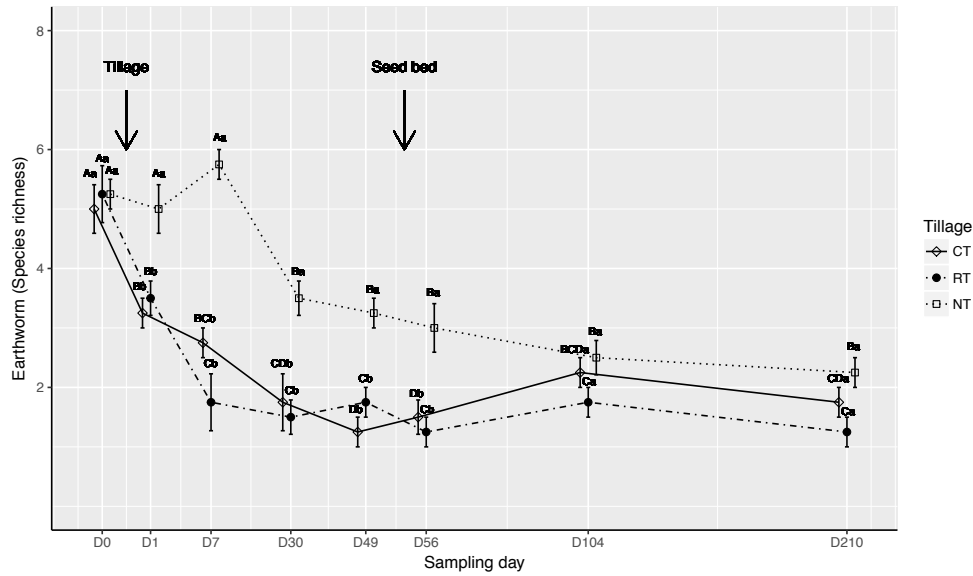


Figure 4-7 : Total species richness of earthworm (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment.

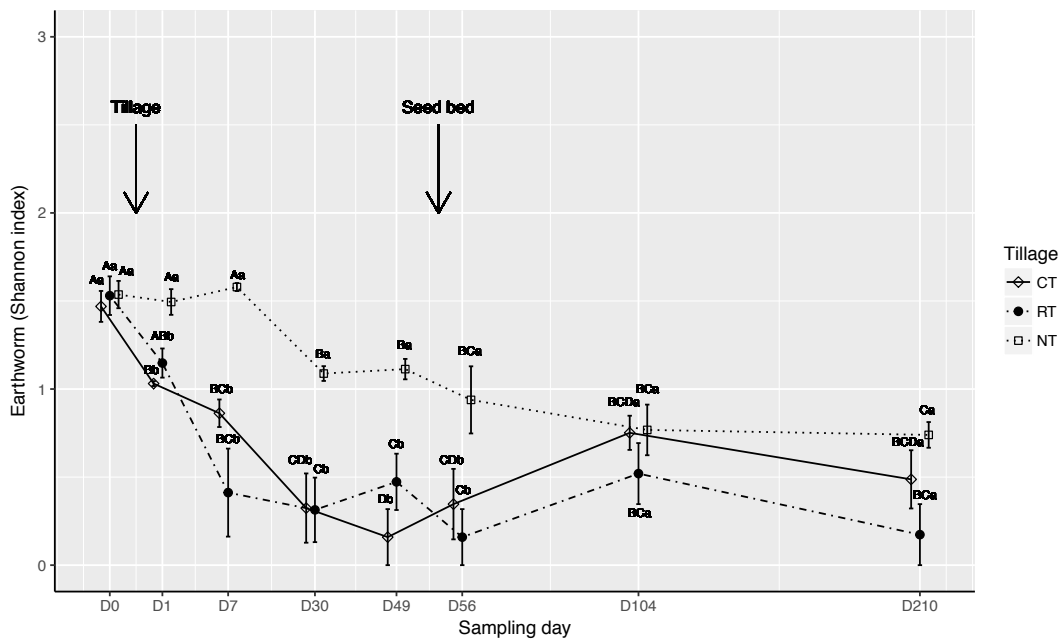


Figure 4-8 : Shannon index of earthworm (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment.

## 3.2. Soil physico-chemical properties

### 3.2.1. pH water

Soil pH water values neither differed over time nor between treatments (Tableau 4-3). They ranged between 7.9 and 8.2.

### 3.2.2. Bulk density (depth = 0 – 0.05 m)

Soil bulk density did not differ with time in NT treatment, but did significantly in CT and RT treatments (sampling day effect, Tableau 4-2).

*Tableau 4-2 : Results of Linear Mixed-Effects Models (LMM) of “the effect of treatment for each sampling date” and “the effect of sampling day for each treatment” on bulk density (0- to 5-cm) and SOC stock (0- to 0.05-m). D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage. CT: Conventional tillage, RT: Reduced tillage and NT: No tillage. The tests values are given. F: F-value, p: p-value, R<sup>2</sup>: variance explained by both fixed and random factors. The rejection level was set at  $\alpha = 0.05$ . \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns  $p > 0.05$ . The location of the significant differences is in Figure 4-9 and Figure 4-10.*

	Tillage effect					
	Bulk density			Stock C		
	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)
D0	0.13	ns	5.93	0.25	ns	5.37
D1	107	***	95.1	3.95	ns	41.8
D7	53.0	***	90.6	18.0	**	76.6
D30	70.6	***	92.8	15.2	**	73.4
D49	25.3	**	82.1	12.6	**	71.7
D56	17.4	**	76.8	14.2	**	72.1
D104	8.45	*	60.8	11.7	**	68.8
D210	0.86	ns	50.1	3.36	ns	41.6
	Sampling day effect					
	Bulk density			Stock C		
	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)
CT	13.5	***	75.3	11.7	***	76.4
RT	22.0	***	83.2	6.02	***	60.8
NT	0.64	ns	12.6	0.67	ns	55.1

The maximum and minimum values of CT were recorded in D1 and D49; and D0 and D56 for RT treatment. This parameter differed significantly between treatments at all sampling dates except for D0 and D210. NT had the highest values except for D1 where the maximum value was recorded in CT (treatment effect, Tableau 4-2, Figure 4-9).

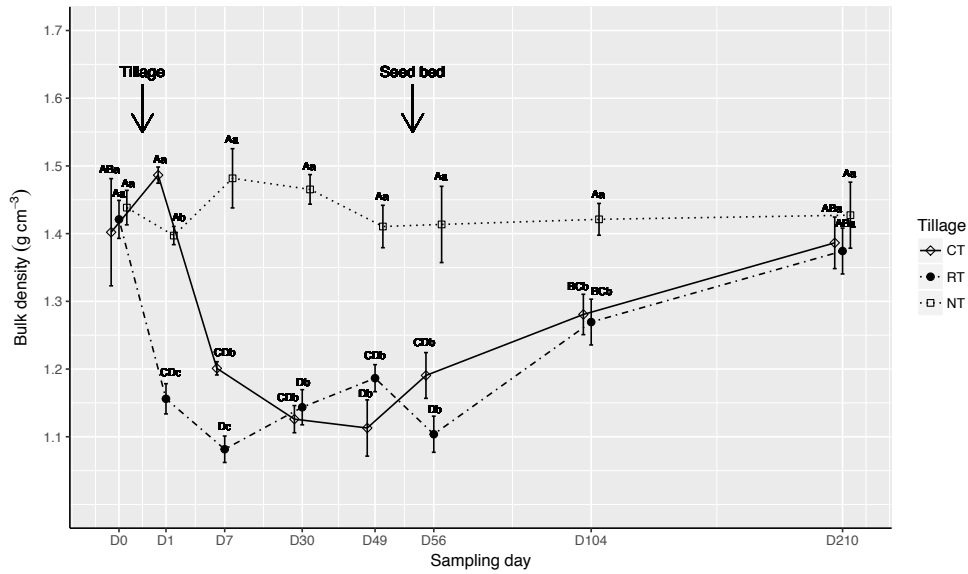


Figure 4-9 : Soil bulk density on 0-5 cm in depth (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment.

### 3.2.3. SOC stocks (depth = 0 - to 0.05 - m)

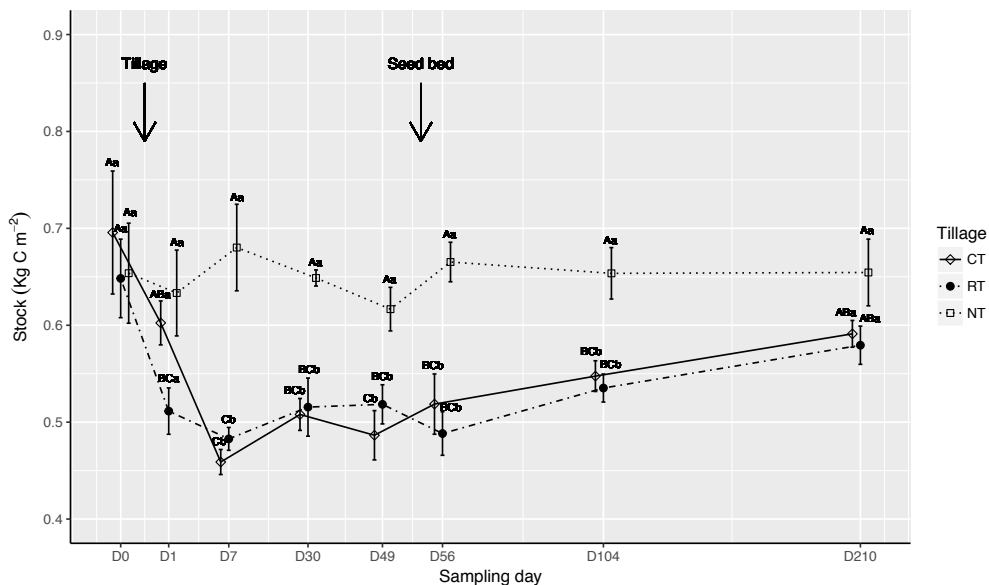


Figure 4-10 : SOC stock on 0- to 5-m in depth (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment.

As bulk density, SOC stocks showed significant temporal variations in CT and RT treatments, but not in NT (sampling day effect, Tableau 4-2, Figure 4-10). For both CT and RT treatments, maximum and minimum values were recorded at D0 and D7. SOC stocks differed significantly between treatments at all sampling dates except at D0, D1 and D210. NT treatment was significantly higher than the two other treatments (treatment effect, Tableau 4-2, Figure 4-10).

### 3.2.4. Mean weight diameter (MWD)

MWD differed significantly between sampling dates in CT and RT treatments, but not in NT (sampling day effect, Table 3). For CT, maximum and minimum values were found before tillage (D0) and to germination (D104), respectively. Accordingly MWD in RT did not change significantly after tillage, differences were observed after the seedbed (D56) and germination (D104) where we recorded the lowest values (2.54 and 2.42 mm, respectively). As for “treatment effect”, this parameter differed statistically between treatments only at D30; D56 and D104, with higher values in NT than in CT and RT except at D56, where RT exhibiting intermediate values (Tableau 4-3).

*Tableau 4-3 : Soil Aggregate mean weight diameter (MWD) and pH water (means  $\pm$  standard errors) of three different tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates for each experimental treatment.*

Physico-chemical properties												
MWD (mm)						pH water						
Sampling date	CT	RT	NT	F	p-value	R2	CT	RT	NT	F	p-value	R2
D0	3.27 $\pm$ 0.06 <sup>Aa</sup>	3.27 $\pm$ 0.09 <sup>Aa</sup>	3.19 $\pm$ 0.06 <sup>Aa</sup>	0.34	ns	5.78	8.2 $\pm$ 0.02 <sup>Aa</sup>	8.1 $\pm$ 0.03 <sup>Aa</sup>	8.1 $\pm$ 0.03 <sup>Aa</sup>	1.12	ns	49.7
D1	2.60 $\pm$ 0.05 <sup>BCa</sup>	3.04 $\pm$ 0.23 <sup>ABa</sup>	3.16 $\pm$ 0.17 <sup>Aa</sup>	3.17	ns	36.6	8.0 $\pm$ 0.03 <sup>Aa</sup>	8.0 $\pm$ 0.01 <sup>Aa</sup>	8.0 $\pm$ 0.03 <sup>Aa</sup>	0.22	ns	3.88
D7	2.88 $\pm$ 0.13 <sup>ABa</sup>	3.32 $\pm$ 0.10 <sup>Aa</sup>	3.21 $\pm$ 0.12 <sup>Aa</sup>	4.78	ns	54.4	8.1 $\pm$ 0.02 <sup>Aa</sup>	8.0 $\pm$ 0.02 <sup>Aa</sup>	8.0 $\pm$ 0.03 <sup>Aa</sup>	2.33	ns	41.4
D30	2.65 $\pm$ 0.13 <sup>BCb</sup>	2.88 $\pm$ 0.07 <sup>ABCb</sup>	3.16 $\pm$ 0.10 <sup>Aa</sup>	11.4	**	74.5	8.0 $\pm$ 0.01 <sup>Aa</sup>	8.0 $\pm$ 0.01 <sup>Aa</sup>	8.0 $\pm$ 0.02 <sup>Aa</sup>	1.51	ns	29.3
D49	2.67 $\pm$ 0.12 <sup>BCa</sup>	2.59 $\pm$ 0.19 <sup>BCDa</sup>	2.92 $\pm$ 0.19 <sup>Aa</sup>	1.41	ns	41.2	8.0 $\pm$ 0.02 <sup>Aa</sup>	7.9 $\pm$ 0.02 <sup>Aa</sup>	7.9 $\pm$ 0.02 <sup>Aa</sup>	4.07	ns	65.9
D56	2.27 $\pm$ 0.12 <sup>CDb</sup>	2.54 $\pm$ 0.13 <sup>CDab</sup>	2.77 $\pm$ 0.09 <sup>Aa</sup>	5.87	*	57.9	7.9 $\pm$ 0.03 <sup>Aa</sup>	7.9 $\pm$ 0.01 <sup>Aa</sup>	7.9 $\pm$ 0.01 <sup>Aa</sup>	0.44	ns	35.2
D104	2.17 $\pm$ 0.11 <sup>D<sup>b</sup></sup>	2.42 $\pm$ 0.08 <sup>D<sup>b</sup></sup>	2.98 $\pm$ 0.10 <sup>Aa</sup>	18.6	**	77.2	7.9 $\pm$ 0.03 <sup>Aa</sup>	8.0 $\pm$ 0.02 <sup>Aa</sup>	7.9 $\pm$ 0.05 <sup>Aa</sup>	3.79	ns	63.8
D210	2.73 $\pm$ 0.08 <sup>Ba</sup>	2.99 $\pm$ 0.11 <sup>ABCa</sup>	3.01 $\pm$ 0.12 <sup>Aa</sup>	2.05	ns	27.2	7.9 $\pm$ 0.01 <sup>Aa</sup>	7.9 $\pm$ 0.02 <sup>Aa</sup>	7.8 $\pm$ 0.02 <sup>Aa</sup>	14.0	ns	81.7
LMM outputs												
F	12.9	8.85	1.67	-	-	-	31.6	16.3	25.9	-	-	-
p-value	***	***	ns	-	-	-	ns	ns	ns	-	-	-
R2	76.1	71.4	28.5	-	-	-	89.5	80.8	88.3	-	-	-

## 3.3. Characterization of the microbial community

### 3.3.1. Microbial biomass carbon (MBC)

MBC varied widely over time in all treatments (sampling day effect, Tableau 4-4). For CT, the highest MBC was observed at D0 and D210 whereas lowest at D56. As for RT and NT treatments, highest MBC was recorded at D1 and lowest at D7. Otherwise, MBC differed significantly between treatments after tillage: D1; D7; D30; D49 (treatment effect, Tableau



4-4). On average, highest values were generally found in RT and NT treatments except at D7 where CT recorded maximum value. No difference was found before tillage (D0) and after seedbed until harvest (D56; D104; D210).

Tableau 4-4 : Soil microbial biomass carbon (MBC) and fungal biomass (FB) (means ± standard errors) of three different tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates for each experimental treatment.

Microbial communities												
Sampling date	MBC ( $\mu\text{g g}^{-1}$ )			LMM outputs			Fungal biomass ( $\mu\text{g g}^{-1}$ )			LMM outputs		
	CT	RT	NT	F	p-value	R <sup>2</sup>	CT	RT	NT	F	p-value R <sup>2</sup>	
D0	408 ± 9.78 <sup>ABa</sup>	418 ± 9.20 <sup>Ba</sup>	428 ± 11.6 <sup>ABa</sup>	0.97	ns	18.9	1.70 ± 0.23 <sup>BCa</sup>	1.81 ± 0.28 <sup>BCa</sup>	1.80 ± 0.24 <sup>CDa</sup>	0.27	ns	78.4
D1	380 ± 28.3 <sup>ABCb</sup>	505 ± 13.8 <sup>Aa</sup>	455 ± 24.8 <sup>Aab</sup>	7.51	*	57.7	1.83 ± 0.07 <sup>BCb</sup>	2.15 ± 0.06 <sup>Ba</sup>	1.95 ± 0.03 <sup>CDb</sup>	8.03	*	59.4
D7	342 ± 21.0 <sup>BCa</sup>	236 ± 21.0 <sup>Db</sup>	217 ± 22.7 <sup>Db</sup>	10.4	*	66.2	1.51 ± 0.04 <sup>Ca</sup>	1.73 ± 0.03 <sup>Ca</sup>	1.71 ± 0.15 <sup>CDa</sup>	1.69	*	23.5
D30	300 ± 18.9 <sup>CDb</sup>	359 ± 6.48 <sup>Ca</sup>	286 ± 16.7 <sup>CDb</sup>	7.21	*	58.6	1.68 ± 0.13 <sup>BCab</sup>	1.86 ± 0.04 <sup>Ca</sup>	1.63 ± 0.06 <sup>Db</sup>	3.85	*	62.3
D49	322 ± 26.3 <sup>Cb</sup>	413 ± 23.3 <sup>Bca</sup>	440 ± 22.4 <sup>Aa</sup>	10.8	*	72.2	2.33 ± 0.17 <sup>ABb</sup>	3.45 ± 0.24 <sup>Aa</sup>	3.70 ± 0.21 <sup>Aa</sup>	14.3	**	73.6
D56	223 ± 18.1 <sup>Da</sup>	282 ± 35.6 <sup>CDa</sup>	259 ± 21.0 <sup>CDa</sup>	3.09	ns	66.4	2.79 ± 0.14 <sup>Aa</sup>	2.81 ± 0.16 <sup>Aa</sup>	2.85 ± 0.18 <sup>ABa</sup>	0.05	ns	10.5
D104	343 ± 16.2 <sup>Bca</sup>	389 ± 27.9 <sup>Bca</sup>	341 ± 30.7 <sup>Bca</sup>	2.21	ns	57.3	2.47 ± 0.07 <sup>Ab</sup>	3.21 ± 0.12 <sup>Aa</sup>	2.74 ± 0.17 <sup>Bab</sup>	9.31	*	63.6
D210	428 ± 13.3 <sup>Aa</sup>	398 ± 12.8 <sup>Bca</sup>	428 ± 14.8 <sup>ABa</sup>	1.57	ns	22.2	2.13 ± 0.24 <sup>ABa</sup>	2.20 ± 0.21 <sup>BCa</sup>	1.93 ± 0.06 <sup>CDa</sup>	0.71	ns	24.2
LMM outputs												
F	10.7	16.0	20.5				8.29	25.4	21.5			
p-value	***	***	***				***	***	***			
R <sup>2</sup>	70.6	78.3	82.5				65.77	86.3	82.9			

### 3.3.2. Fungal biomass

As MBC, fungal biomass varied significantly over time in all treatments (sampling day effect, Tableau 4-4). For CT and RT, minimum values were found 7 days after tillage (at D7) and maximum values were found after seed bed (at D56; D104) in CT and at D49; D56; D104 in RT. For NT, maximum and minimum values were recorded at D49 and D30, respectively. Accordingly, fungal biomass was influenced by experimental treatments only at D1; D30; D49 and D104, with highest values in RT than in CT and NT.

### 3.3.3. Potential C mineralization

Potential C mineralization showed significant temporal variations in all treatments (sampling day effect, Tableau 4-5). In CT, maximum values were found at D1 and minimum values at D0 and D7, the other days exhibiting intermediate values. In RT, higher values were found at D104 and lower values at D0 and D210. In NT, D49 recorded maximum value and minimum values were found at D0 and D210. Potential C mineralization differed significantly between treatments at D7; D30; D49 and D104, with lowest values in CT than in RT and NT.

Tableau 4-5 : C-CO<sub>2</sub> (means  $\pm$  standard errors) of three different tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates for each experimental treatment.

Sampling day	Potential C mineralisation (mg kg <sup>-1</sup> d <sup>-1</sup> )					
	C-CO <sub>2</sub>			LMM outputs		
	CT	RT	NT	F	p-value	R <sup>2</sup>
D0	21.2 $\pm$ 0.71 <sup>Ba</sup>	20.8 $\pm$ 1.16 <sup>Da</sup>	22.6 $\pm$ 1.72 <sup>Ca</sup>	1.02	ns	53.1
D1	25.6 $\pm$ 1.38 <sup>Aa</sup>	27.2 $\pm$ 1.44 <sup>Bca</sup>	23.0 $\pm$ 1.07 <sup>Ca</sup>	2.55	ns	31.7
D7	21.1 $\pm$ 0.67 <sup>Bb</sup>	25.6 $\pm$ 0.76 <sup>Ca</sup>	24.3 $\pm$ 1.13 <sup>BCab</sup>	6.77	*	55.2
D30	23.2 $\pm$ 0.22 <sup>ABb</sup>	25.9 $\pm$ 0.44 <sup>Bca</sup>	24.2 $\pm$ 0.55 <sup>BCb</sup>	9.81	*	64.1
D49	23.3 $\pm$ 0.91 <sup>ABb</sup>	29.4 $\pm$ 0.52 <sup>ABa</sup>	29.0 $\pm$ 0.71 <sup>Aa</sup>	21.3	**	79.5
D56	22.6 $\pm$ 0.64 <sup>ABa</sup>	23.1 $\pm$ 0.56 <sup>CDa</sup>	24.1 $\pm$ 0.48 <sup>BCa</sup>	3.39	ns	62.5
D104	24.2 $\pm$ 0.43 <sup>ABc</sup>	30.9 $\pm$ 0.32 <sup>Aa</sup>	26.7 $\pm$ 0.60 <sup>ABb</sup>	47.3	***	89.6
D210	22.4 $\pm$ 0.73 <sup>ABa</sup>	22.4 $\pm$ 0.57 <sup>Da</sup>	22.7 $\pm$ 0.04 <sup>Ca</sup>	0.10	ns	1.70
LMM outputs						
F	3.66	19.9	8.89	-	-	-
p-value	**	***	***	-	-	-
R <sup>2</sup>	45.2	82.4	71.8	-	-	-

### 3.4. Relationships between soil fauna, soil physico-chemical parameters and microflora

Tableau 4-6 : Results of redundancy analysis of three treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) based on tests of permutations ( $n=999$ ). The values of the first two axis are given.

	Redundancy statistic			Eigenvalues	
	F	p-value	R <sup>2</sup> (%)	axis 1 (%)	axis 2 (%)
CT	3.27	0.001	37.0	91.1	6.67
RT	2.18	0.013	23.3	53.0	21.4
NT	1.11	0.381	2.71	20.0	6.01

#### 3.4.1. Conventional tillage (CT)

In CT system, the proportion of the total variance in the RDA, which is explained by all environmental parameters, is 37.0%. The first axis accounted for 91.1% of variance and the second only for a further 6.67% (Tableau 4-6). Basically, the first axis shows temporal variations after tillage operations (tillage and seed bed, see Figure 4-11). D0; D30 and D210 correlating to high values of collembolan assemblages. Both total density and species richness of Collembola were related to higher values of SOC stock, mean weight diameter (MWD) and pH water. In opposite, D1 and D7 were associated to high values of microbial biomass carbon (MBC), total density and species richness of earthworm. These latter were related to higher

values of bulk density (BD). At D56, soil fauna parameters were lower, only macro-aggregates (MAG) and potential C mineralization were higher values. D49 and D104 were very variable between soil fauna and physico-chemical parameters and microflora.

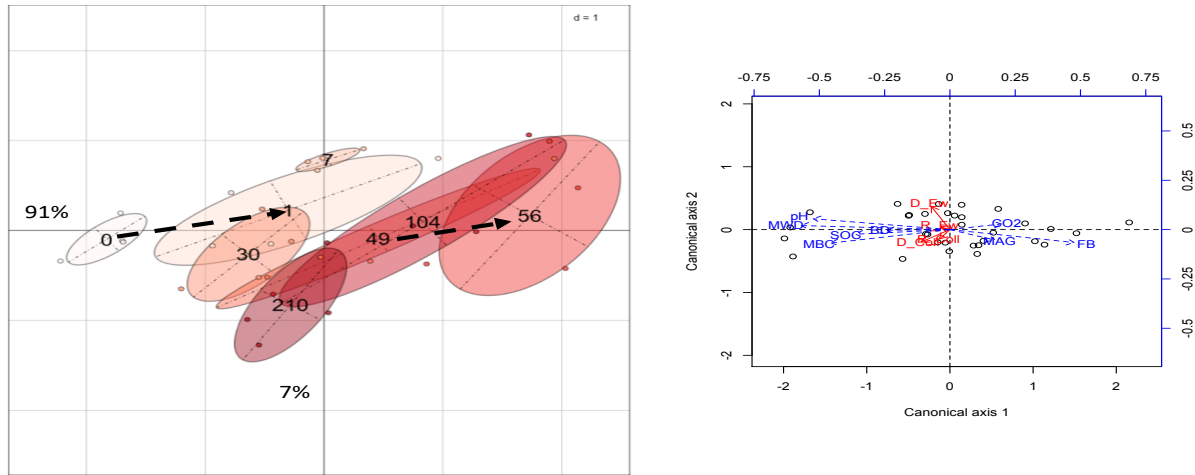


Figure 4-11 : Redundancy analysis (RDA) biplot of the conventional tillage (CT) data showing : a) soil fauna variables (*D\_Ew* : Earthworms density; *R\_Ew* : Earthworms species richness; *D\_Coll*: Collembola density; *R\_Coll* : Collembola species richness; *MBC* : Microbial biomass carbon; *FB* : Fungal biomass), environmental variables (*pH*: pH water; *CO2*: potential C mineralisation; *SOC* : SOC stock on 0- to 5-m; *BD*: Bulk density 0-5 cm; *MWD* : Mean weight diameter; *MAG* : Macro-aggregates or aggregates > 250  $\mu$ m) and b) plotting sampling days (0 : 1 day before tillage; 1; 7; 30 ; 49; 56; 104; 210 respectively after tillage).

### 3.4.2. Reduced tillage (RT)

For RT modality, the proportion of the total variance in the RDA, which is explained by all environmental parameters, is 23.3%. The first axis accounted for 53.0% of variance and the second only for a further 21.4% (Tableau 4-6). The first axis shows effect of mechanical perturbation (Figure 4-12). The first axis opposes D0 and D56, with values higher of macro-aggregates (MAG) and potential C mineralization at D56. On the second axis, firstly, D30; D49; D104 and D210 correlating to high values of collembolan assemblages, microbial biomass carbon (MBC) and fungal biomass (FB). These latter were related to higher values of SOC stock and bulk density (BD). On the other hand, D1 and D7 correlating to high values of total density and species richness of earthworm, which were related to higher values of mean weight diameter (MWD) and pH water.

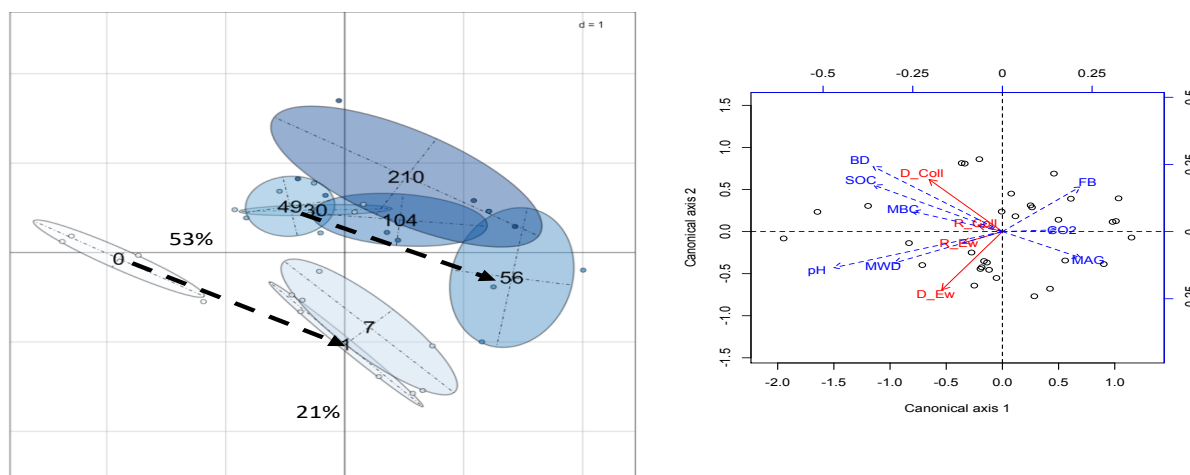


Figure 4-12 : Redundancy analysis (RDA) biplot of the reduced tillage (RT) data showing : a) soil fauna variables ( $D\_Ew$  : Earthworms density;  $R\_Ew$  : Earthworms species richness;  $D\_Coll$ : Collembola density;  $R\_Coll$  : Collembola species richness;  $MBC$  : Microbial biomass carbon;  $FB$  : Fungal biomass), environmental variables ( $pH$ : pH water;  $CO_2$ : potential C mineralisation;  $SOC$  : SOC stock on 0- to 5-m;  $BD$ : Bulk density 0-5 cm;  $MWD$  : Mean weight diameter;  $MAG$  : Macro-aggregates or aggregates > 250  $\mu m$ ) and b) plotting sampling days (0 : 1 day before tillage; 1; 7; 30; 49; 56; 104; 210 respectively after tillage).

### 3.4.3. No tillage (NT)

In NT system, the proportion of the total variance in the RDA, which is explained by all environmental parameters, is 2.71% (Figure 4-13).

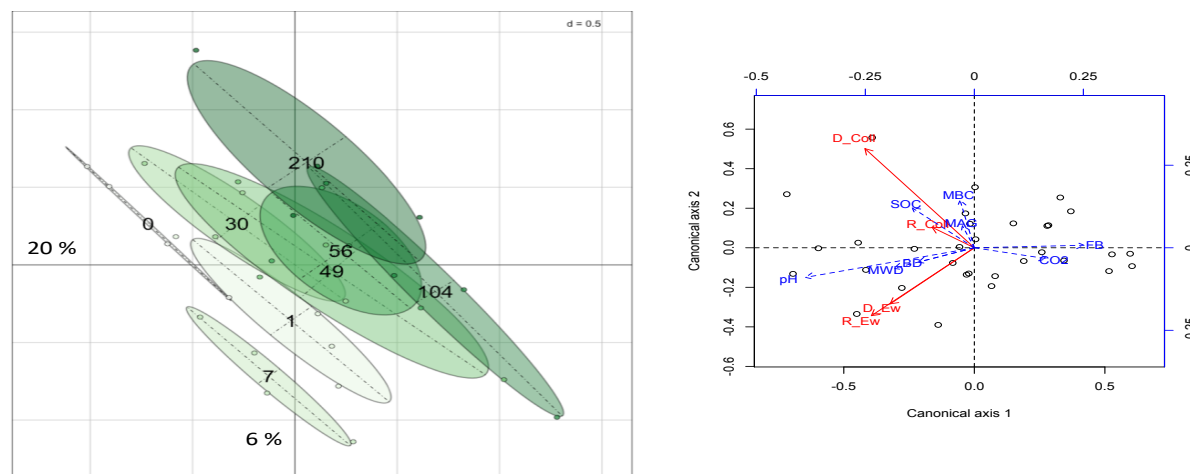


Figure 4-13 : Redundancy analysis (RDA) biplot of the no tillage (NT) data showing : a) soil fauna variables ( $D\_Ew$  : Earthworms density;  $R\_Ew$  : Earthworms species richness;  $D\_Coll$ : Collembola density;  $R\_Coll$  : Collembola species richness;  $MBC$  : Microbial biomass carbon;  $FB$  : Fungal biomass), environmental variables ( $pH$ : pH water;  $CO_2$ : potential C mineralisation;  $SOC$  : SOC stock on 0- to 5-m;  $BD$ : Bulk density 0-5 cm;  $MWD$  : Mean weight diameter;  $MAG$  : Macro-aggregates or aggregates > 250  $\mu m$ ) and b) plotting sampling days (0 : 1 day before tillage; 1; 7; 30; 49; 56; 104; 210 respectively after tillage).

The first axis accounted for 13.4% of variance and the second only for a further 3.65% (Tableau 4-6). Both axes showed temporal variations along the study. Collembola parameters and

microbial biomass carbon (MBC) were related to higher values of SOC stock. These latter were most important at D0, D30 and D210. Total density and species richness of earthworm were correlated with pH water, mean weight diameter (MWD) and bulk density (BD). These latter parameters were most important at D1 and D7. Finally, D49; D56 and D104 correlating to high values of fungal biomass (FB), which was related to higher values of potential C mineralization.

#### **4. Discussion**

We followed during a vegetative season the effects of 3 different tillage practices commonly used in Western Europe. Since all the studied sub-plots were previously managed under conventional tillage (CT) for at least 15 years, this offered us the opportunity to evaluate if shifting from CT towards less intensive management (by minimizing mechanical disturbances) may produce changes in soil fauna assemblages impacting ecological processes.

##### **4.1. Soil fauna**

The average number (density and species richness) of earthworms and Collembola collected in all plots agrees with former published data from similar systems in France (Cortet et al., 2002; Henneron et al., 2014; Ponge et al., 2013) and other parts of Europe (Briones and Schmidt, 2017; Petersen, 2002; van Capelle et al., 2012).

Overall, the results of this study demonstrate that assemblages of earthworm and Collembola are reactive to tillage intensity. The lowest the soil tillage intensity, the highest the Collembola or earthworm assemblage density. This effect was consistent across the three level analysed (density, species richness and Shannon index), which is in accordance with a number of previous studies (Bedano et al., 2006; Brennan et al., 2006; Briones and Schmidt, 2017; Petersen, 2002; van Capelle et al., 2012; Wardle, 1995) and confirms our first hypothesis. This agrees well with a general view that soil biota are usually stimulated by new conservation tillage practices. Nakamoto et al. (2006) found the same results on the numbers of nematodes, but for example Didden et al. (1994) indicate that enchytraeids were unaffected by tillage. However, our kinetic study allowed us to show that Collembola assemblages (density, species richness and Shannon index) differed only after 49 days (D49) between the tillage treatments (for total density) and the second tillage operation (i.e. seedbed, the total densities, richness and Shannon index), unlike earthworms where significant differences were observed from the first tilling operation (from D1). Generally, larger organisms are more sensitive to tillage practices than smaller ones (Wardle, 1995). For example, Briones and Schmidt (2017) state that when soil is ploughed, earthworms are injured and killed directly, exposed to adverse environmental

conditions and predators (Giller et al., 1997), biogenic structures (Pores and burrows) are destroyed and their food sources (litter) have been buried (Chan, 2001). In this context, we suggest that the Collembola may be more resistant than the earthworms and that the repetition of the tillage (i.e. seedbed) causes them to decrease afterwards. The fact that the total densities of Collembola showed significant differences between three soil tillage systems at D49, with higher values in RT and NT compared to CT, is directly related to the effect of tillage as described by earthworms above, but also indirectly through habitat modification. Because, the bare surface exposed after the operation is likely to degrade the soil aggregates when the energy from the raindrops is dissipated (El Titi, 2003; Vršic, 2011), thus causing damage to the total density of Collembola. In one way or another, the effect on Collembola assemblage remains late compared to earthworms. This goes in the same direction as our second hypothesis suggesting that the difference between tillage systems is related to the sampling date.

In the literature, studies have often compared the effect of these three tillage systems on Collembola assemblages (Cortet et al., 2002; Dittmer and Schrader, 2000a; Petersen, 2002; Wardle, 1995; Winter et al., 1990a). They stressed that the latter are promoted by the NT system compared to other tillage systems. However, they often failed to provide information at what time of the season the differences may appear. This is probably clear in our case, as we observed a decrease in Collembola density even in the no-till system at D1, leading to no difference compared to the other two tillage systems. Thus, at D1, the lowest soil temperature value was recorded (as shown in Figure 4-2). We went from 5.7 to 5.3°C (D0 to D1, respectively), and at the same time the average wind speed increased from 1.3 to 2.1 cm second<sup>-1</sup>. It is well known that among abiotic factors, temperature has a direct effect on activity, fecundity and mortality of collembolan (Christiansen, 1964; Eaton et al., 2004).

It is surprising that the total earthworm density was significantly lower in RT than in CT at certain sampling dates (D7, D30, D104 and D210). This is in contradiction with those found by van capelle et al. (2012), but in agreement with the results of Edwards and Lofty (1969). The declines in earthworm community often reported in conventionally tilled soils are associated with undesirable changes in the soil environmental conditions resulting from excessive tillage. However, we often forget the way in which the two tillage systems (CT and RT) have been completed. Indeed, in similar soil types (Luvisol), soil organisms in general, and earthworms in particular, are mostly (more 90%) found in the topsoil (0-10 cm or top ten-centimeter of soil; Coulibaly & Chauvat unpubl). Thus, in the RT system, this soil profile is strongly disturbed by the tool used, which could cause damage to earthworms with direct effects such as injuries,

mortality and exposure to predators (Briones and Schmidt, 2017). The lack of detailed descriptions of tillage practices is also to blame for the contrasting findings reported by the different authors (Chan, 2001). Because, adoption of conservation tillage does not automatically result in an optimal earthworm community in terms of density and diversity.

Another interesting aspect that contributes to the conflicting picture of the effects of tillage on earthworms is the land-use history, that is how many years the soil has been under CT system: what the previous use of the land was and how much time has passed since its last conversion to RT. This is important because the ability of earthworm communities to adapt to a soil that has been ploughed once or several times every year is expected to increase over time, as the more resilient species will remain in the community. Therefore, soon after land-use conversion, mortality rates are expected to be higher than in those soils that have been ploughed for many years, but food supply can also be temporarily higher (Edwards, 1983), and individual fields will differ in their suitability for recolonization by earthworms from field margins (Roarty and Schmidt, 2013). Briones and Schmidt (2017) have shown in their meta-analysis a very strong positive response of earthworm populations to RT operations when the soil had been under RT for a long time (>10 years). Unlike our study covers only one growing season, the farther away from the dates when the mechanical disturbances were applied (D1 et D56), the more we observed lower earthworms density values in RT compared to CT. Therefore, the available literature offers contrasting responses, ranging from prompt recoveries after a few months to soil fauna numbers remaining very low after many years under conventional tillage (more 15 years), but also either increases and decreases at time intervals of just a few weeks.

#### **4.2. Soil physico-chemical parameters and microflora**

Bulk density, SOC stock, MWD, pH, potential C mineralization, microbial biomass carbon (MBC) and fungal biomass (FB) values obtained in our study were within the range of values observed in similar studies within Europe (Groenigen et al. 2010).

Slightly reducing the intensity of soil mechanical perturbation (RT) did not impact abiotic factors. However, when stopping tillage or soil preparation for seedbed, then bulk density, stock C, MWD, increased (NT vs. CT). This fits with the common assumption that mechanical perturbation like tillage is the major cause of physical habitat alteration leading to soil degradation, i.e. organic matter depletion, reduction of soil fertility (Arshad et al., 1999; Reynolds et al., 2007; Six et al., 2000). The decrease in soil bulk density observed at D1 (1 day

after tillage) in NT vs CT was probably due to the inversion of the soil block by CT, which may alter this condition in short term.

Our results showed that between D0 and D1, potential C mineralization increased in RT and CT and no effect was detected for NT. This increase did not last long, since 7 days after tillage we observed a decrease in these systems especially in CT. This result is in perfect agreement with those found by Calderón et al. (2001), which showed the CO<sub>2</sub> increase in tilled soil lasted only 4 days after tillage. Indeed, tillage is known to induce short-lived increases in CO<sub>2</sub> efflux from soil. A plausible explanation is that immediately after tillage, the CO<sub>2</sub>-rich soil atmosphere is flushed with air of relatively low CO<sub>2</sub> content. This causes a reduction in the CO<sub>2</sub> partial pressure in the soil air, which is followed by the degassing of dissolved CO<sub>2</sub> from the soil solution (Ellert and Janzen, 1999; Reicosky et al., 1997; Reicosky and Lindstrom, 1995; Rochette and Angers, 1999). When we look at our kinetic study, reducing and stopping tillage has led to an increase in potential C mineralization (D30, D49, D104). We hypothesize that factors such as the intensity of soil disruption, the amount of initial microbial biomass, and the quantity of previously protected C sources in soil aggregates may determine the impact of tillage on microbial activity.

On the other hand, our results showed that microbial communities are reactive to tillage intensity. The reduction of mechanical disturbance has led to an increase of fungal and microbial biomass (FB and MBC) from the first day after tillage, followed by a decrease 7 days later. This result is in agreement with that of Salinas-Garcia et al. (2002) and Groenigen et al. (2010), but disagree with the results of Calderón et al. (2001), which showed no effect of reduced tillage on microbial biomass in the short term. Due to its dynamic character, microbial biomass responds faster to changes in soil management, because it has the advantage of serving as early signals of soil degradation or soil improvement (Powlson et al., 1987). Shallow non-inversion tillage is carried out using a single pass of a tined stubble cultivator at a depth of 7–10 cm, this may cause an increase in fungal hyphae on the soil surface; thus, it can be suggested that the reduction of tillage may expose previously protected organic matter that may serve as a substrate for microbial growth (Rovira and Greacen, 1957).

Finally at D56, all microbial parameters (MBC, FB and potential C mineralization) showed no significant difference between the three treatments. This could be explained by the application of glyphosate, as its degradation could be co-metabolically performed by the general activity of soil microorganisms (Araújo et al., 2003; Haney et al., 2000; Stratton and Stewart, 1992). Several authors have studied the effects of glyphosate on soil microorganisms, with



controversial results. While, Gomez et al. (2009) observed a decrease of microbial biomass carbon, Haney et al. (2000) observed no effect on either the microbial biomass carbon or nitrogen contents, and yet, Wardle and Parkinson (1990) found a slight increase in these parameters in the first days after application of herbicide.

However, it is interesting to note that at the end of the vegetative season (D210), all these parameters revert to the same level as NT to show no significant difference between the three treatments, due to root development, which could alter soil structure with effects on ecological processes.

#### **4.3. Relationships between soil fauna, physico-chemical parameters and microflora**

Unlike Collembola assemblages, the earthworms were not resilient in the three tillage systems at harvest (D210; H2b rejected for earthworm community), showing progressive decreases in density and diversity since D30. The fact that the two groups of soil organisms have different periods of activity (life cycles) could explain this. Also, this can be explained by a progressive increase of soil temperature at the same time from D30 until D210 (Figure 4-2). It is well known that temperature is a factor of primary importance of earthworms because it determines individual metabolic rates, and can have a major role in determining patterns of earthworm distribution and activity (Cortez, 1998; Curry, 2004). Chan, (2001) showed that increase of the earthworm population could be related to more favorable temperature and humidity conditions. Moreover, in agricultural soils, earthworms affect many soil properties, such as soil structure, dynamics of organic matter (Brown et al., 2004), and can be very sensitive to variations in texture and pH. This is probably the case of our study, because by focusing on our RDA results, total density and species richness earthworms were linked to MWD and pH. These links were stronger when moving away from the tillage dates of the soil or in total absence of tillage. Frey et al. 1999 showed that the mean weight diameter (MWD) of water-stable aggregates decreased significantly with the increase in tillage intensity. As for Collembola, microbial biomass carbon (MBC), SOC stock and bulk density (BD) showed stronger links with their density and diversity when moving away from tillage dates or in the absence of mechanical disturbance. The positive effect of decreasing tillage intensity its dynamics on the microbial biomass (through improved habitat condition) may explain the marked increase of Collembola assemblages as they are known to be rather controlled by bottom-up resources (Henneron et al., 2016; Schneider and Maraun, 2009). Otherwise, the more the soil tillage intensity is increased, especially during the repetition of the mechanical disturbance for the preparation of the seedbed (D56), the greater

the adverse impacts on soil organisms. This was probably due to the decline in coarse pores, because the ergosterol concentration (fungal biomass) was independent of bulk density (see Figure 4-11, Figure 4-12 and Figure 4-13). Also, whatever the tillage system, the decrease of soil organisms has often been accompanied by stimulation of microbial activity with growth on fungal biomass (see (see Figure 4-11, Figure 4-12 and Figure 4-13). Potential C mineralization and FB (fungal biomass) may also be increased due to conditions favourable to vegetal cover and germination, as can be seen in RDA results. These results show that soil structure and decline in habitable pore space are the key parameters in the density and diversity of soil fauna (Larsen et al. 2004).

## 5. Conclusion

This study on a vegetative season allowed us to follow the dynamic of collembolans, earthworms, physico-chemical parameters and microflora in three levels of tillage on a site, which has historically managed under intensive conventional tillage for at least 15 years. Our findings showed that the stopping of tillage has led to an increase in the density and diversity of earthworms and Collembola over time. This change in the endogenous compartment is related to the improvement of some soil conditions such as basic food source (microbial biomass of carbon, stock of soil organic carbon) and the living space/physical structure (bulk density, MWD, aggregates size). Furthermore, assemblages of earthworms and Collembola do not have the same answer as to the comparison of the three systems of tillage over time. The differences occur in the Collembola assemblages only after the repetition of the mechanical disturbance, so the earthworms responded from the first tillage operation. This suggests the resistance of smaller organisms to the effect of tillage compared to larger ones. Thus, Collembola assemblages were more resilient than earthworms due to the role of external driving factors like climate or vegetation growing. Variability demonstrated between sampling dates highlights the importance of multiple samplings in time to ascertain mechanical management effects on edaphic organisms and their associated functions.

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## **Chapitre 5. Relations entre formes de vie des collemboles et communautés microbiennes**

### **Présentation du chapitre**

Le cadre conceptuel de ce chapitre s'appuie sur les conséquences fonctionnelles des changements d'assemblages de faune du sol liés aux différentes pratiques agricoles innovantes précédemment étudiées. L'étude a été menée en conditions contrôlées dans le but d'explorer les interactions biotiques s'établissant entre les différentes formes de vie de collemboles et les communautés microbiennes. Les paramètres microbiens présentés dans ce chapitre ont été analysés au sein des deux unités d'accueil (laboratoire « Ecodiv » et l'unité AGRI'TERR).

Nos résultats ont souligné :

- Une réponse différentielle de chacune des formes de vie de collemboles sur les communautés microbiennes au cours du temps.
- Des effets de complémentarité et de compétition ont été observés entre certains groupes fonctionnels durant l'étude.

# **Collembola functional groups have different effects on soil microbial properties and functions.**

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*Article en préparation*

## **1. Introduction**

Decomposition processes, after primary production is the most important ecosystem function. Indeed, about 90% of the terrestrial net primary production (NPP) enters the soil food webs to be consumed and then decomposed into mineral forms and eventually reabsorbed by plants. Decomposition processes are mainly regulated by environmental drivers including abiotic factors (e.g. water content, temperature), litter quantity and quality, and by the activity of the decomposer biota (Anderson, 1991; Seastedt, 1984; Wardle et al., 2004). Interactions between members of soil food webs strongly impact organic matter recycling and thus affect the quality and quantity of the nutrients available for plants (Bardgett and Cook, 1998; Bardgett and Shine, 1999; Heemsbergen et al., 2004; Mikola et al., 2002; Tiunov and Scheu, 2005).

Although most mineralization of nutrients is governed directly by the activities of bacteria and fungi, their ability to do this is regulated by soil fauna (Chauvat et al., 2014b; Kaneko et al., 1998; Lenoir et al., 2007). Soil fauna can affect the biomass and activity of the microbial community, either directly through selectively feeding on fungi and bacteria, or indirectly by comminution of organic matter, dissemination of microbial propagules, and the alteration of nutrient availability (Griffiths and Bardgett, 1997; Lussenhop, 1992; Moore et al., 1988; Verhoef and Brussaard, 1990). Although studies evidenced such impact, we still lack data on

this point, especially considering how, within a single trophic group, different taxa led to differentially impact rates of litter decomposition (Siepel and Maaskamp, 1994) and nutrient fluxes (Mebes and Filser, 1998). For example, regarding soil Collembola, a dominant soil microarthropod group, recently Caravaca et al. (2014) have shown that different species (3 tested) had a specific grazing intensity on arbuscular mycorrhizal fungi. They relate this observation to the ecological life forms of Collembola. Gisin (1943) described three typical soil collembolan life forms based on morphology and habitat. Epedaphic species are usually large bodied species, have a high metabolic activity, consume a food substrate of a high quality and are surface-dwellers. Conversely, euedaphic species are small deep-living species that consume low-quality food and have a low metabolic activity. Euedaphic species are colourless with reduced appendices (e.g. furca, antennae, leg). Finally, the hemiedaphic group includes species sharing intermediate attributes (Petersen, 2002). Thus, it is common to consider those groups as functional groups, even if we still lack knowledge on the way they perform or drive different functions. In the literature, studies highlighted clear positive relationships between euedaphic and microbial biomass (Perez et al., 2013), while less obvious relationships have been depicted for epedaphic collembolan for example. However, different feeding preferences of epedaphic species upon fungi have been highlighted (Nakano et al., 2017). Furthermore, these functional groups have been shown to express different foraging patterns towards microbial food resources (Chauvat et al., 2014b).

To gain further insight on how functional groups within a single decomposer taxa (i.e. Collembola) impact ecosystem functioning, we conducted a microcosm experiment investigating the response of microbial communities (structurally or functionally) to the different Collembola functional groups, alone or in combination. Previous studies suggested that soil processes are mainly driven by physiological attributes of the dominant decomposer species (Cragg and Bardgett, 2001; Laakso and Setälä, 1999). Thereby we hypothesized that due to their differences in life-history traits, each Collembola functional group has a specific impact on soil microflora by top-down regulation. We hypothesized that the presence of euedaphic species will generate a stronger response of soil microflora than would the presence of epedaphic species compared to a control without Collembola. Furthermore, Eisenhauer et al. (2010) showed that functionally dissimilar decomposer groups could synergistically impact plant performance. We hypothesize that complementarity may occur between different Collembola functional groups for example by using different resources along the soil profile promoting microflora activity on the whole profile. Finally, as time is a determinant aspect of

biotic interactions outcome, we decided to investigate the response of microflora to the different *Collembola* treatments over time during two months.

## **2. Materials and Methods**

### **2.1. Experimental setup**

The experiment was conducted under microcosm (closed glass jar) conditions with 9 cm diameter and 9.5 cm high. Soil, microorganisms and *Collembola* used in this study come from a grazing area since 1968, managed by the Lycée Agricole d'Enseignement Générale et Technique Agricole of Yvetot (north-west France, 0°45'18.76"E, 49° 37 '04.00"N). The climate of the region is temperate oceanic, with an average annual temperature and rainfall of 10 °C and 800 mm, respectively. The original soil was classified as NEOLUVISOL-LUVISOL (pH water = 6.1, clay = 15 %, silt = 65%, sand = 20 %, total carbon = 10.40 g kg<sup>-1</sup>, total nitrogen = 1.04 g kg<sup>-1</sup>; IUSS (2006)) and supported a vegetation dominated by *Agrostis capillaris* (L.), *Lolium perenne* (L.) and *Ranunculus acris* (L.).

#### **2.1.1. Substrate**

The substrate used in the microcosms consisted of a mixture of 1 volume of sand per 5 volumes of soil, which had previously been collected to a depth of 0-15 cm and sieved in a mesh of 5 mm. To eliminate the original fauna and microflora, the substrate was sterilized with two cycles of 105°C in an autoclave every 48 hours. Subsequently, the substrate was dried at 105°C and a sample was removed to determine the field capacity. Finally, each microcosm was filled with 150 g of dry soil.

#### **2.1.2. Microorganisms**

Microorganisms were extracted from soil broth filtrates, prepared by weighing 500 g of sieved fresh soil and dissolved with 2 L of physiological water (0,85% NaCl), according to the adapted protocol of Eisenhauer et al. (2009). Each broth was obtained after orbital stirring for 1 h 30 min and filtration on paper (Durieux filters No. 149).

A volume of 37 ml of microbial filtrate or microbial suspension (corresponding to 70% of the water holding capacity) was inoculated into each microcosm. In order to establish the microbial community, the microcosms were incubated at a temperature of 25°C for 10 days.

### 2.1.3. Collembola extraction and composition of treatments

Collembola were extracted from collected soil (monoliths 15 cm deep) using the Berlese-Tullgren device (Tullgren, 1918). Introduced species therefore come from the natural communities of the Yvetot field (grazed grassland). In order to obtain different treatments used in this study, the monoliths were cut into the depth associated with the habitat of the different life forms of Collembola and each microcosm was placed under the extractor.

First, three treatments corresponding to large groups of collembolan were designed:

- Epedaphic (Ep): litter, vegetation and first layers of soil (2 cm) were used. The extraction took place within a period of 2 days,
- Hemiedaphic (He): the first three layers of soil (0 to 3 cm) were extracted during 5 days. Ideally, the Epedaphic species found in the soil were collected in a separate container for the first two days and the remaining three days were devoted to the extraction of the Hemiedaphic species in the corresponding microcosms.
- Euedaphic (Eu): these organisms were extracted only in the deep layers of the soil (4 to 10 cm) for 7 days.

Secondly, each of these three life forms was associated to construct four treatments (mixed treatments). Ideally, the layers of the soil referring to the corresponding life forms (see above) were extracted:

- Epedaphic and Hemiedaphic (Ep + He): the layers of the soil referring to the two life forms were extracted (0 - 3 cm) were obtained for 5 days.
- Epedaphic and Euedaphic (Ep + Eu): assemblages were obtained (0-2 cm from the ground) for 2 days and 4-10 cm from the soil for 7 days.

Hemiedaphic and Euedaphic (He + Eu): extraction lasted 7 days

- Epedaphic, Hemiedaphic and Euedaphic (Ep + He + Eu): the entire soil layer was extracted (0 -10 cm from the ground) for 10 days

Finally, a control treatment (without Collembola) was added to standardize all the treatments. In total, 8 treatments were designed for our study and each of them was replicated 16 times in microcosms (128 microcosms).

We specify here that in order to avoid contamination of treatments from one form of life to another, different extractors were used and all the microcosms (including control treatment)



were under the extractors for 10 days (extraction time total). After inoculation of the Collembola, the microcosms were moistened at 70% of the field capacity with milli-Q water, closed and stored in an incubator at a temperature of 18 ° C and 12 h of photoperiod for 60 days but open every week for aeration (10 seconds) and humidification. Subsequently, we measured the parameters at 30 and 60 days after Collembola was inoculated.

Prior to the establishment of the experiment, tests were carried out to verify the number and species of Collembola introduced into each treatment (Tableau 5-1).

*Tableau 5-1 : Mean density of Collembola (number of individuals) introduced in each treatment. The most dominant species per life forms were : Ep (Isotoma anglicana, Lepidocyrtus violaceus, Isotomurus palustris gr); He (Parisotoma notabilis, Sminthurinus aureus, Ceratophysella denticulata); Eu (Folsomia fimetaria, Protaphorura armata gr, Mesaphorura spp). Ep: Epedaphic, He: Hemiedaphic; Eu : Euedaphic*

Treatment	Total density	Abd Life forms		
		Ep	He	Eu
Ep	19,9	15,6	3,3	1,0
He	15,7	1,1	13,1	1,4
Eu	23,7	4,8	0,0	18,9
Ep + He	17,3	8,5	7,3	1,4
Ep+Eu	15,2	8,7	0,8	5,7
He + Eu	23,5	0,0	7,7	15,8
Ep + He + Eu	19,0	7,8	3,8	7,5

## 2.2. Characterization of the microbial community

Soil analyses were carried out twice at t = 30 days and t = 60 days after the introduction of Collembola. At each time, every 30 days, 64 microcosms (including all treatments) were dismantled. Half (32 microcosms) were dedicated to the extraction of the Collembola, allowed us to confirm that the collembolan assemblages, in terms of abundance, were maintained even if inevitably compositional changes appeared. The remaining 32 microcosms were used to determine structure and activity of microbial communities:

### 2.2.1. Microbial community structure

- Phospholipid fatty acid analysis (PLFA)

Freeze-dried soil samples (10 g) were extracted with 15.2 mL Bligh and Dyer mixture of chloroforme : methanol : phosphate buffer : ( 1 : 2 : 0.8 , v/v/v) on a Multi Reax vortex mixer for 2 h, at 1500rpm, at room temperature. After centrifugation for 20 min at 2500 rpm, the supernatant was transferred to a borosilicate glass tube and the soil residue was re-extracted for 30 min with 7.6 mL Bligh and Dyer extractant. The combined supernatant was split into two phases

by adding 3.1 mL chloroform and 3.1 mL phosphate buffer and left overnight to separate. The organic layer at the bottom was then transferred to a vial and evaporated to dryness under N<sub>2</sub> at 37°C.

Phospholipids were separated from neutral lipids and glycolipids On a solid phase extraction (SPE) Si column Bond Elut. The column was first conditioned with CHCl<sub>3</sub> (5 ml). The lipids were then transferred into the column with CHCl<sub>3</sub> (500 µL, then 3×250 µl). Neutral lipids and glycolipids were eluted with chloroform (6 ml) and acetone (6 ml) successively.

Phospholipids were obtained from methanol elution (3x3 ml) and evaporated to dryness under N<sub>2</sub> at 37°C. Lipidic extracts were redissolved in 2 x 500 µL methanol : toluene (1 : 1, v : v), transferred in a glass centrifuge tube, 500 µL C19 at 76 nmol mL<sup>-1</sup> was then added as internal standard.

The polar lipids were trans-esterified to the fatty acid methyl esters by a mild alkaline methanolysis (Guckert et al., 1985) with a methanol:toluene (1 ml) and potassium hydroxide methanol solution (0.2 M, 1 ml) in the glass centrifuge tube and incubated at 37 °C for 30 min. After methylation, acetic acid (0.3 ml) and H<sub>2</sub>O (2 ml) were added. Fatty acid methyl esters were extracted in 2x2 mL hexane : chloroform (4:1, v/v) and dried under N<sub>2</sub>. Samples were then dissolved in hexane (200 µL) with C13 at 47.73 nmol/mL and transferred in a GC vial insert and analysed in a Varian CP 3800 Gas Chromatograph fitted with a flam ionisation detector. The column was a Thermo Scientific 260 M 142 P ( 30 m x 0.25 mm x 0.25 µm capillary column. Helium was the carrier gas. The GC temperature progression was set so : 100°C to 165°C (5°C/min) to 183 °C (2°C/min) to 240°C (5°C/min) and during 20 min at 240°C. The fatty acid 19:0 was added as an internal standard before methylation and 13:0 before analysis in GC. Fatty acid methyl esters were identified using relative retention times; the peaks having previously been identified by GC/MS and BAME 26 standards Sigma. The results were expressed as nmol PLFA g<sup>-1</sup> dry soil.

We retained the following 16 PLFAs as indicators of the microbial community structure (Fanin et al., 2016) : branched and saturated PLFAs i15:0, a15:0, i16:0 and i17:0 (Gram-positive bacteria); mono-unsaturated and cyclopropyl PLFAs 16:1ω7c (16:1ω9), cy17:0, (Gram-negative bacteria) 18:1ω9c, 18:1ω9t, 18:2ω6,9 (fungi), 10me-16: 0 and 10me-18:0 (Actinobacteria); and 14:0, 15:0, 16:0, 17:0, 18:0 (general indicators).

### 2.2.2. Heterotrophic soil activity

- Microbial activity

The microbial activity was assessed by CO<sub>2</sub> evolution at 30 and 60 days after the introduction of Collembola (Anderson and Domsch, 1978). A flask containing 20 ml of 0.5M NaOH was placed in each microcosm prior to incubation. The CO<sub>2</sub> content emitted at each date was measured 10 days after the incubation by electrical conductivity. The standard curve was carried out with 0.25 mol L<sup>-1</sup> Na<sub>2</sub>CO<sub>3</sub> solution, with concentrations ranging from 0 to 20 mM (21 points in the curve) and the electrical conductivity of each point was then determined. The data were expressed in µg CO<sub>2</sub> g<sup>-1</sup>dry soil h<sup>-1</sup>.

- Enzymatic activities

We estimated different enzymatic activities, specifically the β-glucosidase activity involved in the C cycle, the urease involved in the N cycle, and the hydrolysis of the fluorescein dihydrate (FDA). FDA is hydrolysed by different enzymes such as lipases, esterases and proteases, so this is a method of measuring overall activity potential.

The β-glucosidase was evaluated by the method using the p-nitrophenyl-β-d-glucopyranoside (pNPG) substrate (Eivazi and Tabatabai, 1988). 1 g of wet soil was weighed in duplicate and each sample was incubated for 2 hours at 25 ° C. with stirring with 1 ml substrate (5 nM pNPG) and 4 ml universal buffer solution adjusted to pH 6.0. The reaction was terminated by adding 1 ml of 0.5 mol L<sup>-1</sup> CaCl<sub>2</sub> and 4 ml of 0.5 molar L<sup>-1</sup> NaOH. The mixture was vortexed and centrifuged for 3 minutes at 9000 rpm. The β-glucosidase activity was based on the levels of p-nitrophenol released during the reaction, which was determined by spectrophotometry (410 nm). The standard curve was performed with p-nitrophenol (50 µg mL<sup>-1</sup>) at the concentration of 0; 25; 50; 100; 150; 200 µg. The data were expressed in µg pNPG<sup>-1</sup> dry soil h<sup>-1</sup>

The urease activity was determined according to the method proposed by Kandeler (1988). Urease, an enzyme linked to the conversion of the amine (NH<sub>2</sub>) to ammonium (NH<sub>4</sub><sup>+</sup>), is measured from two samples of 2 g of soil, in which 2 ml of urea 1) and 2 mL of ultra-pure water incubated for 2 hours at 37 ° C. The activity of the urease was measured by the ammonium released from this reaction, extracted with KCl 2 mol L<sup>-1</sup>, Measured by spectrophotometry by the acid-salicylic method, at 690 nm (Bundy and Meisinger, 1994). The standard curve was carried out using a NH<sub>4</sub>Cl solution in the following concentrations: 0; 0.56; 1.11; 2.23; 5.57; 8.9; 13.38; 17.85; 22.31 µmol L<sup>-1</sup> NH<sub>4</sub><sup>+</sup>, respectively. The data were expressed in µg N-NH<sub>4</sub> g<sup>-1</sup> dry soil h<sup>-1</sup>.

The FDA activity proposed by Schnurer and Rosswall (1982) was measured on 2 g of moist soil in the presence of 15 ml of 60 nM potassium phosphate buffer and 200  $\mu\text{l}$  of substrate (solution of 1000  $\mu\text{g mL}^{-1}$  of The FDA). The samples were incubated for 20 min at 30 ° C. with stirring, then the reaction was quenched by adding 15 ml of a chloroform / methanol mixture (2: 1: v: v). The control samples did not receive any substrate prior to incubation after adding chloroform: methanol. All samples were centrifuged at 2000 rpm for 3 minutes and the fluorescein was read at 490 nm by spectrophotometry. The standard curve was performed using a fluorescein solution (20  $\mu\text{g mL}^{-1}$ ) in the following concentrations: 0; 10; 20; 30; 40; 50; 60; 70; 80; 90; 100  $\mu\text{g}$ , respectively. The data were expressed in  $\mu\text{g}$  fluorescein  $\text{g}^{-1}$  dry soil  $\text{h}^{-1}$ .

### 2.3. Statistical analysis

Statistical analyses were achieved with the R-software (Team, n.d.). Normality and homoscedasticity of the data set were tested (Shapiro-Wilk and Bartlett,  $\alpha = 0.05$ ) to decide whether parametric tests (in case data met both assumptions) or non-parametric tests (in case at least one of these assumptions was not met) had to be used. Finally, we opted for non-parametric tests. A Kruskal-Wallis test was used to examine effects of treatments (Control, Ep, He, Eu, Ep+He, Ep+Eu, He+Eu, Ep+He+Eu) on measured variables over the whole course of the experiment. The function “Print kruskal” was used to identify the differences between treatments at the 5% level. The calculations were performed with the libraries ade4 (Dray and Dufour, 2007) and vegan (Oksanen et al., 2013), agricolae (De Mendiburu, 2014).

For mixed treatments (Ep+He, Ep+Eu, He+Eu and Ep+He+Eu), since we did not have the same number of Collembola for each treatment (cf. Tableau 5-1), we used the Collembola biomass per treatment to standardize the comparisons. Subsequently, we calculated the predicted values from the observed data for each microbial variable. The predicted data were reported per unit of Collembola (in  $\mu\text{g}$ ). Means between observed and predicted values were compared with Pairwise t-tests. Significance was tested with  $\alpha = 0.05$ . In addition, we tested the conformity of the distribution of observed values and those predicted using the Chi 2 test compliance ( $\alpha = 0.05$ ). The calculations were performed with the library ade4.

In order to summarize/visualize the effect of Collembola life forms on the 16 PLFA indicators, we performed a principal component analysis (PCA) for each sampling time ( $t= 30$  days and  $t=60$  days). PCA were computed on transformed data according to Hellinger (library vegan) and using the ADE-4 package.

### 3. Results

#### 3.1. PLFA

##### 3.1.1. Total PLFA

For the first month, total PLFAs differed significantly between treatments (Figure 5-1).

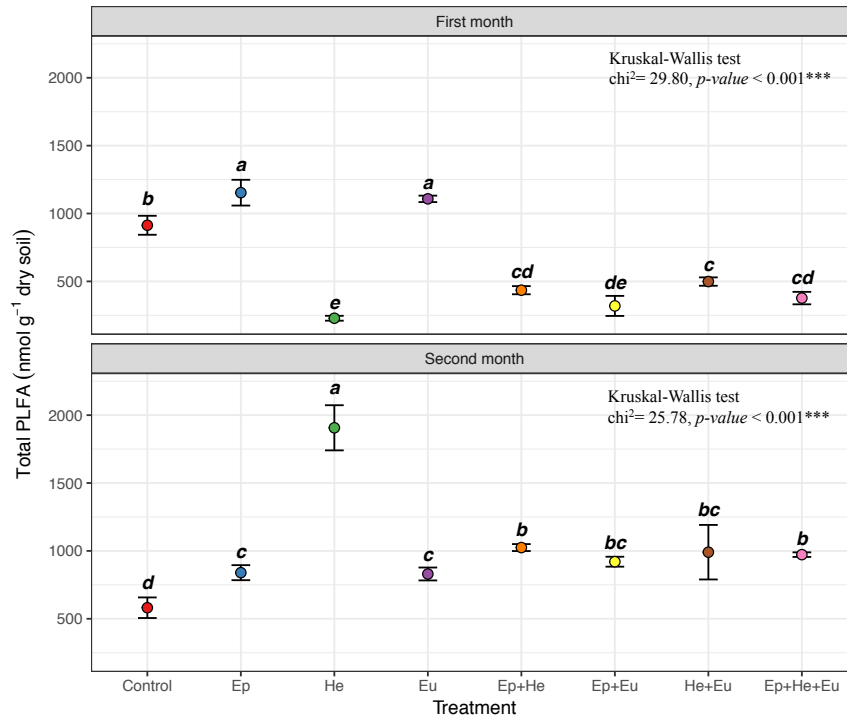


Figure 5-1 : Total PLFA (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, one, two and all life forms following Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic.  $n = 4$ .

All treatments with Collembola (one, two and all life forms) significantly influenced total PLFA compared to the control treatment without life-forms of Collembola. “Ep” and “Eu” treatments positively influenced this parameter with higher values (with an average of 1154 and 1108 nmol g<sup>-1</sup> dry soil, respectively) compared to control (913 nmol g<sup>-1</sup> dry soil in average value); as well as the other five experimental treatments (which averaged 372 nmol g<sup>-1</sup> dry soil). As for these last treatments, i.e. He, Ep+He, Ep + Eu, He + Eu and Ep + He + Eu, they negatively influenced total PLFA with lower values compared to control (372 vs. 913 nmol g<sup>-1</sup> dry soil). The “He” treatment seems to show the lowest total PLFA value (with mean 229 nmol g<sup>-1</sup> dry soil) among all the treatments studied for this first month. On the other hand, the mixed treatments (two and three life forms) showed predicted values significantly higher than those observed (t-test,

Tableau 5-2). Also, only Ep+Eu and Ep+He+Eu treatments showed that the observed values did not conform to the predicted /theoretical (chisq-test, Tableau 5-2).

*Tableau 5-2 : Qualitative comparison between predicted net effects (based on Collembola biomass) and observed effects on total PLFAs, bacterial, fungal and general indicators (mean ± standard deviation) of the first month in function of mixed treatments (two and three life forms). The values are in nmol g<sup>-1</sup>. The tests values are given Chi-square compliance and t-test. The rejection level was set at  $\alpha = 0.05$ . \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns  $p > 0.05$ . The different letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between observed and predicted values for each treatment. Ep = Epedaphic; He = Hemiedaphic; Eu = Euedaphic. Predicted value = microbial parameter / mean biomass of Collembola functional groups considered. Observed value =really measured value.*

	Ep + He		Ep + Eu		He + Eu		Ep + He + Eu	
	Observed	Predicted	Observed	Predicted	Observed	Predicted	Observed	Predicted
<b>Total PLFA</b>	435.1 ± 29.98 <sup>b</sup>	766.3 ± 43.70 <sup>a</sup>	319.3 ± 73.80 <sup>b</sup>	985.3 ± 36.27 <sup>a</sup>	498.7 ± 30.77 <sup>b</sup>	1059 ± 23.77 <sup>a</sup>	377.0 ± 45.89 <sup>b</sup>	1087 ± 35.88 <sup>a</sup>
t-test		-12.50***		-16.20***		-28.82***		-24.37***
chisq-test		6.902 <sup>ns</sup>		42.26***		4.077 <sup>ns</sup>		11.35**
<b>Bacterial PLFA</b>	212.6 ± 12.84 <sup>b</sup>	375.3 ± 30.63 <sup>a</sup>	158.21 ± 34.09 <sup>b</sup>	495.4 ± 23.29 <sup>a</sup>	247.6 ± 26.96 <sup>b</sup>	600.1 ± 20.13 <sup>a</sup>	209.7 ± 30.71 <sup>b</sup>	560.4 ± 21.13 <sup>a</sup>
t-test		-9.798***		-16.33***		-20.96***		-18.82***
chisq-test		3.878 <sup>ns</sup>		19.09***		11.28*		11.64**
<b>Fungal PLFA</b>	181.6 ± 20.71 <sup>b</sup>	267.1 ± 19.93 <sup>a</sup>	138.3 ± 33.44 <sup>b</sup>	348.7 ± 19.59 <sup>a</sup>	198.6 ± 3.80 <sup>b</sup>	398.8 ± 14.91 <sup>a</sup>	153.5 ± 25.49 <sup>b</sup>	389.5 ± 18.95 <sup>a</sup>
t-test		-5.944**		-10.86***		-26.01***		-14.86***
chisq-test		11.62**		21.95***		1.861 <sup>ns</sup>		12.08**
<b>General indicators PLFA</b>	40.91 ± 8.66 <sup>b</sup>	114.6 ± 11.40 <sup>a</sup>	22.80 ± 15.98 <sup>b</sup>	131.6 ± 14.60 <sup>a</sup>	52.54 ± 9.130	60.35 ± 17.09	13.87 ± 0.95 <sup>b</sup>	128.5 ± 15.18 <sup>a</sup>
t-test		-10.30***		-11.22***		-0.806 <sup>ns</sup>		-15.07***
chisq-test		5.735 <sup>ns</sup>		16.11**		21.08***		0.309 <sup>ns</sup>

*Tableau 5-3 : Qualitative comparison between predicted net effects (based on Collembola biomass) and observed effects on total PLFAs, bacterial, fungal and general indicators (mean ± standard deviation) of the second month in function of mixed treatments (two and three life forms). The values are in nmol g<sup>-1</sup>. The tests values are given Chi-square compliance and t-test. The rejection level was set at  $\alpha = 0.05$ . \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns  $p > 0.05$ . The different letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between observed and predicted values for each treatment. Ep = Epedaphic; He = Hemiedaphic; Eu = Euedaphic; Control = no Collembola added. Predicted value = microbial parameter / mean biomass of Collembola functional groups considered. Observed value =really measured value.*

	Ep + He		Ep + Eu		He + Eu		Ep + He + Eu	
	Observed	Predicted	Observed	Predicted	Observed	Predicted	Observed	Predicted
<b>Total PLFA</b>	1024 ± 25.64 <sup>b</sup>	1523 ± 112.4 <sup>a</sup>	920.4 ± 36.59 <sup>a</sup>	717.1 ± 44.68 <sup>b</sup>	990.5 ± 201.0 <sup>b</sup>	1813 ± 115.2 <sup>a</sup>	972.5 ± 16.95 <sup>b</sup>	1293 ± 79.47 <sup>a</sup>
t-test		-8.648**		7.042***		-7.099**		-7.884**
chisq-test		18.44***		6.230ns		99.56***		16.52***
<b>Bacterial PLFA</b>	502.5 ± 12.66	524.6 ± 61.22	463.4 ± 28.11 <sup>a</sup>	358.6 ± 30.63 <sup>b</sup>	494.5 ± 101.8	641.3 ± 76.52	444.0 ± 99.13	521.0 ± 53.51
t-test		-0.707ns		5.041**		-2.305ns		-1.367 ns
chisq-test		27.93***		10.13*		31.82***		123.5***
<b>Fungal PLFA</b>	373.4 ± 20.15 <sup>b</sup>	816.9 ± 74.31 <sup>a</sup>	325.9 ± 9.48 <sup>a</sup>	258.6 ± 9.64 <sup>b</sup>	353.2 ± 74.59 <sup>a</sup>	937.4 ± 69.24 <sup>a</sup>	324.1 ± 46.39 <sup>b</sup>	604.1 ± 35.33 <sup>a</sup>
t-test		-11.52***		9.959***		-11.48***		-9.604***
chisq-test		9.337*		0.070ns		51.24***		31.36***
<b>General indicators PLFA</b>	148.6 ± 8.93 <sup>b</sup>	181.4 ± 20.82 <sup>a</sup>	131.1 ± 4.37 <sup>a</sup>	99.91 ± 6.16 <sup>b</sup>	142.9 ± 30.77 <sup>b</sup>	234.0 ± 23.90 <sup>a</sup>	138.4 ± 7.23 <sup>b</sup>	167.7 ± 11.49 <sup>a</sup>
t-test		-2.895*		8.256***		-4.679**		-4.313**
chisq-test		11.69**		0.554 <sup>ns</sup>		26.44***		5.057 <sup>ns</sup>

For the second month, the total PLFA were also significantly different between the treatments tested (Figure 5-1). All treatments with Collembola (one, two and all life forms) positively influenced this parameter with higher values compared to control (1069 vs. 581nmol g<sup>-1</sup> dry soil in average value). The “He” treatment seems to show the highest total PLFA value (with

average 1907 nmol g<sup>-1</sup> dry soil) among all treatments studied for this second month. Ep + He and Ep + He + Eu were higher compared to Ep and Eu (1025 & 973 vs. 840 & 830 nmol g<sup>-1</sup> dry soil in average value, respectively); “Ep + Eu” and “He + Eu” treatments showed intermediate values, but stronger than the control treatment. For mixed treatments (two and three life forms), only Ep + Eu treatment showed significantly higher observed values than those predicted (t-test, , Tableau 5-3). The distribution of the observed data was conformed to that of the predicted data (Chisq test, , Tableau 5-3). The other treatments showed the opposite effect (t-test and Chisq test, Tableau 5-3).

### 3.1.2. PLFA diversity: Shannon index

For the first month, PLFA diversity differed significantly between experimental treatments (Figure 5-2). The diversity of PLFA was arranged as follows: Ep > Eu > Control, He, Ep + He > Ep + Eu, He + Eu, Ep + He + Eu. The He treatment was the most weakly diversified.

For the second month, the diversity of PLFA showed significant differences between the experimental treatments (Figure 5-2). The greatest diversity was observed in the Eu treatment. Subsequently, He + Eu, Ep + He + Eu > Ep + Eu, Ep > Ep + He, control > He. Thus the He treatment had the lowest diversity.

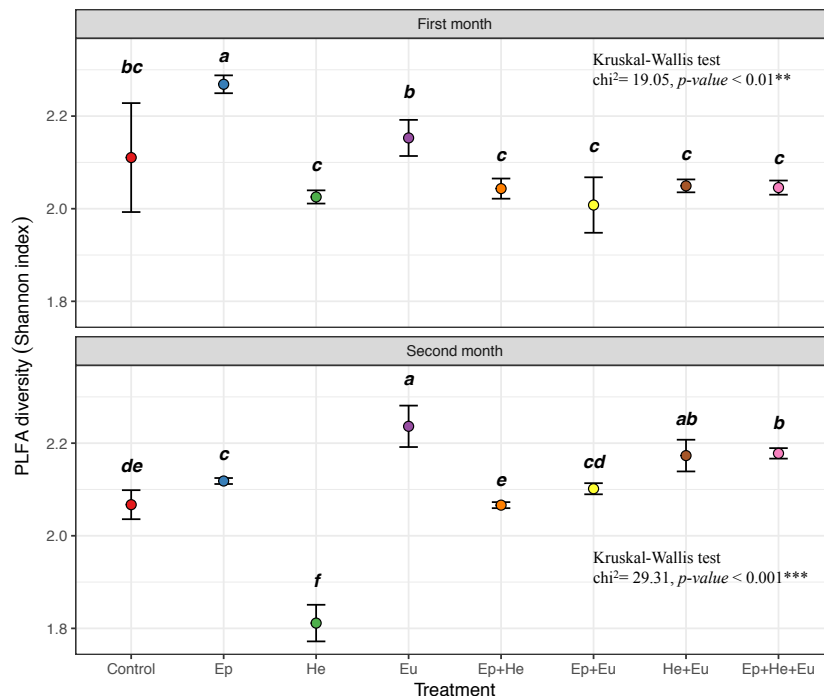


Figure 5-2 : PLFA diversity based on Shannon index (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, one, two and all life forms following Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic. n= 4.

### 3.1.3. PLFA groups

- Bacterial PLFA

For the first month, bacterial PLFA differed significantly between treatments (Figure 5-3). Only the Ep treatment was not different from the control. Eu treatment showed higher bacterial PLFA values compared to control (625 vs. 523 nmol g<sup>-1</sup> dry soil in average value). The He, Ep + He, Ep + Eu, He + Eu and Ep + He + Eu treatments showed lower values compared to control. The "He" treatment seems to show the lowest value of bacterial PLFA (133 nmol g<sup>-1</sup> of dry soil on average) among all the treatments studied for this first month. On the other hand, the mixed treatments (two and three life forms) showed predicted values significantly higher than those observed (t-test, Tableau 5-2). Only Ep+He treatment showed that the distribution of the observed data was conforming to that of the predicted data (Chisq test, Tableau 5-2).

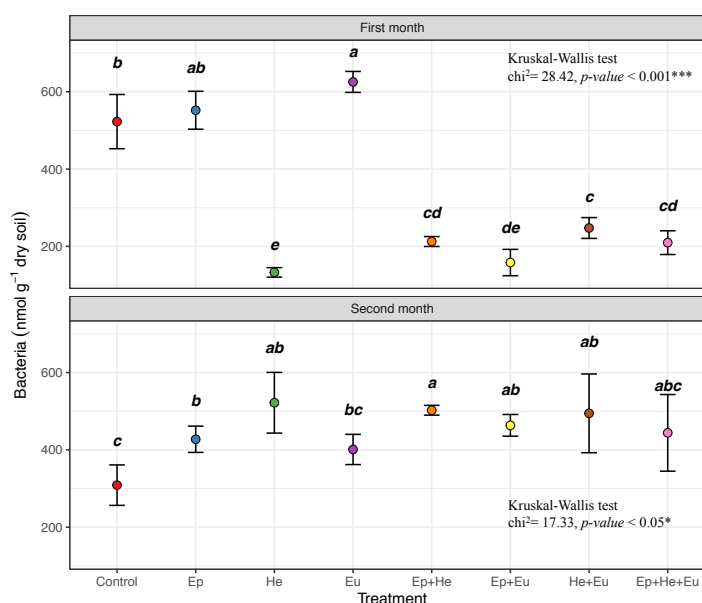


Figure 5-3: Bacterial PLFA (means and standard deviation) of eight experimental treatments over a period of two months. For each date, different minuscule letters (i.e. "a", "b") indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, one, two and all life forms following Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic.  $n = 4$ .

For the second month, bacterial PLFA differed significantly between treatments (Figure 5-3). The treatments Eu and Ep + He + Eu, were very variable and did not show significant differences compared to the control treatment. In addition, all other treatments with Collembola (Ep, He, Ep + He, Ep + Eu and He + Eu) had higher PLFA values than the control. For mixed treatments (two and three life forms), only Ep + Eu treatment showed significantly higher observed values than those predicted. The other treatments showed no effect (t-test, Table 4).



Moreover for each of the mixed treatments, the distribution of the observed data did not conforming to that of the predicted data (Chisq test, Tableau 5-3).

- Fungal PLFA

For the first month, fungal PLFA differed significantly between treatments (Figure 5-4). The He, Ep + He, Ep + Eu, He + Eu and Ep + He + Eu treatments showed lower values compared to the Ep, Eu and control treatments (152 vs 382 nmol g<sup>-1</sup> of dry soil on average). The He treatment recorded the lowest fungal PLFA value with an average of 86 nmol g<sup>-1</sup> of dry soil. Focusing on the mixed treatments (two and three life forms), we note that predicted values significantly were higher than those observed (t-test, Tableau 5-2). Also, only He+Eu treatment showed that the observed values did conform to the predicted /theoretical (chisq-test, Tableau 5-2).

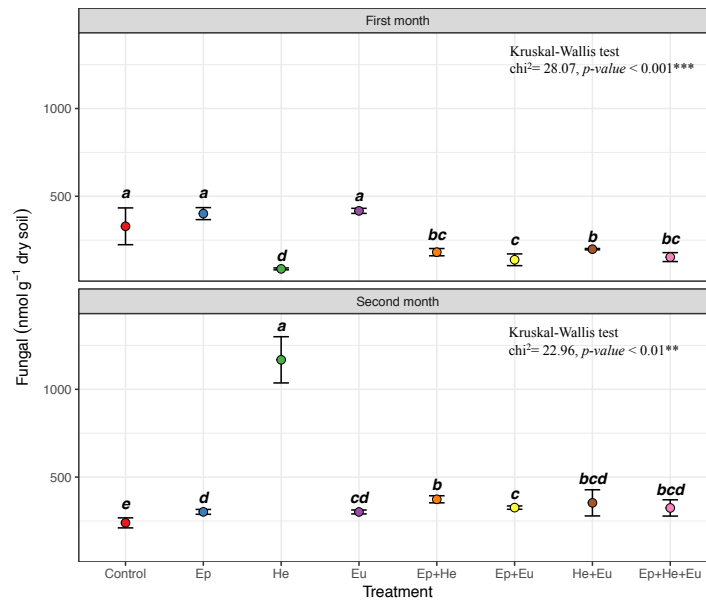


Figure 5-4 : Fungal PLFA (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, one, two and all life forms following Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic. n= 4.

For the second month, fungal PLFAs were influenced by experimental treatments (Figure 5-4). All treatments with Collembola showed stronger values than the control treatment. The highest value was noted in the He treatment with an average of 1168 nmol g<sup>-1</sup> of dry soil. For mixed treatments (two and three life forms), only Ep+Eu treatment showed significantly higher observed values than those predicted. The distribution of the observed data was conforming to that of the predicted data (Chisq test, Tableau 5-3). The other treatments showed the opposite effect (t-test, table and Chisq test, Tableau 5-3).

- General indicators PLFA

For the first month, general indicators PLFA differed significantly between treatments (Figure 5-5). The He, Ep + Eu and Ep + He + Eu treatments showed lower values compared to the Ep, Eu and control treatments (15.4 vs 127 nmol g<sup>-1</sup> of dry soil on average). The He treatment recorded the lowest general indicators PLFA value with an average of 9.43 nmol g<sup>-1</sup> of dry soil. For mixed treatments (two and three life forms), only He+Eu treatment showed no effect between observed and predicted values, the other treatments presented predicted values significantly higher than those observed (t-test, Tableau 5-2). The distribution of observed data was conforming to that of the predicted data for Ep+He and Ep+He+Eu, but not for Ep+Eu and He+Eu (Chisq test, Tableau 5-2).

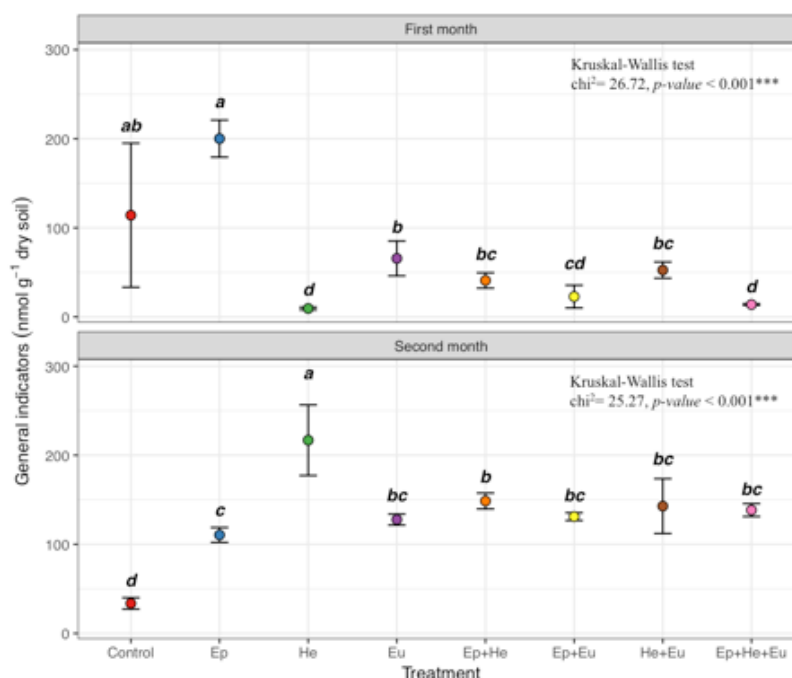


Figure 5-5 : General indicators of PLFA (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, one, two and all life forms following Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic. n= 4.

For the second month, general indicators PLFA were influenced by experimental treatments (Figure 5-5). All treatments with Collembola showed stronger values than the control treatment. The highest value was noted in the He treatment with an average of 217-nmol g<sup>-1</sup> of dry soil. For mixed treatments (two and three life forms), only Ep+Eu treatment showed significantly higher observed values than those predicted. The other treatments showed the opposite effect (t-test, table and Chisq test, Tableau 5-3). The distribution of the observed data was conforming

to that of the predicted data (Chisq test, Tableau 5-3) for Ep+Eu and Ep+He+Eu, but not for Ep+He and He+Eu.

### 3.1.4. Principal component analysis

For the first month, the proportion of the total variance in the PCA (Figure 5-6), which is explained by all PLFAs, is 67%. The first axis accounted for 41% of variance, the second 17%, and the third 15%. Generally, Control, Ep and Eu treatments were separated from the treatments He, Ep+He+Eu, Ep+He, Ep+Eu and He+Eu along the first axis. Second axis showed a differentiation between two life forms treatments and He with Ep+He+Eu treatment in intermediate position. Indeed, Control, Ep and Eu were correlated with higher values of C16.1.9, C18, C15, C14, C15a and C15i, while He were related to higher values of C18.2, C17D, C16i. Two life forms treatments (Ep+He, Ep+Eu and He+Eu) were only correlated with higher values of C18.1.c, C16, and C18.1.t.

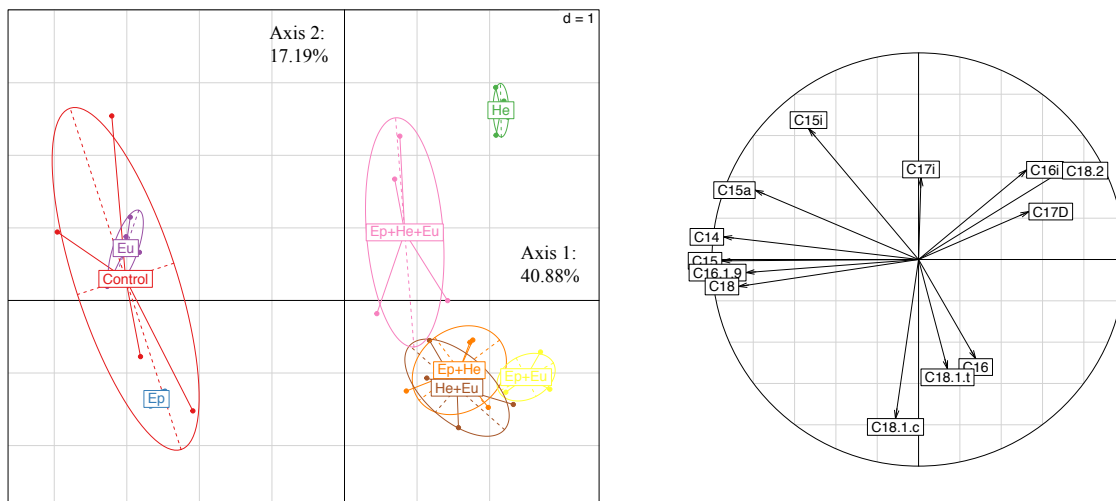


Figure 5-6 : Principal Component Analysis (PCA) of PLFA mixed of first month. . Control= no Collembola added, Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic

For the second month, the proportion of the total variance in the PCA (Figure 5-7), which is explained by all PLFAs, is 60%. The first axis accounted for 45% of variance, the second 16%, and the three 11%. He treatment was separated from the treatments with Collembola (Ep, Ep+He, Ep+Eu, Eu, He+Eu and Ep+He+Eu) along the first axis. Second axis showed a differentiation between control and Eu, He+Eu, Ep+He+Eu treatments. Ep, Ep+He, Ep+Eu treatment in intermediate. Indeed, He correlated with higher values of C18.1.c and C18.1.t (fungal indicators); Ep+He was related to higher values of C18.2 (fungal indicator). Ep, Ep+Eu were correlated with higher values of C15a, C15i, C16i, C17i (bacterial Gram+). Eu, He+Eu and Ep+He+Eu were related to higher values of C14, C16, C15, C18 and C16.1.9 (General

indicators and bacterial Gram-). Control only correlated with higher values of C17D (bacterial Gram-).

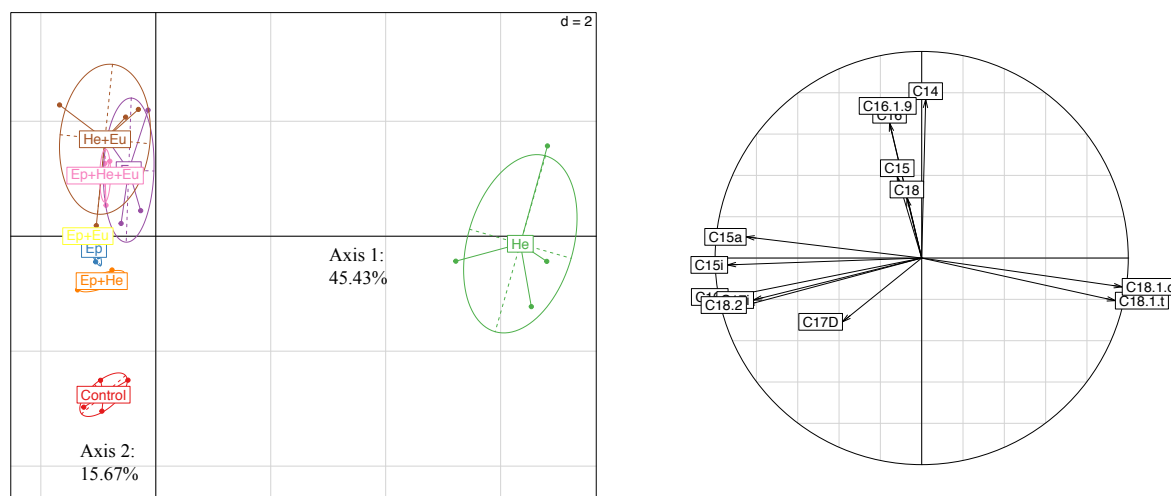


Figure 5-7 : Principal Component Analysis (PCA) of PLFA mixed of second month. . Control= no Collembola added, Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic.

### 3.2. Heterotrophic soil activity

#### 3.2.1. Microbial activity: Carbon mineralization

For the first month, CO<sub>2</sub> activity differed significantly between treatments (Figure 5-8). Except the Ep treatment, all other treatments with Collembola have influenced CO<sub>2</sub> activity. The Ep + He treatment influenced positively by showing higher values compared to control (298 vs. 233  $\mu\text{g CO}_2 \text{ g}^{-1}$  dry soil). While other treatments (He, Eu, Ep + He, and He + Eu + Eu + He Ep) were lower compared to the control (Figure 5-8). For mixed treatments (two and three life forms), we observed that predicted values significantly higher than those observed except for Ep+He treatment, where the opposite trend was found (t-test, Tableau 5-4). Also, only He+Eu and Ep+He+Eu treatments showed that the observed values did not conform to the predicted /theoretical values, while the Ep+He and Ep+Eu treatments were compliant (chisq-test, Tableau 5-4).

Tableau 5-4 : Qualitative comparison between predicted net effects (based on Collembola biomass) and observed effects CO<sub>2</sub> activity and three enzymatic activities (mean ± standard deviation) of the first month in function of mixed treatments (two and three life forms). The tests values are given Chi-square compliance and t-test. The rejection level was set at α = 0.05. \*\*\*p<0.001, \*\*p<0.01, \*p<0.05, ns p>0.05. The different letters (i.e. “a”, “b”) indicated significant differences (α = 0.05) between observed and predicted values for each treatment. Ep = Epedaphic; He = Hemiedaphic; Eu = Euedaphic; Control = no Collembola added. Predicted value = microbial parameter / mean biomass of Collembola functional groups considered. Observed value =really measured value.

	Ep + He		Ep + Eu		He + Eu		Ep + He + Eu	
	Observed	Predicted	Observed	Predicted	Observed	Predicted	Observed	Predicted
Carbon mineralization								
<b>CO<sub>2</sub> activity (µg g<sup>-1</sup>)</b>	298.4 ± 24.96 <sup>a</sup>	188.0 ± 4.98 <sup>b</sup>	95.71 ± 9.83 <sup>b</sup>	181.8 ± 9.16 <sup>a</sup>	70.61 ± 7.39 <sup>b</sup>	138.4 ± 29.79 <sup>a</sup>	94.39 ± 13.65 <sup>b</sup>	198.51 ± 11.17 <sup>a</sup>
x-squared		8.675 **		-12.81 ***		-4.416 *		-11.81 ***
p		6.518 <sup>ns</sup>		4.440 <sup>ns</sup>		18.23 ***		9.657 *
Enzymatic activities								
<b>FDA (µg g<sup>-1</sup> h<sup>-1</sup>)</b>	43.44 ± 10.89 <sup>b</sup>	76.36 ± 7.88 <sup>a</sup>	74.04 ± 4.69 <sup>a</sup>	58.71 ± 5.50 <sup>b</sup>	35.22 ± 11.22 <sup>b</sup>	94.84 ± 16.56 <sup>a</sup>	52.54 ± 10.42 <sup>b</sup>	80.38 ± 8.59 <sup>a</sup>
x-squared		-4.898 **		4.241 **		-5.911 **		-4.122 **
p		3.351 <sup>ns</sup>		0.210 <sup>ns</sup>		23.32 ***		2.756 <sup>ns</sup>
<b>B-glucosidase (µg g<sup>-1</sup> h<sup>-1</sup>)</b>	8.702 ± 0.58 <sup>b</sup>	12.64 ± 1.46 <sup>a</sup>	6.509 ± 1.89	6.240 ± 1.20	7.066 ± 0.97 <sup>b</sup>	13.87 ± 1.60 <sup>a</sup>	12.32 ± 1.51	10.63 ± 0.95
x-squared		-4.997 **		0.237 ns		-7.269 ***		1.888 <sup>ns</sup>
p		0.584 <sup>ns</sup>		0.529 ns		0.014 ns		1.604 <sup>ns</sup>
<b>Urease (µg g<sup>-1</sup> h<sup>-1</sup>)</b>	31.97 ± 2.37	35.16 ± 4.26	22.69 ± 4.04	25.59 ± 4.26	35.75 ± 4.24	33.77 ± 4.39	36.30 ± 4.69	33.66 ± 4.50
x-squared		-1.311 <sup>ns</sup>		-0.987 <sup>ns</sup>		0.650 <sup>ns</sup>		0.810 <sup>ns</sup>
p		0.866 <sup>ns</sup>		6.181 <sup>ns</sup>		0.324 <sup>ns</sup>		1.415 <sup>ns</sup>

Tableau 5-5 : Qualitative comparison between predicted net effects (based on Collembola biomass) and observed effects CO<sub>2</sub> activity and three enzymatic activities (mean ± standard deviation) of the Second month in function of mixed treatments (two and three life forms). The tests values are given Chi-square compliance and t-test. The rejection level was set at α = 0.05. \*\*\*p<0.001, \*\*p<0.01, \*p<0.05, ns p>0.05. The different letters (i.e. “a”, “b”) indicated significant differences (α = 0.05) between observed and predicted values for each treatment. Ep = Epedaphic; He = Hemiedaphic; Eu = Euedaphic; Control = no Collembola added. Predicted value = microbial parameter / mean biomass of Collembola functional groups considered. Observed value =really measured value.

	Ep + He		Ep + Eu		He + Eu		Ep + He + Eu	
	Observed	Predicted	Observed	Predicted	Observed	Predicted	Observed	Predicted
Carbon mineralization								
<b>CO<sub>2</sub> activity (µg g<sup>-1</sup>)</b>	155.1 ± 10.10 <sup>a</sup>	134.3 ± 12.90 <sup>b</sup>	84.24 ± 23.52	72.19 ± 10.75	114.41 ± 20.04 <sup>b</sup>	164.7 ± 12.95 <sup>a</sup>	200.1 ± 28.16 <sup>a</sup>	120.95 ± 10.04 <sup>b</sup>
x-squared		2.542 *		0.932 <sup>ns</sup>		-4.218 **		5.292 **
p		10.31 *		5.640 <sup>ns</sup>		12.45 **		11.02 *
Enzymatic activities								
<b>FDA (µg g<sup>-1</sup> h<sup>-1</sup>)</b>	43.78 ± 8.60 <sup>b</sup>	75.52 ± 3.87 <sup>a</sup>	28.97 ± 4.21 <sup>b</sup>	50.85 ± 3.60 <sup>a</sup>	63.90 ± 7.82 <sup>b</sup>	87.05 ± 3.27 <sup>a</sup>	44.54 ± 8.84 <sup>b</sup>	73.22 ± 2.66 <sup>a</sup>
x-squared		-6.732 **		-7.897 ***		-5.464 **		-6.216 **
p		4.335 <sup>ns</sup>		3.979 <sup>ns</sup>		4.271 <sup>ns</sup>		4.541 <sup>ns</sup>
<b>B-glucosidase (µg g<sup>-1</sup> h<sup>-1</sup>)</b>	9.81 ± 1.47	11.79 ± 0.75	6.84 ± 0.84	8.26 ± 0.81	14.87 ± 1.74 <sup>a</sup>	10.75 ± 0.57 <sup>b</sup>	4.28 ± 0.68 <sup>b</sup>	10.94 ± 0.65 <sup>a</sup>
x-squared		-2.404 <sup>ns</sup>		-2.429 <sup>ns</sup>		-4.503 *		-14.15 ***
p		0.716 <sup>ns</sup>		0.848 <sup>ns</sup>		1.227 <sup>ns</sup>		0.178 <sup>ns</sup>
<b>Urease (µg g<sup>-1</sup> h<sup>-1</sup>)</b>	24.70 ± 3.26	23.39 ± 3.01	22.02 ± 4.19	16.68 ± 2.83	22.28 ± 2.49 <sup>b</sup>	26.75 ± 1.24 <sup>a</sup>	26.55 ± 2.34	23.23 ± 2.72
x-squared		0.589 <sup>ns</sup>		2.108 <sup>ns</sup>		-3.207 *		1.855 <sup>ns</sup>
p		0.334 <sup>ns</sup>		4.582 <sup>ns</sup>		0.692 <sup>ns</sup>		1.016 <sup>ns</sup>

For the second month, CO<sub>2</sub> activity was influenced by experimental treatments (Figure 5-8). All treatments with Collembola showed stronger values than the control treatment. The highest value was noted in the Ep + He + Eu treatment with an average of 200 µg CO<sub>2</sub> g<sup>-1</sup> dry soil. For mixed treatments (two and three life forms), we noted that observed values significantly higher

than those predicted for Ep+He and Ep+He+Eu treatments, He+Eu treatment showed the opposite trend, while Ep+Eu showed no effect (t-test, Tableau 5-5). Also, except Ep+Eu treatment, the distribution of the observed data did not conforming to that of the predicted data (Chisq test, Tableau 5-5).

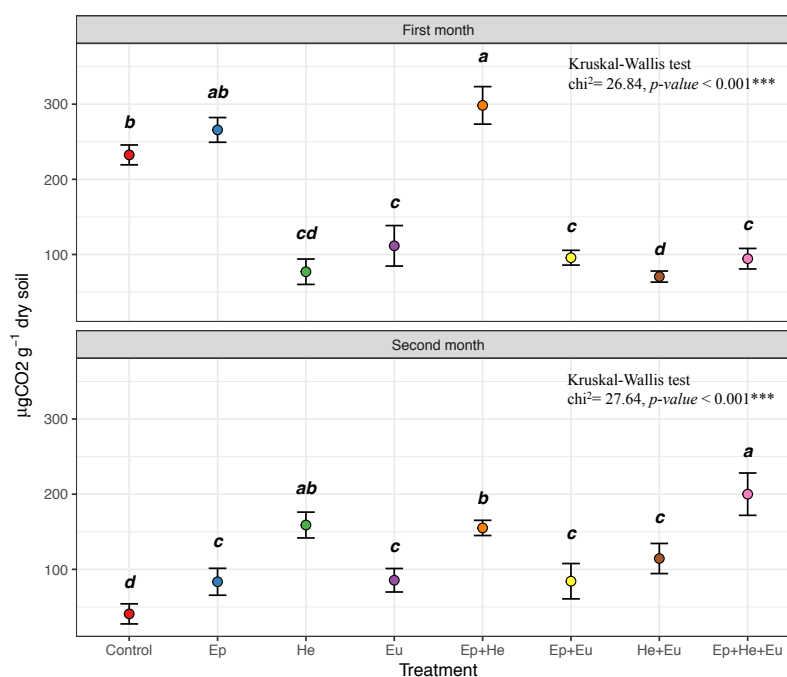


Figure 5-8 : CO<sub>2</sub> activity (means and standard deviation) of eight experimental treatments over a period of two months. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic.

### 3.2.2. Enzymatic activities

- FDA activity

For the first month, FDA activity was significantly affected by treatment (Figure 5-9). The highest value was noted in the Ep + Eu treatment. For mixed treatments (two and three life forms), only Ep+Eu treatment showed significantly higher observed values than those predicted. The Other treatments showed the opposite effect (t-test, table and Chisq test, Tableau 5-4). The distribution of the observed data was conforming to that of the predicted data for all treatments except He+Eu (Chisq test, Tableau 5-4).

As for the second month, the latter (Ep+Eu treatment) was lower compared to all other treatments studied. And the highest value was recorded by the He treatment (Figure 5-9). On the other hand, the mixed treatments (two and three life forms) showed predicted values significantly higher than those observed (t-test, , Tableau 5-5). Also, for each these treatments,

the distribution of the observed data did conforming to that of of the predicted data (Chisq test, Tableau 5-5).

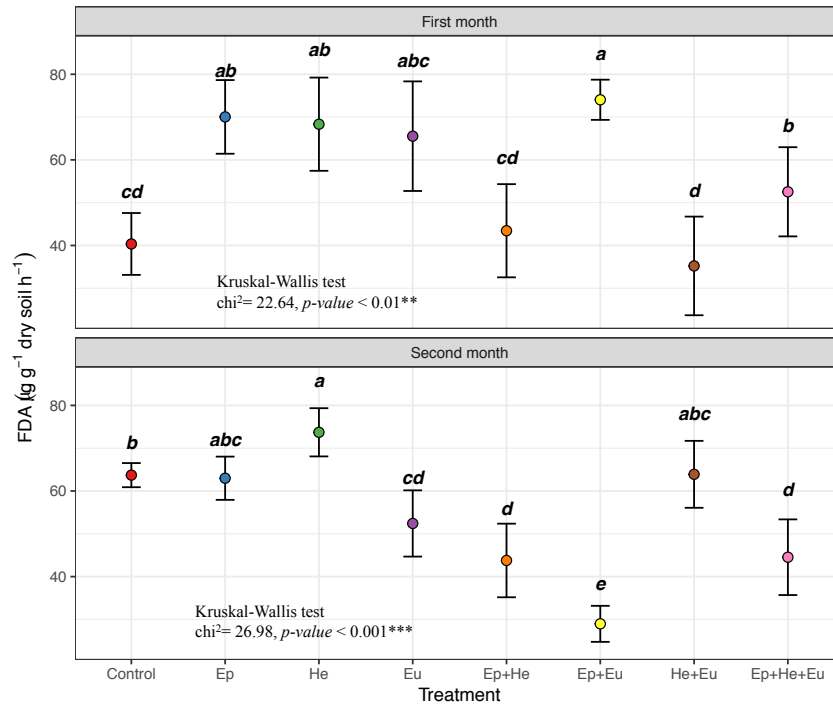


Figure 5-9 : FDA activity (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic.

- Glucosidase activity

For the first month,  $\beta$ -Glucosidase activity differed significantly between treatments (Figure 5-10). The “He” and “Ep + He + Eu” treatments showed higher values compared to the other treatments studied (13.6 vs. 7.09  $\mu\text{g g}^{-1}$  dry soil on average). For mixed treatments (two and three life forms), Ep+He and He+Eu treatments showed significantly higher predicted values than those observed, while Ep + Eu and Ep + He + Eu showed no effect (t-test, table and Chisq test, Tableau 5-4). The distribution of the observed data was conforming to that of the predicted data for all treatments (Chisq test, Tableau 5-4).

For the second month,  $\beta$ -Glucosidase activity was influenced by experimental treatments (Figure 5-10). The lowest and highest values were recorded in treatments Ep + He + Eu (4.28  $\mu\text{g g}^{-1}$  dry soil) and He + Eu (14.9  $\mu\text{g g}^{-1}$  dry soil), respectively. On the other hand, the mixed treatments (two and three life forms) showed predicted values significantly higher than those observed for Ep+He+Eu, He+Eu had the opposite effect, and while Ep+He and Ep+Eu showed

no effect (t-test, Tableau 5-5). Also, for each these treatments, the distribution of the observed data did conforming to that of of the predicted data (Chisq test, Tableau 5-5).

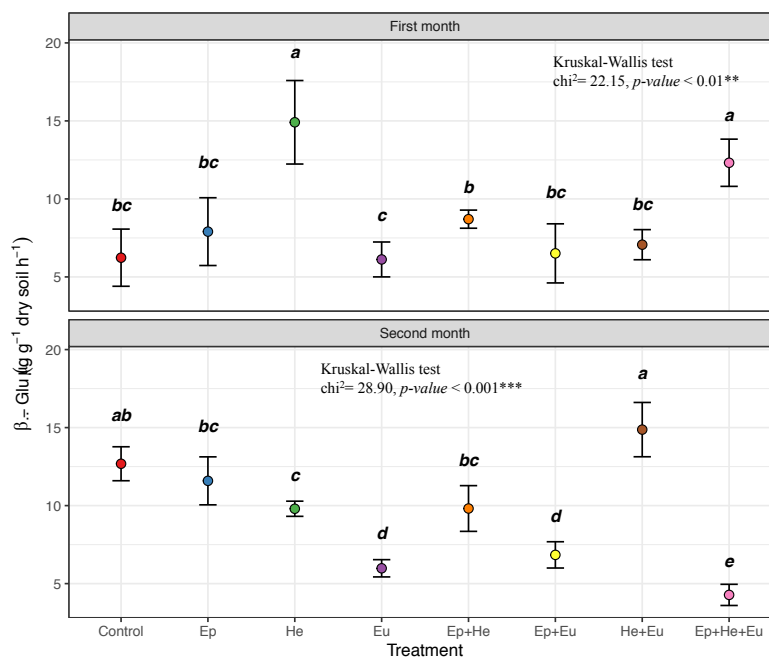


Figure 5-10 :  $\beta$ -Glucosidase activity (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, Ep = *Epedaphic*, He= *Hemiedaphic*, Eu= *Euedaphic*.

- Urease activity

For the first month, Urease activity was significantly affected by treatments (Figure 5-11). Urease activity was arranged from 20.2-to 36.3- $\mu\text{g g}^{-1}$  dry soil  $\text{h}^{-1}$ . Ep, Ep+He, He+Eu and Ep+He+Eu treatments showed higher values compared to the Eu and Ep + Eu treatments (on average 34.7 vs. 21.5  $\mu\text{g g}^{-1}$  dry soil  $\text{h}^{-1}$ ). The other treatments (control and He) had intermediate values. For mixed treatments (two and three life forms), no effects were showed between predicted and observed values (t-test, Tableau 5-4). Also, the distribution of the observed data was conforming to that of the predicted data for all treatments (Chisq test, Tableau 5-4).

For the second month, Urease activity differed significantly between experimental treatments (Figure 5-11). Urease activity was arranged from 16.9-to 26.6- $\mu\text{g g}^{-1}$  dry soil  $\text{h}^{-1}$ . Ep+He+Eu treatment had the highest value and the lowest was attributed to the Eu treatment. On the other hand, the mixed treatments (two and three life forms), except He+Eu treatment where the observed value was lower than that predicted, the other treatments showed no effect (t-test,



Table 6). Also, all treatments, the distribution of the observed data did conforming to that of of the predicted data (Chisq test, Tableau 5-5).

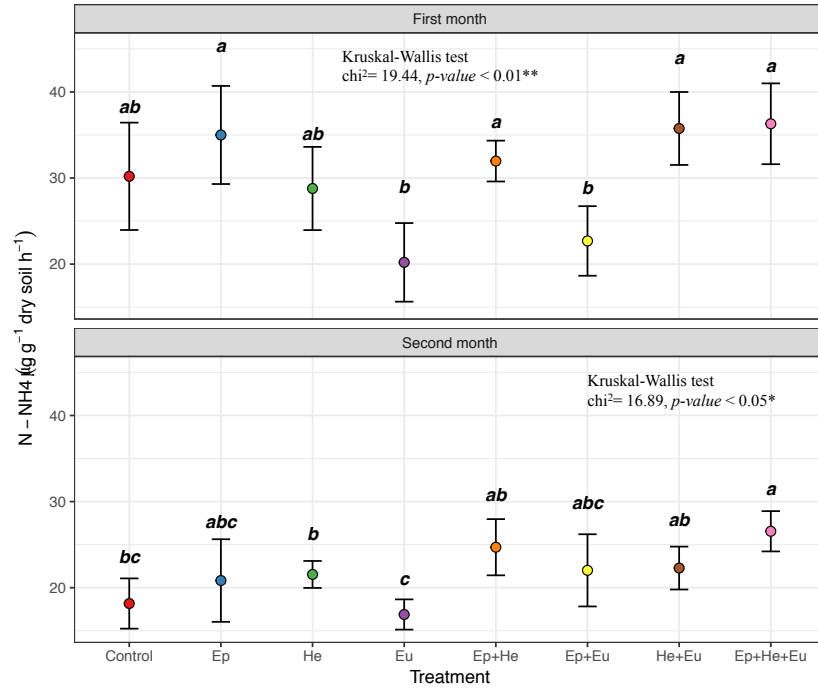


Figure 5-11 : Urease activity (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic.

#### 4. Discussion

Our present experiment over two months had for objective to determine whether varying the composition of the life-forms of Collembola has effects on microbial community of the soil (modifying its biomass, composition and activity), resulting in potentially important effects on ecosystem processes.

Our results showed that one-month after the start of the experiment, all treatments with Collembola significantly influenced the total PLFA. The Ep and Eu treatments stimulated it by showing stronger values compared to treatment control, whereas the others such as He, Ep + He, Ep + Eu, He + Eu and Ep + He + Eu inhibited it. In the same way, PCA ordination of the experimental treatments over the first month on all PLFAs mixed (Figure 5-6) revealed a clear differentiation between Control, Ep and Eu on one side and Ep+He+Eu, Ep+He, Ep+Eu and He+Eu on the other side of the first axis. The He treatment became quite isolated according to the second axis. We note that the combination of the different life forms of Collembola as well as hemiedaphic Collembola lead to a decrease in total PLFA. These decreases by these

treatments were found in the different groups of PLFA (bacterial, fungal and general indicators) and that overall the Hemiedaphic treatment showed lower values thus reflecting their effect of grazing on the microbial communities in the first 30 days of experience. This was not the case of Collembola ep- and euedaphic, since in these treatments, they generally stimulated the microbial community. These distinctions could be explained based on the identity of these three Collembola groups. Collembola ep- and euedaphic are two most dissimilar groups in terms of biological traits and microhabitats, whereas the hemiedaphic group includes intermediate attributes sharing ep- and euedaphic (Petersen, 2002; Rusek, 1998). Therefore, the hemiedaphic have access to both soil microhabitats (surface and deep), thus controlling trophic resources until depletion. That is why when they are associated with the other two forms of life, we observe decreases. These results could be explained by the considerable increase in  $\beta$ -glucosidase and FDA activity, but also the decrease of CO<sub>2</sub> activity in He treatment (see Figure 5-8, Figure 5-9 and Figure 5-10). As for Urease activity, we noted that He treatment had intermediate values, which might suggest their effect on the carbon cycle.

By the same token, after 60 days of experience (second month), total PLFAs were stimulated by Collembola treatments showing higher values compared to control treatment. And He treatment, which had lower values in the first month, showed this time the highest values (total, bacterial, fungal and general indicators) in the second month, but very slightly diversified (see Figure 5-2). Focusing on the results of PCA of the second month (Figure 5-7), the He treatment was only linked to two PLFA markers (indicators) such as C18.1.c and C18.1.t. These are considered as specific markers of fungal. A third fungal marker (C18.2) was more related to the Ep+He treatment along the first axis. This allowed us to see the effect of Collembola hemiedaphic on fungal communities. At the same time, we found that Collembola ep- and euedaphic and their association was correlated with bacterial and general markers. Specifically, the Ep, Ep + Eu treatments were linked to Gram+ bacteria (C15a, C15i, C16i, C17i), whereas the Eu, He+Eu and Ep+He +Eu treatments were rather related to general and Gram- bacteria markers (C14, C16, C15, C18 and C16.1.9). Overall, the second month of this experiment allowed a specialization of microbial communities with respect to the variation of the different forms of Collembola life and their association. We can say that the first month is linked to the quantity of resources and the second month is associated with the specialization of different experimental treatments with respect to trophic resources (quality of resources).

Focusing on the combination of the different life-forms of Collembola, we noted at the end of the first 30 days of the experiment, observed values of total PLFA, bacterial, fungal and general

indicators well below those predicted (Tableau 5-2), thus reflecting complementarity effects (facilitation) between life-forms. While facilitation has been clearly identified for plants (Brooker et al. 2008, journal of ecology), only few examples emerge from soil fauna. Our study supports the hypothesis of Heemsbergen et al. (2004) stating that the nature of the interspecific interactions plays the most significant role in the direction and magnitude of their response.

However, at the end of the experiment (at the end of the second month), only the Ep + Eu treatment had observed values higher than the predicted values on total PLFAs, bacterial, fungal and general indicators (Tableau 5-3). Thus, at the end of the second month the Collembola ep- and euedaphic showed that they departed especially general indicators and bacteria (as described above), therefore their association could result in effects of competitions for the same trophic resources.

## **5. Conclusion**

Our study conducted under controlled conditions (microcosms), showed that the different functional groups of Collembola, alone or combined interact differently on microbial communities over time. Taking into account the time in such an experiment is an important factor to fully appreciate the relationships that are established within a food web



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## **CONCLUSION GENERALE ET PERSPECTIVES**

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L'objectif principal de ce travail de thèse visait à explorer les réponses de la faune du sol aux pratiques agricoles innovantes développées en Normandie et en Picardie et d'anticiper les conséquences fonctionnelles de ces changements.

Le but de ce chapitre est de répondre aux questions formulées dans la partie introductive de ce manuscrit (rappelées ci-dessous), et de synthétiser et discuter l'ensemble des résultats.

- Comment le couplage de deux pratiques innovantes favorise-t-il la fonctionnalité des sols agricoles ? Quelle pratique produit le plus d'effet sur la faune du sol ? Observe-t-on une réponse similaire sur les différents groupes faunistiques aux pratiques mises en place ? (Chapitre 2)
- Existe-t-il une dissemblance de structure et de composition des assemblages de collemboles entre cinq régimes de gestion au cours des quatre années de l'étude (à long terme) ? Si oui, quelle est la modalité de gestion la plus importante (celle imprimant la trajectoire observée) ? (Chapitre 3)
- Quel est l'effet de la conversion du travail du sol sur les communautés de vers de terre et de collemboles au cours d'une saison de végétation ? Existe-t-il une résistance et/ou une résilience fonctionnelle de ces communautés quant à l'intensité du travail du sol ? (Chapitre 4)
- Quelle est l'influence différentielle de chacune des formes de vie de collemboles sur les communautés de microorganismes ? Existe-t-il une complémentarité fonctionnelle entre les différentes formes de vie ? (Chapitre 5)

## **I. Synthèse des résultats**

### **1. Introduction des légumineuse et réduction du travail du sol (Chapitre 2)**

Ce chapitre avait pour objectif de tester dans les conditions réelles d'exploitation agricole, l'effet combiné de deux pratiques innovantes (l'intégration des légumineuses dans la rotation de culture et la réduction du travail du sol) sur plusieurs communautés de la faune du sol (vers de terre, collemboles, microorganismes avec les bactéries et champignons) et les teneurs en éléments nutritifs (carbone, azote). Cette étude s'est déroulée à une échelle spatio-temporelle régionale couvrant la Normandie et sur des méthodes d'exploitations en place depuis plus de cinq années.

Nous avons étudié six modalités expérimentales comprenant la présence et la position de la légumineuse (féverole, Faba bean) dans la rotation de culture (pas de féverole, féverole en n-1

et féverole en n-3) couplées à deux systèmes de travail du sol (labour profond vs peu profond). Nos résultats ont montré que les communautés des vers de terre et des collemboles répondent différemment aux pratiques culturales innovantes. L'abondance et la biomasse des collemboles ont augmenté, tandis que les vers de terre n'ont pas été influencés. Cette augmentation constatée dans la structure des assemblages de collemboles suite à l'adoption des deux pratiques innovantes est surtout expliquée en termes de groupes fonctionnels. En effet, chaque forme de vie (épédaphique, hémiédaphique et euédaphique) témoigne d'une réponse différente aux facteurs agronomiques testés : réduction du travail du sol, introduction de légumineuses, et leur interaction. L'abondance et la biomasse des collemboles épédaphiques ont augmenté lors de la réduction du travail du sol et l'introduction de la féverole et cela à très court terme (n-1). Pour les euédaphiques, leur abondance et leur biomasse n'ont pas été influencées par l'introduction des légumineuses, mais elles ont augmenté suite à la réduction de la profondeur du travail du sol et lors de l'interaction des deux pratiques à moyen terme (n-3). Cela était dû surtout à l'augmentation marquée de l'ADN et l'ARN fongique, et témoigne le fait que les collemboles euédaphiques soient contrôlés par les ressources trophiques « bottom-up effect » (Henneron et al., 2016; Schneider and Maraun, 2009). Quant aux collemboles hémiédaphiques, seule l'introduction de légumineuses dans les rotations de culture a favorisé leur abondance et leur biomasse, dont l'effet n'a duré qu'à court terme (n- 1). Ces différences de réponses dans les groupes fonctionnels de collemboles suite à l'adoption des pratiques innovantes au cours du temps pourraient être liées à leurs stratégies biologiques basées sur certaines caractéristiques comme la reproduction, le développement et la mobilité (Siepel, 1994). Le faible niveau de réponse observé sur les collemboles hémiédaphique peut être expliqué par leurs caractéristiques intermédiaires (stratégie rK). En effet, certaines de leurs espèces peuvent être favorisées à l'inverse d'autres défavorisées ou bien présentant une réponse neutre. Globalement, les hémiédaphiques présentent moins de variations suite à l'adoption des pratiques mise en place.

Par ailleurs, un point étonnant de nos résultats est que les teneurs en éléments nutritifs (carbone, azote) n'ont pas réagi à l'adoption des pratiques agricoles innovantes, et notamment le fait d'incorporer les légumineuses dans les rotations de culture. Or plusieurs études soutiennent une augmentation des quantités d'azote à l'issue de l'introduction des légumineuses (Brockwell et al., 1995; D'Annibale et al., 2017; Nemecek et al., 2008; Sileshi et al., 2008). Ce qui n'a pas été le cas de notre étude, puisque nous n'avons pas pu dénouer un effet global de cette pratique légumineuse sur le cycle des nutriments. Au terme, de ces résultats, il s'avère que certains effets bénéfiques de ces pratiques innovantes ne peuvent être envisagés sans prendre en compte la



manière dont elles ont été mises en œuvre à l'échelle des rotations culturales (itinéraires techniques) ainsi que l'historique des pratiques anciennement employées dans chacune des parcelles prospectées.

## **2. Réduction du travail du sol, gestion des résidus de culture, diminution de la fertilisation azotée (Chapitre 3)**

Suite aux résultats observés dans le chapitre précédent, cela nous a permis de suivre dans les mêmes conditions pédoclimatiques (échelle spatiale plus réduite) et mêmes itinéraires techniques, l'effet à long terme (quatre ans) de cinq régimes de gestion différents sur les communautés de collemboles. Les traitements comprenaient des combinaisons de différentes cultures (annuelles, pérennes) avec des taux de fertilisation azotée différents (ajout de N, réduction de N), des résidus de culture (incorporation ou élimination de résidus) et intensités de labour contrastées (labour profond vs peu profond).

En réponse aux questions, nos résultats démontrent que le passage d'un système conventionnel à un système de conservation a un fort effet positif sur la richesse spécifique et la densité des collemboles. Plus précisément, tous les traitements avec une réduction de l'intensité du travail du sol ont favorisé les assemblages de collemboles. À la fin de notre étude, la densité et la richesse en espèces étaient 3 à 4 fois plus élevées en travail superficiel que dans le labour conventionnel. Néanmoins, la différenciation entre les assemblages de collemboles ne s'est produite qu'au bout de 2 ans, avec une différence croissante jusqu'à la fin de l'étude. À la dernière date d'échantillonnage, tous les traitements présentaient des assemblages de collemboles significativement différents. Parallèlement, nous avons remarqué des changements dans la structure fonctionnelle des assemblages, même si globalement, toutes les formes de vie ont été favorisées par un labour réduit. Ces changements sont particulièrement marqués pour le groupe des euédaphiques où la densité et la richesse sont plus fortes dans la culture pérenne à la dernière date d'échantillonnage grâce à l'augmentation de la biomasse microbienne.

Ainsi, il apparaît que les assemblages de collemboles soient plus sensibles à l'intensité du travail du sol qu'à la gestion des résidus ou à la fertilisation azotée.

## **3. Réduction et arrêt de la perturbation mécanique (Chapitre 4)**

Dans ce chapitre, le but principal était de suivre sur une saison de végétation l'effet de la conversion du travail du sol conventionnellement utilisé, sur les communautés d'organismes du sol (vers de terre, collemboles, microorganismes) et sur certains paramètres abiotiques (densité

apparente, stock de carbone organique, taille des agrégats). L'expérimentation a intégré trois niveaux de travail du sol : labour profond (état habituel), labour peu profond et non labour (états convertis). Ce suivi s'est déroulé à une échelle spatio-temporelle plus réduite : sur un seul site, sur une saison de végétation dont deux opérations de perturbations mécaniques (uniquement dans les systèmes de travail du sol). Cela a permis un suivi important des changements s'opérant au sein des communautés en réponse aux différents modes de travail du sol.

Nos résultats montrent que l'arrêt du travail du sol a entraîné une augmentation de la taille des populations (abondance et diversité) de vers de terre et de collemboles au cours du temps. Ce changement dans le compartiment endogé était lié à l'amélioration de la distribution de la matière organique et à l'accessibilité de cette dernière comme source alimentaire de base (stock de COS, biomasse microbienne et fongique et leur activité potentielle de minéralisation C), de la structure physique du sol et de la distribution des tailles de pores comme espace de vie (densité apparente, MWD et taille des agrégats). De plus, les organismes du sol semblent répondre différemment quant à l'effet de la perturbation mécanique (Labour profond vs peu profond). La diversité des vers de terre diminue juste après réduction du travail du sol alors que les collemboles ne montrent aucune réponse jusqu'à la répétition du travail du sol où leur diversité a significativement baissé. A la fin de l'expérimentation, nous avons observé dans chacun des systèmes de travail du sol, une augmentation des populations de collemboles contrairement à celles des vers de terre qui continuaient à baisser en effectifs.

#### **4. Relations entre les groupes fonctionnels de collemboles et les communautés microbiennes (Chapitre 5)**

Les précédents résultats montrent des changements importants dans les communautés de faune du sol en lien avec les itinéraires agricoles. Ces changements ont été observés principalement au niveau des formes de vie de collemboles. Au vu des fonctions écosystémiques assurées par ce groupe d'organismes, nous avons réalisé une expérience ex situ ciblant les conséquences fonctionnelles des changements d'assemblages de faune du sol liés aux différentes pratiques agricoles innovantes. Pour cela, nous avons décidé de caractériser dans une approche mécaniste les actions des différentes formes de vie de collemboles (Epédaphique, Hemiédaphique et Euédaphique) sur les communautés de microorganismes du sol (bactéries et champignons). Comme le temps est un facteur déterminant des interactions biotiques, nous avons décidé d'étudier la réponse de la microflore aux différents traitements de collemboles au cours du temps pendant deux mois.

Nos résultats ont montré qu'un mois après le début d'expérience, les différentes formes de vie de collemboles influencent différemment les communautés microbiennes. Par comparaison avec un témoin sans collemboles, les collemboles épé- et euédaphiques ont augmenté l'activité microbienne en termes de dégagement de CO<sub>2</sub>, tandis que les hémiedaphiques ont engendré une diminution de la biomasse bactérienne et fongique. Au deuxième mois, nous avons observé que chacune des formes de vie avait une influence positive sur les communautés microbiennes. Les hémiedaphiques avaient très fortement augmenté la biomasse microbienne, en comparaison des groupes d'épé- et euédaphiques (tendance inverse par rapport au premier mois).

Toutefois en associant les différentes formes de vie, par rapport à un témoin sans collemboles, des diminutions en termes de diversité, de biomasse et d'activité sont observées pour la communauté microbienne au premier mois, alors qu'une augmentation de ces différents paramètres est constatée au deuxième mois. De plus au premier mois, nous avons noté une complémentarité entre les formes de vie, tandis qu'au deuxième mois les groupes les plus distincts (épé- et euédaphiques) ont montrés des effets de compétition.

## **5. Bilan des travaux**

Dans nos différentes expérimentations in situ, nous avons suivi les assemblages de vers de terre et de collemboles en réponses à l'adoption de certaines pratiques agricoles innovantes. Il paraît évident que les deux groupes d'organismes du sol, n'ont pas la même réponse vis-à-vis des pratiques agricoles étudiées. Les collemboles ont montré une réponse positive en augmentant leur abondance et leur diversité, tandis que les vers de terre ont eu peu ou pas de réponses (Figure 6.1). Cela démontre la réponse rapide des collemboles aux changements du couvert végétal et des conditions microclimatiques du sol tels que l'habitat et la ressource (Chauvat et al., 2007; Ponge et al., 1993). En général, des effets positifs des nouvelles pratiques agricoles de conservation sur les communautés de collemboles ont été observés (Cortet et al., 2002; Petersen, 2002; Winter et al., 1990b). Dans la faune du sol, les organismes plus gros (comme les vers de terre) sont plus sensibles aux changements des pratiques agricoles que les plus petits (Wardle, 1995). De plus, certaines études ont montré que l'adoption des systèmes de gestion plus durables n'entraîne pas toujours une augmentation de l'abondance et de la diversité des vers de terre (Bernier et al., 2008; Chan, 2001). Très récemment, Briones et Schmidt (2017) ont montré une réponse positive des vers de terre lorsque les systèmes étaient soumis à une agriculture de conservation depuis plus de 10 ans. Or dans nos différents cas d'étude, les systèmes ont récemment été convertis (<10 ans), ce qui pourrait expliquer le faible niveau de réponse des vers de terre sur nos sites d'étude (Figure 6.1). De plus, dans nos différents cas

d'études, plus de 75% des vers de terre étaient des juvéniles, couplés aux régimes de perturbations récurrents dans les systèmes étudiés, cela pourrait retarder leur développement. Dans la littérature, les études ont souvent associé l'augmentation des assemblages de vers de terre par rapport à la diminution de l'intensité du travail du sol (Holland, 2004; Pelosi et al., 2009). Les résultats du chapitre 4 confirment cela, puisque l'arrêt total de toute perturbation mécanique a entraîné une augmentation de leur population (Figure 6-1). Cependant, il a fallu une légère perturbation mécanique pour constater une diminution dans les assemblages de vers de terre. Ce qui n'a pas été le cas des collemboles puisqu'ils ont résisté jusqu'à la répétition du travail du sol et par la suite, augmentent progressivement. Nous notons ainsi une résistance et une résilience plus forte par rapport au travail du sol chez les collemboles comparativement aux vers de terre.

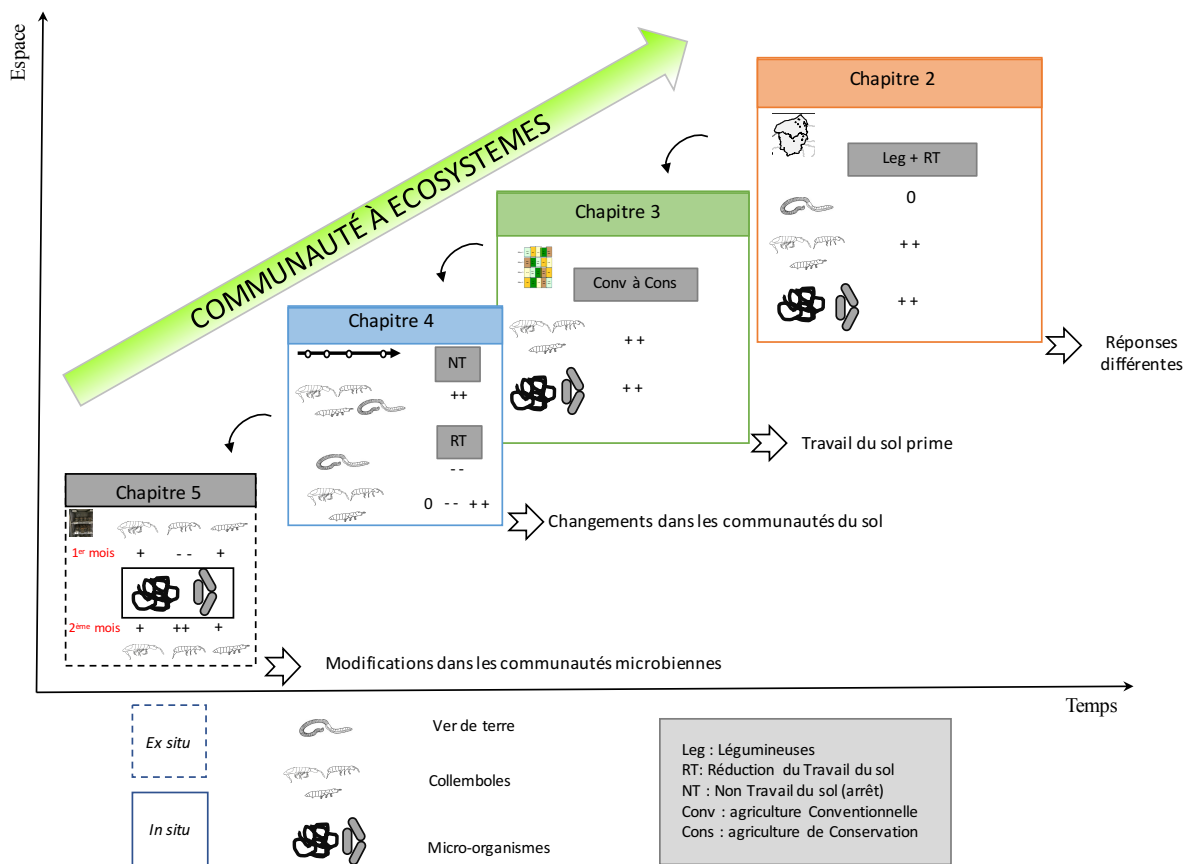


Figure 6-1: Représentation schématique des différents résultats obtenus selon une échelle spatio-temporelle. La taille des carrés est proportionnelle aux échelles de temps et d'espace. Les groupes faunistiques étudiés dans chaque chapitre sont figurés.

Ces changements dans les structures des communautés d'organismes du sol, notamment chez les collemboles, se reflètent dans les modifications en termes de groupes fonctionnels. Les résultats des chapitres 2 et 3 en attestent. En effet, suite à l'application des pratiques agricoles

innovantes, les épé- et les hémiedaphiques présentent une réponse à court terme tandis que les euédaphiques augmentent progressivement au cours du temps (effet tardif). Cette différenciation de réponse entre les groupes fonctionnels semble surtout être lié à leurs interactions avec les communautés microbiennes, dont la résultante de ces interactions pourrait influencer les processus de l'écosystème tels que le recyclage des éléments nutritifs (Chauvat et al., 2014b; Kaneko et al., 1998). Eisenhauer et al. (2010) ont montré que des groupes de décomposeurs fonctionnellement dissemblables pouvaient avoir une incidence synergique sur la performance de plantes.

Enfin, notre approche en fonction des formes de vie de collembolles a démontré des effets variables sur les communautés microbiennes au cours du temps (Figure 6 1). Cette distinction dans le temps peut être associée à la quantité et à la qualité des ressources trophiques (communautés microbiennes).

## **II. Perspectives**

Comme dans tout travail scientifique, les réponses aux questions soulevées dans cette thèse ne s'arrêtent pas aux conclusions exposées dans ce chapitre. Nous proposons ici quelques pistes de réflexions qui pourraient approfondir nos résultats obtenus :

- Introduction des légumineuses, réduction du travail du sol

L'absence d'effet des pratiques agricoles innovantes sur certaines propriétés du sol (comme sur le carbone et azote) permet de mettre l'accent sur la variabilité apportée par la mise en place de ces dernières à l'échelle des rotations culturales (itinéraires techniques), mais aussi celle adressée par la distance géographique qui pourrait traduire le type du sol et les conditions microclimatiques (pédoclimatiques). Afin d'approfondir nos résultats, il serait nécessaire d'effectuer un échantillonnage, prenant en compte les conditions pédoclimatiques et les itinéraires techniques des exploitants (changement des cultures dans la rotation, gestion des résidus, différents produits, phytosanitaires, changement du mode de travail du sol). L'objectif serait de garder le multi-site, mais avec les différentes modalités de l'étude pour chaque site. Ce qui représenterait un nombre de répétitions important et rendrait plus robustes les analyses statistiques. De plus, une telle étude pourrait être complétée par l'étude de l'effet d'une autre variété de légumineuse sur les communautés d'organismes du sol et leur fonctionnement, puisque l'identité des cultures joue un rôle déterminant dans le fonctionnement du compartiment endogé (Chauvat et al., 2014a).

- Réduction du travail du sol, gestion des résidus de culture, diminution de la fertilisation azotée : Echelle spatiale plus réduite

En accord avec des études antérieures, nous avons observé que le passage d'un système de culture conventionnel à un système de conservation changeait la structure et la composition des assemblages de collemboles (Petersen, 2002; Wardle, 1995). De plus, notre approche dynamique nous a permis de montrer que ce changement dans la structure fonctionnelle des collemboles augmente avec la différenciation des pratiques agronomiques au cours du temps. Et cela a permis des réponses complexes des collemboles du sol aux pratiques agricoles innovantes. Ainsi comme reporté par Vandewalle et al. (2010), le développement d'indicateurs utilisant des traits fonctionnels des collemboles pourrait compléter nos résultats. De cette manière, la comparaison de l'effet des changements d'utilisation des terres sur organismes du sol pourrait être facilitée et devrait affiner notre compréhension sur les réponses observées.

- Réduction et arrêt du travail du sol

L'un des résultats majeurs qui émerge de cette thèse est l'effet de la perturbation mécanique lors du travail du sol sur les communautés édaphiques et leurs fonctions associées. De nombreuses études ont montré que la suppression du travail du sol a des effets positifs sur les services fournis par le sol, dont la biodiversité du sol, améliorant ainsi la qualité et l'état des sols (Bedano et al., 2006; Brennan et al., 2006; Briones and Schmidt, 2017; van Capelle et al., 2012). Cependant d'autres études montrent des résultats contradictoires (Berner et al., 2008; Chan, 2001). Cette image conflictuelle pourrait résulter de l'absence d'examen des effets de changements des pratiques agricoles dans un schéma plus large comprenant les niveaux du labour, intrants agrochimiques, gestion des résidus de culture, facteurs du sol (texture, pH, humidité du sol) et climat (Chan, 2001). La variabilité démontrée entre les dates d'échantillonnage dans notre étude, souligne l'importance des échantillonnages multiples dans le temps.

Cependant, nous pensons que certains points ont manqué à nos résultats, notamment le suivi de la composition des communautés d'organismes étudiés suite à la conversion du travail du sol. Ainsi, nos futures recherches devront par exemple envisager des analyses de beta diversité temporelle afin de quantifier le gain et la perte d'espèce entre dates d'échantillonnage. Puisque les changements qui s'opèrent dans les communautés d'organismes du sol sont dynamiques et donc fluctuent au cours du temps, il est donc important de prendre en compte la dynamique de population si nous voulons apprécier pleinement les aspects. Aussi, notre étude s'effectuant uniquement dans une échelle spatio-temporelle réduite (un site et une seule saison végétative),

il serait nécessaire d'envisager un suivi à long terme afin de d'appréhender les réponses escomptées sur les pratiques agricoles novatrices. En effet, il s'avère que certains groupes comme les vers de terre répondent plus tardivement aux effets du travail du sol (Briones and Schmidt, 2017).

- Relations entre groupes fonctionnels de collemboles et communautés microbiennes

Il est important de rappeler que l'expérimentation ex situ mise en place dans cette thèse avait pour but de mieux comprendre les conséquences fonctionnelles des changements d'assemblages de faune du sol liés aux différentes pratiques agricoles novatrices sur les processus de l'écosystème. Cela s'est passé au travers les interactions s'établissant entre formes de vie de collemboles et microorganismes. Nos résultats ont montré que les différents groupes fonctionnels de collemboles (formes de vie) interagissaient différemment avec les communautés microbiennes. Le lien étroit que nous observons entre les différentes formes de vie de collemboles et les communautés microbiennes est très intéressant et tend à supporter que les interactions biotiques qui s'opèrent entre les organismes des réseaux trophiques sont fortement guidées par les traits de réponses des individus au détriment de la classification en termes de groupes fonctionnels. Ainsi, on pourrait se demander au sein d'un même groupe fonctionnel (d'une même forme de vie), quel est l'effet des différents assemblages sur les communautés microbiennes ? Cela nécessite la compréhension des différentes caractéristiques (traits) qui composent le groupe fonctionnel, puisque chaque groupe est composé de différentes espèces avec des caractéristiques qui pourraient être différentes en termes de taille, mobilité, nombre d'ocelles etc. Tout ceci pourrait plaider en faveur d'une meilleure connaissance des relations biotiques et leurs conséquences sur les processus de l'écosystème.

### **III. Transfert de connaissances : préconisations quant aux pratiques agricoles novatrices**

Au regard de nos résultats, l'adoption des pratiques culturales novatrices a entraîné des effets bénéfiques sur les sols et son fonctionnement. En somme, il est important de comprendre que ce travail de thèse a été réalisé sur des cas d'étude. Dans ce sens, nous modérons nos conclusions et leur généralisation doit passer par d'autres cas d'études (sites d'étude dans des contextes différents, l'utilisation d'autres groupes d'organismes du sol etc). Néanmoins, cela n'enlève rien à la qualité des résultats présentés, puis que les effets positifs des pratiques agricoles innovantes sur le compartiment endogé font généralement consensus (Briones and Schmidt, 2017; Dittmer and Schrader, 2000a; Hobbs, 2007; Nakamoto et al., 2006). Cependant,

la comparaison de ces effets nécessite d'avoir des conditions pédoclimatiques semblables, mêmes itinéraires techniques et d'effectuer un suivi temporel (dynamique). La plupart des études ne prennent pas en compte le facteur temps alors que cette approche pourrait affiner notre compréhension des réponses de la faune du sol aux changements environnementaux (Chauvat et al., 2014a) et les conséquences subséquentes sur les processus écologiques (Petersen, 2002).

Il est important de souligner que l'agriculture moderne doit continuer à repenser la gestion des systèmes agricoles, et la nécessité d'intégrer les processus écologiques dans les systèmes de production alimentaire doit être la pierre angulaire de l'agroécologie (Wezel et al., 2014). Une attention particulière doit être accordée à la biodiversité des sols, qui, longtemps a été sous-estimée dans les systèmes de culture, mais dont la conservation est maintenant reconnue comme essentielle pour maintenir ou améliorer les capacités de fonctionnement du sol, comme la décomposition de la litière et le cycle des nutriments (de Graaff et al., 2015; Kibblewhite et al., 2008).





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## Liste des figures

Figure 1-1: Nombre de publications par an relatives à (a) l'effet du travail du sol sur les organismes endogés Topic : « soil tillage effect on soil organisms », (b) agriculture de conservation Topic : « conservation agriculture ». Le point bleu indique l'état pour l'année 2017. (Web of Science, 2017/12/01 ; Timespan = All Years. Databases=SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH, ESCI)... 3	3
Figure 1-2 : Les principes fondamentaux de l'agriculture de conservation (FAO, 2015)..... 8	8
Figure 1-3 : Représentation des principaux groupes taxonomiques d'organismes du sol classé suivant leur taille (Extrait de Decaëns, 2010) d'après Swift and Anderson (1979)..... 12	12
Figure 1-4 : Représentation schématique de la structure des réseaux trophiques du sol : « micro-réseau », « transformateur de litière » et « ingénieur des écosystèmes ». Les flèches indiquent la direction du flux d'énergie (extrait de Lavelle et al., 1995; Wardle, 2002). ..... 13	13
Figure 1-5 : Représentation schématique des différentes pratiques agricoles étudiées en lien avec les chapitres de résultats de la thèse. Q1, Q2, Q3, Q4 indiquent les différentes questions posées respectivement dans les quatre chapitres de résultats. .... 16	16
Figure 1-6 : Représentation schématique des différents dispositifs expérimentaux étudiés selon une échelle spatio-temporelle. La taille des carrés est proportionnelle aux échelles de temps et d'espace. Les groupes faunistiques et les paramètres abiotiques étudiés dans chaque chapitre sont figurés..... 19	19
Figure 2-1 :(a) Empirical experimental design studied. CT: Conventional tillage; RT: Reduced tillage; Leg-1: Faba Bean as previous crop of wheat; Leg-3: Faba Bean sown three years before wheat; None: rotation without Faba Bean and without any leguminous at least during the preceding five years, (b) location of plots: (Seine Maritime and Eure)..... 26	26
Figure 2-2 : pH, CEC: Cation exchange capacity, moisture, NT: total nitrogen; TOC: total organic carbon; POXC: active carbon (means and standard error) according to the different methods studied combining the tillage (CT: conventional tillage-black barplot; RT: reduced tillage-grey barplot) and legume factor (Leg-1: Faba Bean as previous crop of wheat; Leg-3: Faba Bean sown three years before wheat; None: rotation without Faba Bean and without any leguminous at least during the preceding five years.). Different minuscule letters (i.e. "a", "b") indicated significant differences ( $\alpha = 0.05$ ) between "Tillage modalities". Different minuscule letters (i.e. "x", "y") indicated significant differences ( $\alpha = 0.05$ ) between "Leguminous (Leg) modalities". Different capital letters (i.e. "A", "B") showed significant differences ( $\alpha = 0.05$ ) between "interactions (Tillage x Leg) modalities"..... 31	31
Figure 2-3 : Fungal DNA, bacterial DNA; fungal RNA and bacterial RNA (means and standard error) according to the different methods studied combining the tillage (CT: conventional tillage-black barplot; RT: reduced tillage-grey barplot) and legume factor (Leg-1: Faba Bean as previous crop of wheat; Leg-3: Faba Bean sown three years before wheat; None: rotation without Faba Bean and without any leguminous at least during the preceding five years.). Different minuscule letters (i.e. "a", "b") indicated significant differences ( $\alpha = 0.05$ ) between "Tillage modalities". Different minuscule letters (i.e. "x", "y") indicated significant differences ( $\alpha = 0.05$ ) between "Leguminous (Leg) modalities". Different capital letters (i.e. "A", "B") showed significant differences ( $\alpha = 0.05$ ) between "interactions (Tillage x Leg) modalities"..... 32	32
Figure 2-4 : Total density, biomass, species richness and Shannon index of earthworms (means and standard error) according to the different methods studied combining the tillage (CT: conventional tillage-black barplot; RT: reduced tillage-grey barplot) and legume factor (Leg-1: Faba Bean as previous crop of wheat; Leg-3: Faba Bean sown three years before wheat; None: rotation without Faba Bean and without any leguminous at least during the preceding five years.). Different minuscule letters (i.e. "a", "b") indicated significant differences ( $\alpha = 0.05$ ) between "Tillage modalities". Different minuscule letters (i.e. "x", "y") indicated significant differences ( $\alpha = 0.05$ ) between "Leguminous (Leg) modalities". Different capital letters (i.e. "A", "B") showed significant differences ( $\alpha = 0.05$ ) between "interactions (Tillage x Leg) modalities"..... 34	34

Figure 2-5 : Figure 5: Density, biomass and species richness of functional groups of earthworms (means and standard error) according to the different methods studied combining the tillage (CT: conventional tillage-black barplot; RT: reduced tillage-grey barplot) and legume factor (Leg-1: Faba Bean as previous crop of wheat; Leg-3: Faba Bean sown three years before wheat; None: rotation without a Faba Bean and without any leguminous at least during the preceding five years.). Different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between “Tillage modalities”. Different minuscule letters (i.e. “x”, “y”) indicated significant differences ( $\alpha = 0.05$ ) between “Leguminous (Leg) modalities”. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between “interactions (Tillage x Leg) modalities” ..... 35

Figure 2-6 : Non-metric multidimensional scaling (NMDS) plot based on Bray-Curtis dissimilarity indices derived from abundance of earthworms species recorded in six different modalities. CT-None: conventional tillage - rotation without Faba Bean and without any leguminous at least during the preceding five years.; CT-Leg-1: conventional tillage - Faba Bean as previous crop of wheat; CT-Leg-3 : conventional tillage - Faba Bean sown three years before wheat; RT-None : reduced tillage - rotation without Faba Bean and without any leguminous at least during the preceding five years.; RT-Leg-1: reduced tillage - Faba Bean as previous crop of wheat; RT-Leg-3 : reduced tillage - Faba Bean sown three years before wheat ..... 36

Figure 2-7 : Earthworms community compositions of the plots displayed using NMDS. Stress of the ordination is 0.18. Significant variables ( $P < 0.05$ ) are shown by arrows whose length is proportional to the strength of the correlation, and they are shown in bold in the table ..... 36

Figure 2-8 : Relationship between earthworm assemblages (based on bray Curtis distance) and geographical distances (based on Euclidian distance). ..... 37

Figure 2-9 : Total density, biomass, species richness and Shannon index of Collembola (means and standard error) according to the different methods studied combining the tillage (CT: conventional tillage-black barplot; RT: reduced tillage-grey barplot) and legume factor (Leg-1: Faba Bean as previous crop of wheat; Leg-3: Faba Bean sown three years before wheat; None: rotation without Faba Bean and without any leguminous at least during the preceding five years.). Different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between “Tillage modalities”. Different minuscule letters (i.e. “x”, “y”) indicated significant differences ( $\alpha = 0.05$ ) between “Leguminous (Leg) modalities”. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between “interactions (Tillage x Leg) modalities” ..... 38

Figure 2-10 : Density, biomass and species richness of functional groups of Collembola (means and standard error) according to the different methods studied combining the tillage (CT: conventional tillage-black barplot; RT: reduced tillage-grey barplot) and legume factor (Leg-1: Faba Bean as previous crop of wheat; Leg-3: Faba Bean sown three years before wheat; None: rotation without Faba Bean and without any leguminous at least during the preceding five years.). Different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between “Tillage modalities”. Different minuscule letters (i.e. “x”, “y”) indicated significant differences ( $\alpha = 0.05$ ) between “Leguminous (Leg) modalities”. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between “interactions (Tillage x Leg) modalities” ..... 39

Figure 2-11 : Non-metric multidimensional scaling (NMDS) plot based on Bray-Curtis dissimilarity indices derived from abundance of Collembola species recorded in six different modalities. CT-None: conventional tillage - rotation without Faba Bean and without any leguminous at least during the preceding five years.; CT-Leg-1: conventional tillage -Faba Bean as previous crop of wheat; CT-Leg-3 : conventional tillage - Faba Bean sown three years before wheat; RT-None : reduced tillage - rotation without Faba Bean and without any leguminous at least during the preceding five years.; RT-Leg-1: reduced tillage - Faba Bean as previous crop of wheat; RT-Leg-3 : reduced tillage - Faba Bean sown three years before wheat ..... 40

Figure 2-12 : Collembola community compositions of the plots displayed using NMDS. Stress of the ordination is 0.19. Significant variables ( $P < 0.05$ ) are shown by arrows whose length is proportional to the strength of the correlation, and they are shown in bold in the table ..... 41

Figure 2-13 : Relationship between Collembola assemblages (based on bray Curtis distance) and geographical distances (based on Euclidian distance).....	41
Figure 3-1 : Total density (grey boxplots) and species richness (white boxplots) of Collembola assemblages between years (y+2: 2012, y+3: 2013 and y+4: 2014) for five different agricultural treatments (North of France). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced. P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Different letters for a single parameter indicate significant Turkey's HSD differences between treatments at $\alpha=0.05\%$ .....	56
Figure 3-2 : Total density (grey boxplots) and species richness (white boxplots) of Collembola assemblages of five different agricultural treatments (North of France) over a 4-year period (2a: y+2: 2012. 2b: y+3: 2013 and 2c: y+4: 2014). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Different letters for a single parameter indicate significant Turkey's HSD differences between treatments at $\alpha=0.05\%$ .....	58
Figure 3-3 : Shannon index (grey boxplots) and Evenness (white boxplots) of Collembola assemblages of five different agricultural treatments (North of France) followed over 4 years (3a: y+2: 2012. 3b: y+3: 2013 and 3c: y+4: 2014). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Different letters for a single parameter indicate significant Turkey's HSD differences between treatments at $\alpha=0.05\%$ .....	59
Figure 3-4 : Non-metric multidimensional scaling (NMDS) plot based on Bray-Curtis dissimilarity indices derived from abundance of collembolan species recorded in five different agricultural practices (North of France) across a 4-year period (y+2: 2012. y+3: 2013 and y+4: 2014). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal.....	60
Figure 3-5: Density (grey boxplots) and species richness (white boxplots) of the three Collembola functional groups recorded in five different agricultural treatments across a 4-year period (y+2. y+3 and y+4). Ep: Epedaphic, He: Hemiedaphic, Eu: Euedaphic. CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Different letters within a single parameter denote significant differences between treatments at $\alpha=0.05\%$ (Turkey's HSD).....	62
Figure 3-6 : Redundancy analysis (RDA) based on Total density of Collembola (D_tot), total species richness (R_tot), density and richness of each of the three life forms (D_Ep, D_He, D_Eu, R_Ep, R_He, R_Eu), microbial C biomass (Cbiom), microbial activity (CO <sub>2</sub> ), soil moisture (HUM), soil temperature (TEMP) and soil pH (pHwater). All variables were measured in five different agricultural treatments (north of France) 2 to 4 years (y+2: 2012, y+3: 2013 and y+4: 2014) after experimental set-up. CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal.....	63
Figure 4-1: Design of the experiment set-up and samplings schedule. 12 sub-plots in total, each sub-plot is 9 m long and 6 m wide; CT = Conventional Tillage, RT = Reduced Tillage, NT = No Tillage. Samplings: 0: 1 day before Tillage, 1: 1 day after Tillage (aT), 2: 7 days aT, 3: 30 days aT, 4: 49 days aT, 5: 56 days aT, 6: 104 days aT, 7: 210 days aT.....	74
Figure 4-2 : Ombrothermic diagram of Cumulative mean temperature and total rainfall values on 7 days before each sampling date on the experimental site, SOERE ACBB, Estrées-Mons, Picardie, France. D0 is the start of the experiment (la date) and D210 (Date) is the end of the experiment 210 days after D0. ....	75
Figure 4-3 : Total density of Collembola assemblages (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. "a", "b") indicated significant differences ( $\alpha = 0.05$ ) between treatments.	

Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment..... 79

Figure 4-4 : Total species richness of Collembola assemblages (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment..... 80

Figure 4-5 : Shannon index of Collembola assemblages (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment..... 81

Figure 4-6 : Total density of earthworm (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment. .... 82

Figure 4-7 : Total species richness of earthworm (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment. .... 83

Figure 4-8 : Shannon index of earthworm (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment. .... 83

Figure 4-9 : Soil bulk density on 0-5 cm in depth (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment. .... 85

Figure 4-10 : SOC stock on 0- to 5-m in depth (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment. .... 85

Figure 4-11 : Redundancy analysis (RDA) biplot of the conventional tillage (CT) data showing : a) soil fauna variables (D_Ew : Earthworms density; R_Ew : Earthworms species richness; D_Coll: Collembola density; R_Coll : Collembola species richness; MBC : Microbial biomass carbon; FB : Fungal biomass), environmental variables (pH: pH water; CO2: potential C mineralisation; SOC : SOC stock on 0- to 5-m; BD: Bulk density 0-5 cm; MWD : Mean weight diameter; MAG : Macro-aggregates or aggregates > 250 $\mu$ m) and b) plotting sampling days (0 : 1 day before tillage; 1; 7; 30 ; 49; 56; 104; 210 respectively after tillage). .....	89
Figure 4-12 : Redundancy analysis (RDA) biplot of the reduced tillage (RT) data showing : a) soil fauna variables (D_Ew : Earthworms density; R_Ew : Earthworms species richness; D_Coll: Collembola density; R_Coll : Collembola species richness; MBC : Microbial biomass carbon; FB : Fungal biomass), environmental variables (pH: pH water; CO2: potential C mineralisation; SOC : SOC stock on 0- to 5-m; BD: Bulk density 0-5 cm; MWD : Mean weight diameter; MAG : Macro-aggregates or aggregates > 250 $\mu$ m) and b) plotting sampling days (0 : 1 day before tillage; 1; 7; 30 ; 49; 56; 104; 210 respectively after tillage). .....	90
Figure 4-13 : Redundancy analysis (RDA) biplot of the no tillage (NT) data showing : a) soil fauna variables (D_Ew : Earthworms density; R_Ew : Earthworms species richness; D_Coll: Collembola density; R_Coll : Collembola species richness; MBC : Microbial biomass carbon; FB : Fungal biomass), environmental variables (pH: pH water; CO2: potential C mineralisation; SOC : SOC stock on 0- to 5-m; BD: Bulk density 0-5 cm; MWD : Mean weight diameter; MAG : Macro-aggregates or aggregates > 250 $\mu$ m) and b) plotting sampling days (0 : 1 day before tillage; 1; 7; 30 ; 49; 56; 104; 210 respectively after tillage). .....	90
Figure 5-1 : Total PLFA (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, one, two and all life forms following Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic. n= 4.....	107
Figure 5-2 : PLFA diversity based on Shannon index (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, one, two and all life forms following Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic. n= 4.....	109
Figure 5-3: Bacterial PLFA (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, one, two and all life forms following Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic. n= 4.....	110
Figure 5-4 : Fungal PLFA (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, one, two and all life forms following Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic. n= 4.....	111
Figure 5-5 : General indicators of PLFA (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, one, two and all life forms following Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic. n= 4.....	112
Figure 5-6 : Principal Component Analysis (PCA) of PLFA mixed of first month. . Control= no Collembola added, Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic.....	113
Figure 5-7 : Principal Component Analysis (PCA) of PLFA mixed of second month. . Control= no Collembola added, Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic.....	114
Figure 5-8 : CO <sub>2</sub> activity (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic.....	116

Figure 5-9 : FDA activity (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic. .... 117

Figure 5-10 :  $\beta$ -Glucosidase activity (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic. .... 118

Figure 5-11 : Urease activity (means and standard deviation) of eight experimental treatments over a period of two month. For each date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Control= no Collembola added, Ep = Epedaphic, He= Hemiedaphic, Eu= Euedaphic. .... 119

## Liste des tableaux

Tableau 2-1 : Results of Linear Mixed-Effects Models (LMM) of “tillage effect”, “leguminous effect” and “interaction effect” on physicochemical variables (pH, CEC: Cation exchange capacity, moisture, NT: total nitrogen; TOC: total organic carbon; POXC: active carbon). The tests values are given. F: F-value, p: p-value. ***p<0.001, **p<0.01, *p<0.05, ns p>0.05. The rejection level was set at $\alpha = 0.05$ . The location of the significant differences is in Figure 2-2.....	30
Tableau 2-2 : Results of Linear Mixed-Effects Models (LMM) of “tillage effect”, “leguminous effect” and “interaction effect” on microbial variables. The tests values are given. F: F-value, p: p-value. The rejection level was set at $\alpha = 0.05$ . ***p<0.001, **p<0.01, *p<0.05, ns p>0.05. The location of the significant differences is in Figure 2-3.....	31
Tableau 2-3 : Results of Linear Mixed-Effects Models (LMM) of “tillage effect”, “leguminous effect” and “interaction effect” on total density, biomass, species richness and Shannon index of earthworms. The tests values are given. F: F-value, p: p-value. The rejection level was set at $\alpha = 0.05$ . ***p<0.001, **p<0.01, *p<0.05, ns p>0.05. The location of the significant differences is in Figure 2-4.....	33
Tableau 2-4 : Results of Linear Mixed-Effects Models (LMM) of “tillage effect”, “leguminous effect” and “interaction effect” on total density, biomass, species richness of functional groups of earthworms. An: Anecic, En: Endogeic. The tests values are given. F: F-value, p: p-value. The rejection level was set at $\alpha = 0.05$ . ***p<0.001, **p<0.01, *p<0.05, ns p>0.05. The location of the significant differences is in Figure 2-5.....	35
Tableau 2-5 : Results of Linear Mixed-Effects Models (LMM) of “tillage effect”, “leguminous effect” and “interaction effect” on total density, biomass, species richness and Shannon index of Collembola. The tests values are given. F: F-value, p: p-value. The rejection level was set at $\alpha = 0.05$ . ***p<0.001, **p<0.01, *p<0.05, ns p>0.05. The location of the significant differences is in Figure 2-9.....	37
Tableau 2-6 : Results of Linear Mixed-Effects Models (LMM) of “tillage effect”, “leguminous effect” and “interaction effect” on total density, biomass, species richness of functional groups of Collembola. Ep: Epedaphic; He: Hemiedaphic; Eu: Euedaphic. The tests values are given. F: F-value, p: p-value. The rejection level was set at $\alpha = 0.05$ . ***p<0.001, **p<0.01, *p<0.05, ns p>0.05. The location of the significant differences is in Figure 2-10.....	38
Tableau 2-7 : Results of ANOSIM analyses between Collembola assemblages within six different modalities. p-values after correction of Bonferroni are given. CT-None: conventional tillage - rotation without Faba Bean and without any leguminous at least during the preceding five years.; CT-Leg-1: conventional tillage - Faba Bean as previous crop of wheat; CT-Leg-3 : conventional tillage - Faba Bean sown three years before wheat; RT-None : reduced tillage - rotation without Faba Bean and without any leguminous at least during the preceding five years.; RT-Leg-1: reduced tillage - Faba Bean as previous crop of wheat; RT-Leg-3 : reduced tillage - Faba Bean sown three years before wheat.....	40
Tableau 3-1 : Description of the 5 investigated treatments of the SOERE ACBB located in Estrées-Mons, France, according to three main practices: soil tillage, crop residue management, and N fertilization rate.....	52
Tableau 3-2 : Results of Linear Mixed-Effects Models (LMM) of the effect of year (y+2, y+3 and y+4) on total density, species richness of Collembola assemblages for each agricultural treatment (CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal). The tests values are given. Chisq : Chi-squared, p : p-value, R2 : variance explained by both fixed and random factors. Degree of freedom = 4. The rejection level was set at $\alpha = 0.05$ . ***p<0.001, **p<0.01, *p<0.05, ns p>0.05.....	55
Tableau 3-3 : Results of Linear Mixed-Effects Models (LMM) of the effect of treatment on total density, species richness, Shannon index and evenness of Collembola assemblages sampled at three different sampling dates (y+2, y+3 and y+4). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop	



residues removal. The tests values are given. Chisq : Chi-squared, p : p-value, R2 : variance explained by both fixed and random factors. Degree of freedom = 4. The rejection level was set at  $\alpha = 0.05$ . \*\*\*p<0.001, \*\*p<0.01, \*p<0.05, ns p>0.05..... 57

Tableau 3-4 : Results of ANOSIM analyses between collembolan assemblages within five different agricultural treatments (North of France) after 3 (y+3) and 4 years (y+4) following experimental set-up. CT: Conventional tillage; CT-RN: Conventional tillage and nitrogen reduced. P-BC: Perennial and Bioenergy Crop. RT: Reduced tillage; RT-RR: Reduced tillage and crop residues removal. P-value and R-values (within brackets) are given. For clarity, significant results are in bold. .... 60

Tableau 3-5 : Results of Linear Mixed-Effects Models (LMM) of the effect of the factor treatment on the density and species richness of the three functional groups after 2 (y+2), 3 (y+3) and 4 years (y+4). CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Chisq: Chi-square value. p : p-value. R2: variance explained by both fixed and random factors. Degree of freedom = 4. The rejection level was set at  $\alpha = 0.05$ . \*\*\*p<0.001. \*\*p<0.01. \*p<0.05. ns p>0.05..... 62

Tableau 4-1: Results of Linear Mixed-Effects Models (LMM) of “the effect of treatment for each sampling date” and “the effect of sampling day for each treatment” on total density, species richness and Shannon index of Collembola and earthworm. D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage. CT: Conventional tillage, RT: Reduced tillage and NT: No tillage. The tests values are given. F: F-value, p: p-value, R2: variance explained by both fixed and random factors. The rejection level was set at  $\alpha = 0.05$ . \*\*\*p<0.001, \*\*p<0.01, \*p<0.05, ns p>0.05. The location of the significant differences is in Figure 4-3, Figure 4-4, Figure 4-5, Figure 4-6, Figure 4-7and Figure 4-8..... 78

Tableau 4-2 : Results of Linear Mixed-Effects Models (LMM) of “the effect of treatment for each sampling date” and “the effect of sampling day for each treatment” on bulk density (0- to 5-cm) and SOC stock (0- to 0.05-m). D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage. CT: Conventional tillage, RT: Reduced tillage and NT: No tillage. The tests values are given. F: F-value, p: p-value, R2: variance explained by both fixed and random factors. The rejection level was set at  $\alpha = 0.05$ . \*\*\*p<0.001, \*\*p<0.01, \*p<0.05, ns p>0.05. The location of the significant differences is in Figure 4-9 and Figure 4-10. .... 84

Tableau 4-3 : Soil Aggregate mean weight diameter (MWD) and pH water (means  $\pm$  standard errors) of three different tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates for each experimental treatment. .... 86

Tableau 4-4 : Soil microbial biomass carbon (MBC) and fungal biomass (FB) (means  $\pm$  standard errors) of three different tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates for each experimental treatment. .... 87

Tableau 4-5 : C-CO2 (means  $\pm$  standard errors) of three different tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates for each experimental treatment..... 88

Tableau 4-6 : Results of redundancy analysis of three treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) based on tests of permutations (n=999). The values of the first two axis are given..... 88

Tableau 5-1 : Mean density of Collembola (number of individuals) introduced in each treatment. The most dominant species per life forms were : Ep (*Isotoma anglicana*, *Lepidocyrtus violaceus*, *Isotomurus palustris* gr); He (*Parisotoma notabilis*, *Sminthurinus aureus*, *Ceratophysella denticulata*); Eu (*Folsomia fimetaria*, *Protaphorura armata* gr, *Mesaphorura* spp). Ep: Epedaphic, He: Hemiedaphic; Eu : Euedaphic ..... 103

Tableau 5-2 : Qualitative comparison between predicted net effects (based on Collembola biomass) and observed effects on total PLFAs, bacterial, fungal and general indicators (mean  $\pm$  standard deviation) of the first month in function of mixed treatments (two and three life forms). The values are in nmol g-1. The tests values are given Chi-square compliance and t-test. The rejection level was set at  $\alpha = 0.05$ . \*\*\*p<0.001, \*\*p<0.01, \*p<0.05, ns p>0.05. The different letters (i.e. "a", "b") indicated significant differences ( $\alpha = 0.05$ ) between observed and predicted values for each treatment. Ep = Epedaphic; He = Hemiedaphic; Eu = Euedaphic. Predicted value = microbial parameter / mean biomass of Collembola functional groups considered. Observed value =really measured value. .... 108

Tableau 5-3 : Qualitative comparison between predicted net effects (based on Collembola biomass) and observed effects on total PLFAs, bacterial, fungal and general indicators (mean  $\pm$  standard deviation) of the second month in function of mixed treatments (two and three life forms). The values are in nmol g-1. The tests values are given Chi-square compliance and t-test. The rejection level was set at  $\alpha = 0.05$ . \*\*\*p<0.001, \*\*p<0.01, \*p<0.05, ns p>0.05. The different letters (i.e. "a", "b") indicated significant differences ( $\alpha = 0.05$ ) between observed and predicted values for each treatment. Ep = Epedaphic; He = Hemiedaphic; Eu = Euedaphic; Control = no Collembola added. Predicted value = microbial parameter / mean biomass of Collembola functional groups considered. Observed value =really measured value. .... 108

Tableau 5-4 : Qualitative comparison between predicted net effects (based on Collembola biomass) and observed effects CO2 activity and three enzymatic activities (mean  $\pm$  standard deviation) of the first month in function of mixed treatments (two and three life forms). The tests values are given Chi-square compliance and t-test. The rejection level was set at  $\alpha = 0.05$ . \*\*\*p<0.001, \*\*p<0.01, \*p<0.05, ns p>0.05. The different letters (i.e. "a", "b") indicated significant differences ( $\alpha = 0.05$ ) between observed and predicted values for each treatment. Ep = Epedaphic; He = Hemiedaphic; Eu = Euedaphic; Control = no Collembola added. Predicted value = microbial parameter / mean biomass of Collembola functional groups considered. Observed value =really measured value. .... 115

Tableau 5-5 : Qualitative comparison between predicted net effects (based on Collembola biomass) and observed effects CO2 activity and three enzymatic activities (mean  $\pm$  standard deviation) of the Second month in function of mixed treatments (two and three life forms). The tests values are given Chi-square compliance and t-test. The rejection level was set at  $\alpha = 0.05$ . \*\*\*p<0.001, \*\*p<0.01, \*p<0.05, ns p>0.05. The different letters (i.e. "a", "b") indicated significant differences ( $\alpha = 0.05$ ) between observed and predicted values for each treatment. Ep = Epedaphic; He = Hemiedaphic; Eu = Euedaphic; Control = no Collembola added. Predicted value = microbial parameter / mean biomass of Collembola functional groups considered. Observed value =really measured value. .... 115



## **ANNEXES**

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## APPENDIX A- Chapitre 2

Table A1: Species list, relative abundance (values in%) and total abundances of Collembola considering the tillage factor. CT: Conventional tillage; RT: Reduced tillage.

Taxa	CT	RT
<i>Lepidocyrtus violaceus</i>	23.99	27.53
<i>Parisotoma notabilis</i>	20.17	10.28
<i>Folsomia spinosa</i>	13.59	10.44
<i>Protaphorura armata</i>	12.53	19.46
<i>Megalothorax minimus</i>	8.92	6.01
<i>Stenacidia violacea</i>	8.49	13.92
<i>Folsomia candida</i>	5.73	5.22
<i>Mesaphorura sp</i>	3.18	4.11
<i>Pseudosinella alba</i>	1.7	1.27
<i>Isotomiella minor</i>	1.06	0.95
<i>Anurida tullbergi</i>	0.42	0.16
<i>Friesea truncata</i>	0.21	0.47
<i>Entomobrya lanuginosa</i>	0	0.16
Total epedaphic	33.12	42.25
Total hemiedaphic	35.46	21.99
Total euedaphic	31.42	35.76
Total abundance per m2	5333.19	7156.19

Table A2: Species list, relative abundance (values in%) and total abundances of Collembola considering the leguminous factor. Leg-1: Faba Bean as previous crop of wheat; Leg-3: Faba Bean sown three years before wheat; None: rotation without Faba Bean and without any leguminous at least during the preceding five years.

Taxa	None	Leg-1	Leg-3
<i>Parisotoma notabilis</i>	23.84	14.18	5.51
<i>Stenacidia violacea</i>	16.37	9.27	11.4
<i>Protaphorura armata</i>	15.3	17.45	15.81
<i>Lepidocyrtus violaceus</i>	12.81	31.27	29.04
<i>Megalothorax minimus</i>	8.9	3.09	13.97
<i>Folsomia spinosa</i>	8.19	15.27	8.46
<i>Folsomia candida</i>	4.98	5.45	5.88
<i>Mesaphorura sp</i>	4.98	2.18	5.51
<i>Pseudosinella alba</i>	2.49	0.36	2.57
<i>Friesea truncata</i>	1.07	0.18	0
<i>Isotomiella minor</i>	0.71	0.91	1.47
<i>Anurida tullbergi</i>	0.36	0.36	0
<i>Entomobrya lanuginosa</i>	0	0	0.37
Total epedaphic	30.61	41.09	40.81
Total hemiedaphic	34.52	29.82	16.54
Total euedaphic	34.88	29.09	42.65
Total abundance per m2	4772.7	9341.58	4619.85

Table A3 : Species list, relative abundance (values in%) and total abundances of Collembola considering the interaction of two factors. Leg-1: Faba Bean as previous crop of wheat; Leg-3: Faba Bean sown three years before wheat; None: rotation without Faba Bean and without any leguminous at least during the preceding five years. CT: Conventional tillage; RT: Reduced tillage.

Taxa	None		Leg-1		Leg-3	
	CT	RT	CT	RT	CT	RT
<i>Parisotoma notabilis</i>	34.7	15.3	20.3	9.55	3.6	6.83
<i>Protaphorura armata</i>	25	7.64	6.36	25.8	11.7	18.6
<i>Megalothorax minimus</i>	12.1	6.37	4.66	1.91	14.4	13.7
<i>Stenacidia violacea</i>	8.87	22.3	6.36	11.5	12.6	10.6
<i>Mesaphorura sp</i>	4.84	5.1	2.12	2.23	3.6	6.83
<i>Folsomia candida</i>	4.03	5.73	5.93	5.1	7.21	4.97
<i>Pseudosinella alba</i>	4.03	1.27	0.85	0	0.9	3.73
<i>Lepidocyrtus violaceus</i>	3.23	20.4	28.4	33.4	37.8	23
<i>Folsomia spinosa</i>	0.81	14	22.9	9.55	8.11	8.7
<i>Isotomiella minor</i>	0.81	0.64	1.69	0.32	0	2.48
<i>Anurida tullbergi</i>	0.81	0	0.42	0.32	0	0
<i>Friesea truncata</i>	0.81	1.27	0	0.32	0	0
<i>Entomobrya lanuginosa</i>	0	0	0	0	0	0.62
Total epedaphic	13.7	43.9	35.2	45.5	50.5	34.2
Total hemiedaphic	39.5	30.6	44.1	19.1	12.6	19.2
Total euedaphic	46.8	25.5	20.8	35.3	36.9	46.6
Total abundance per m2	4212	5333	8017	10666	3771	5469

## APPENDIX B- Chapitre 3

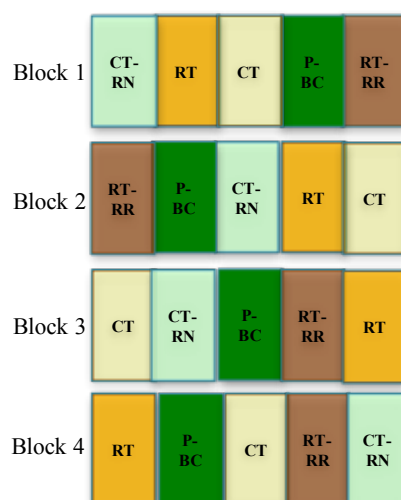


Figure B1: Experimental platform SOERE-ACBB. CT: Conventional Tillage; CT-RN: Conventional Tillage and Reduced N fertilization; RT: Reduced tillage; RT-RR: Reduced Tillage and crop Residues Removal; P-BC: Perennial and Bioenergy Crop.

Table B.1: Contribution of the first five Collembola species to the dissimilarity between assemblages of treatments in y+3. Cont %: Contribution percentage to dissimilarity. Cum %: Cumulative percentage of contribution to dissimilarity. CT: Conventional tillage; CT-RN: Conventional tillage and nitrogen reduced. P-BC: Perennial and Bioenergy Crop. RT: Reduced tillage; RT-RR: Reduced tillage and crop residues removal.

Taxa	CT vs.		CT-RN vs.		P-BC vs.	
	RT-RR	RT	RT-RR	RT	RT-RR	RT-RR
	con %	con %	con %	con %	con %	con %
<i>Protaphorura armata</i>	30.0	18.8	25.6	16.8	21.4	
<i>Parisotoma notabilis</i>	23.8	26.6	27.8	28.7	30.9	
<i>Mesaphorura sp</i>	12.2	–	12.8	11.0	11.8	
<i>Megalothorax minimus</i>	10.3	12.8	10.6	–	9.85	
<i>Lepidocyrtus violaceus</i>	7.60	16.5	7.96	16.0	–	
<i>Isotomurus unifasciatus</i>	–	7.22	–	7.03	7.92	
cum %	83.9	81.9	84.8	79.5	81.9	

Table B2: Contribution of the first five Collembola species to the dissimilarity between assemblages of treatments in y+4. Cont %: Contribution percentage to dissimilarity. Cum %: Cumulative percentage of contribution to dissimilarity. CT: Conventional tillage; CT-RN: Conventional tillage and nitrogen reduced. P-BC: Perennial and Bioenergy Crop. RT: Reduced tillage; RT-RR: Reduced tillage and crop residues removal.

Taxa	CT vs.			CT-RN vs.			RT vs.		P-BC vs.
	RT	RT-RR	P-BC	RT	RT-RR	P-BC	RT-RR	P-BC	RT-RR
	con %	con %	con %	con %	con %	con %	con %	con %	con %
<i>Megalothorax minimus</i>	39.1	10.9	–	37.9	12.3	–	19.3	19.2	7.37
<i>Parisotoma notabilis</i>	19.9	25.4	6.42	19.5	25.3	6.76	19.7	10.6	15.5
<i>Protaphorura armata</i>	8.03	8.70	7.67	6.99	8.50	7.50	7.49	–	–
<i>Sphaeridia pumilis</i>	6.48	–	–	6.18	–	–	–	–	–
<i>Mesaphorura sp</i>	6.39	9.82	40.8	5.56	8.44	38.8	6.92	29.1	23.5
<i>Sminthurinus elegans</i>	–	–	15.8	–	–	15.0	–	11.1	8.56
<i>Paratublergia callipygos</i>	–	–	9.34	–	–	9.40	–	7.16	–
<i>Isotoma anglicana</i>	–	19.6	–	–	19.6	–	19.3	–	12.7
cum %	80.0	74.5	80.1	76.1	74.1	77.4	72.7	77.1	67.7

Table B 3: Species list, relative abundance (values in %) and total abundances of Collembola in five treatments in y+3 and y+4. CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, P-BC: Perennial and Bioenergy Crop, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal. Ep : Epedaphic, He : Hemiedaphic, Eu : Euedaphic.

	y+3					y+4				
	CT	CT-RN	RT	RT-RR	P-BC	CT	CT-RN	RT	RT-RR	P-BC
<i>Anurida tullbergi</i> (Ep)	–	–	–	–	–	0	0	0	0	0.41
<i>Dicyrtomina minuta</i> (Ep)	0	0	0.93	1.28	0	0	0	0	0	0.83
<i>Deuterosminthurus</i> sp (Ep)	0	0	0.93	0	0	–	–	–	–	–
<i>Isotoma anglicana</i> (Ep)	2.92	0	0	0	0	2.68	9.12	0.60	19.1	1.66
<i>Isotoma viridis</i> (Ep)	0	0	7.46	0	1.98	0	0	0	0	0.82
<i>Isotomurus maculatus</i> (Ep)	–	–	–	–	–	0	1.80	0	2.84	0
<i>Isotomurus unifasciatus</i> (Ep)	2.92	0	5.61	6.45	0	0	3.60	0	0	2.90
<i>Lepidocyrtus violaceus</i> (Ep)	2.92	0	15.0	7.11	1.98	8.11	5.46	5.41	3.25	0.41
<i>Orchesella flavescens</i> (Ep)	0	4.30	0	4.51	0	–	–	–	–	–
<i>Stenacidia violacea</i> (Ep)	–	–	–	–	–	0	0	1.21	0	0
<i>Parisotoma notabilis</i> (He)	44.1	34.8	29.9	28.4	10.0	32.4	25.4	22.9	26.8	6.23
<i>Pseudosinella alba</i> (He)	0	0	0	0.64	1.98	2.68	3.66	1.81	4.87	0.41
<i>Sminthurinus elegans</i> (He)	0	0	0	0	3.96	0	3.60	1.81	3.66	15.3
<i>Sphaeridia pumilis</i> (He)	–	–	–	–	–	0	0	5.41	0.81	4.98
<i>Folsomia fimetaria</i> (Eu)	0	0	0.93	0	0	0	3.66	3.62	3.25	1.25
<i>Megalothorax minimus</i> (Eu)	8.84	0	11.2	9.04	10.0	29.8	20.0	41.6	14.2	3.72
<i>Mesaphorura</i> sp (Eu)	26.5	21.7	8.41	12.9	38.0	16.2	18.2	7.23	10.2	41.9
<i>Paratullbergia callipygos</i> (Eu)	–	–	–	–	–	0	0	1.21	2.03	10.4
<i>Protaphorura armata</i> (Eu)	11.8	39.2	19.6	29.7	32.0	8.11	5.46	7.23	8.85	8.72
Total epedaphic	8.75	4.30	29.9	19.3	3.96	10.8	20.0	7.22	25.2	7.04
Total hemiedaphic	44.1	34.8	29.9	29.0	16.0	35.1	32.7	31.9	36.2	27.0
Total euedaphic	17.1	60.9	40.2	51.6	80.1	54.1	47.3	60.9	38.6	66.0
Total abundance per m <sup>2</sup>	1441	978	4543	6580	2122	1571	2334	7045	10438	10229

Table B4: Mean  $\pm$  standard error of soil chemical proprieties and microbial communities (Cbiom: microbial carbon biomass; CO<sub>2</sub>: microbial activity; pHwater; HUM: soil moisture; and TEMP: soil temperature) of five different agricultural treatments (CT: Conventional tillage, CT-RN: Conventional tillage and nitrogen reduced, RT: Reduced tillage, RT-RR: Reduced tillage and crop residues removal, P-BC: Perennial and Bioenergy Crop) after 2 (y+2), 3 (y+3) and 4 years (y+4), with blocks as random factors. Chisq: Chi-square value. p : p-value. R<sup>2</sup>: variance explained by both fixed and random factors. Degree of freedom = 4. The rejection level was set at  $\alpha = 0.05$ . \*\*\*p<0.001. \*\*p<0.01. \*p<0.05. ns p>0.05.

		CT	CT-RN	RT	RT-RR	P-BC	LMM outputs		
							Chisq	p	R <sup>2</sup> (%)
y+2	Cbiom (mg kg <sup>-1</sup> )	243 $\pm$ 21.4 <sup>d</sup>	249.1 $\pm$ 10.3 <sup>d</sup>	346 $\pm$ 3.64 <sup>b</sup>	317 $\pm$ 17.2 <sup>c</sup>	388 $\pm$ 6.89 <sup>a</sup>	336	***	94.65
	CO <sub>2</sub> (mg kg <sup>-1</sup> )	18.7 $\pm$ 2.79	20.2 $\pm$ 3.92	23.1 $\pm$ 3.65	20.3 $\pm$ 5.25	23.0 $\pm$ 4.89	6.20	ns	54.67
	pHwater	7.70 $\pm$ 0.10	7.80 $\pm$ 0.10	7.70 $\pm$ 0.10	7.70 $\pm$ 0.20	7.75 $\pm$ 0.16	3.60	ns	52.89
	HUM (%)	23.3 $\pm$ 1.94	22.4 $\pm$ 1.83	22.6 $\pm$ 1.85	21.9 $\pm$ 2.43	22.9 $\pm$ 1.14	5.61	ns	79.23
	TEMP (°C)	8.21 $\pm$ 1.50 <sup>a</sup>	7.97 $\pm$ 1.46 <sup>a</sup>	7.98 $\pm$ 1.38 <sup>a</sup>	8.05 $\pm$ 1.44 <sup>a</sup>	6.84 $\pm$ 1.15 <sup>b</sup>	138	***	98.34
y+3	Cbiom (mg kg <sup>-1</sup> )	255 $\pm$ 19.4 <sup>b</sup>	251.7 $\pm$ 8.71 <sup>b</sup>	435 $\pm$ 31.82 <sup>a</sup>	428 $\pm$ 44.89 <sup>a</sup>	399 $\pm$ 42.6 <sup>a</sup>	154	***	89.27
	CO <sub>2</sub> (mg kg <sup>-1</sup> )	16.5 $\pm$ 3.61 <sup>b</sup>	15.7 $\pm$ 2.42 <sup>b</sup>	29.0 $\pm$ 9.01 <sup>a</sup>	32.0 $\pm$ 2.67 <sup>a</sup>	25.4 $\pm$ 1.79 <sup>a</sup>	69.5	***	81.87
	pHwater	7.60 $\pm$ 0.38 <sup>b</sup>	7.90 $\pm$ 0.10 <sup>a</sup>	7.85 $\pm$ 0.15 <sup>ab</sup>	7.90 $\pm$ 0.12 <sup>ab</sup>	7.85 $\pm$ 0.22 <sup>ab</sup>	11.1	*	49.53
	HUM (%)	22.5 $\pm$ 2.33 <sup>ab</sup>	22.6 $\pm$ 0.94 <sup>b</sup>	24.1 $\pm$ 0.13 <sup>a</sup>	24.5 $\pm$ 0.08 <sup>a</sup>	24.7 $\pm$ 0.54 <sup>a</sup>	13.8	*	42.03
	TEMP (°C)	3.89 $\pm$ 0.13	3.75 $\pm$ 0.12	3.91 $\pm$ 0.17	3.82 $\pm$ 0.25	3.53 $\pm$ 0.50	6.29	ns	36.24
y+4	Cbiom (mg kg <sup>-1</sup> )	258 $\pm$ 18.20 <sup>c</sup>	237 $\pm$ 4.31 <sup>c</sup>	376 $\pm$ 25.4 <sup>b</sup>	387 $\pm$ 13.23 <sup>ab</sup>	418 $\pm$ 25.0 <sup>a</sup>	335	***	94.67
	CO <sub>2</sub> (mg kg <sup>-1</sup> )	28.5 $\pm$ 5.40 <sup>ab</sup>	25.1 $\pm$ 6.01 <sup>b</sup>	32.9 $\pm$ 2.82 <sup>ab</sup>	32.7 $\pm$ 8.76 <sup>ab</sup>	35.2 $\pm$ 7.87 <sup>a</sup>	15.0	**	69.18
	pHwater	7.79 $\pm$ 0.14	7.86 $\pm$ 0.13	7.57 $\pm$ 0.28	7.73 $\pm$ 0.25	7.70 $\pm$ 0.31	6.06	ns	52.44
	HUM (%)	22.9 $\pm$ 1.95	23.4 $\pm$ 2.02	24.3 $\pm$ 1.42	23.6 $\pm$ 1.23	24.8 $\pm$ 0.31	8.88	ns	63.66
	TEMP (°C)	7.50 $\pm$ 0.75 <sup>a</sup>	7.18 $\pm$ 0.74 <sup>b</sup>	7.58 $\pm$ 0.80 <sup>a</sup>	7.64 $\pm$ 0.87 <sup>a</sup>	6.84 $\pm$ 0.96 <sup>c</sup>	157	***	98.56



## Appendix C – Chapitre 4

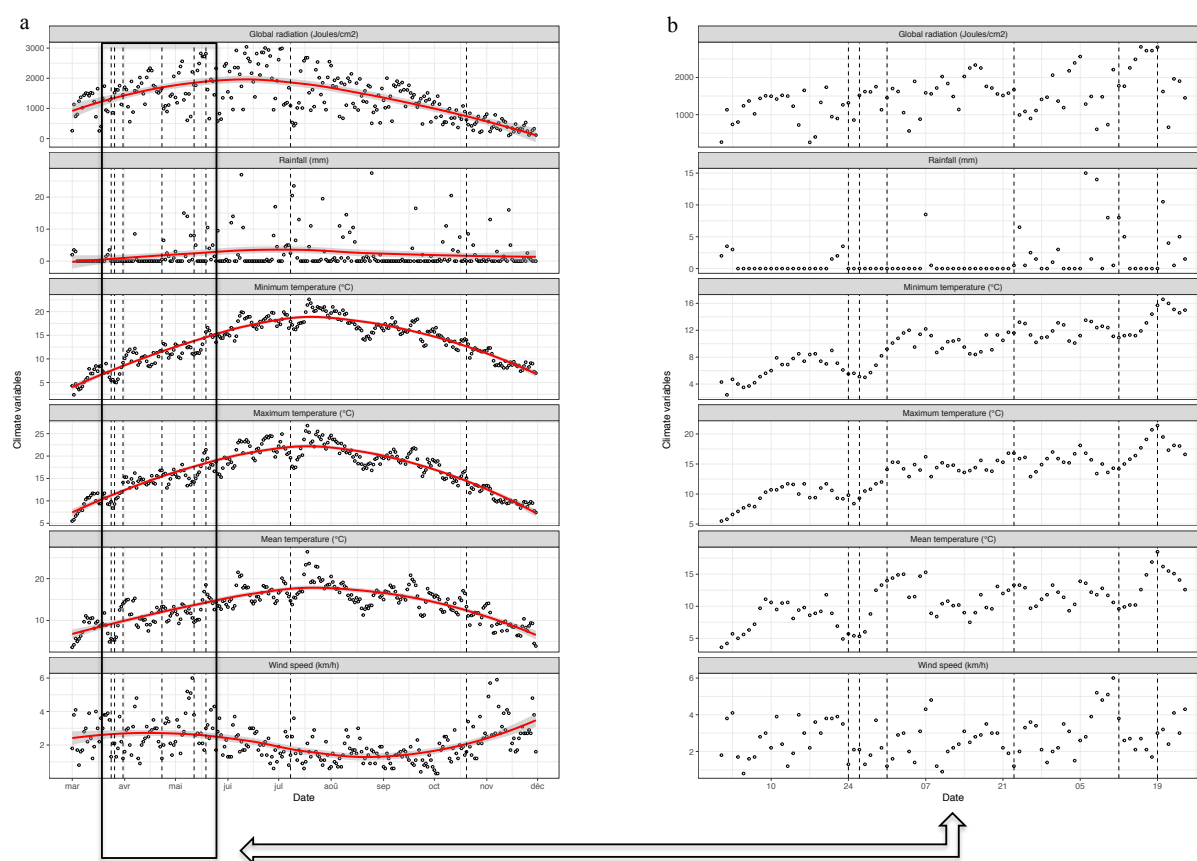


Figure C1: Daily weather data throughout the experimental period the site SOERE ACBB, Estrées-Mons, Picardy, France. Vertical dashed lines represent the sampling dates. a) Daily weather data from March to November; and (b) daily weather data on the closest sampling dates.

Table C1: Results of Linear Mixed-Effects Models (LMM) of “the effect of sampling day for each treatment” on soil organic carbon and bulk density in four different depths of soil (0-5, 5-10, 10-20, 20-30 cm). CT: Conventional tillage, RT: Reduced tillage and NT: No tillage. The tests values are given. F: F-value, p: p-value, R<sup>2</sup>: variance explained by both fixed and random factors. The rejection level was set at  $\alpha = 0.05$ . \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns $p > 0.05$ . The location of the significant differences is in Appendix C–Figure C2 and C3.

Depth (cm)	Sampling day effect																	
	CT						RT						NT					
	Soil organic carbon			Bulk density			Soil organic carbon			Bulk density			Soil organic carbon			Bulk density		
	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)
0 - 5	13.9	***	85.6	13.9	***	76.6	0.70	ns	32.6	22.8	***	84.3	1.03	ns	74.3	0.85	ns	16.7
5 - 10	3.20	*	40.1	25.9	***	85.9	1.71	ns	44.3	5.98	***	60.9	1.52	ns	78.4	1.99	ns	34.0
10 - 20	1.21	ns	76.4	0.99	ns	32.2	1.99	ns	48.1	7.87	**	66.4	2.91	*	56.8	0.19	ns	31.1
20 - 30	2.21	ns	48.5	4.64	*	54.7	0.30	ns	37.5	1.38	ns	55.3	2.56	*	59.4	0.86	ns	16.4

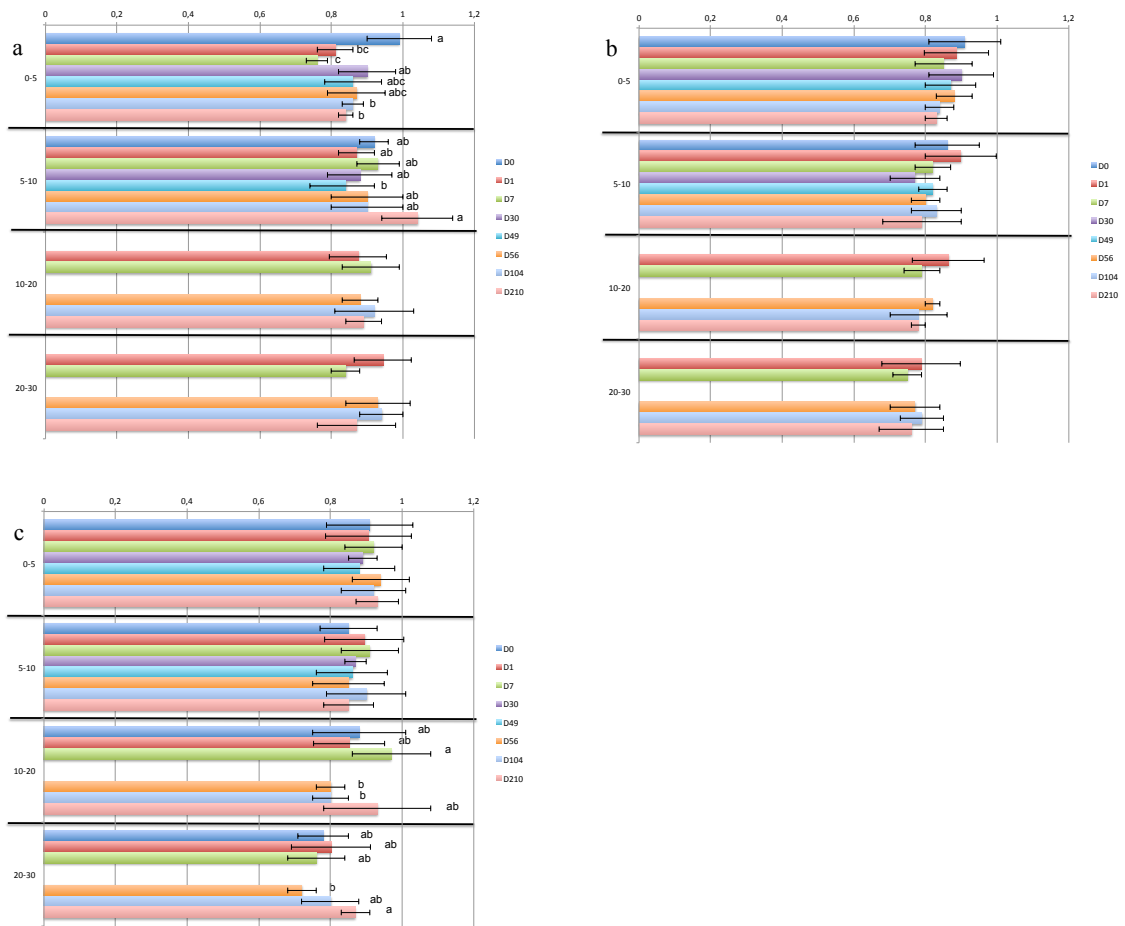


Figure C2: Soil organic carbon (means and standard deviation) of three tillage treatments (a- CT: Conventional tillage; b- RT: Reduced tillage; c- NT: No-tillage over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) for each of the four depths of the soil (0-5, 5-10, 10-20, 20-30 cm) performed in Estrées-Mons, Picardie, France. Different letters (i.e. “a”, “b”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment.

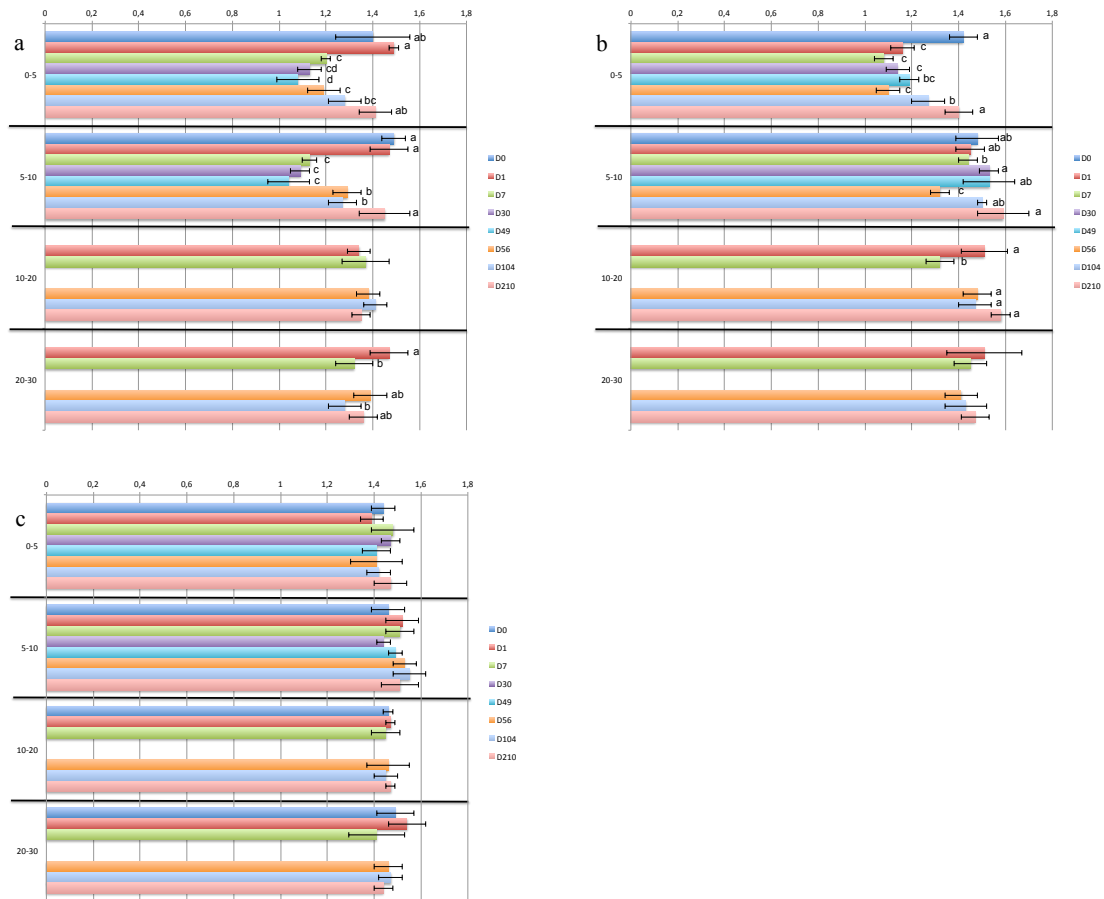


Figure C3: Bulk density (means and standard deviation) of three tillage treatments (a- CT: Conventional tillage; b- RT: Reduced tillage; c- NT: No-tillage over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) for each of the four depths of the soil (0-5, 5-10, 10-20, 20-30 cm) performed in Estrées-Mons, Picardie, France. Different letters (i.e. “a”, “b”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment.

Table C2: Results of Linear Mixed-Effects Models (LMM) of “the effect of treatment for each sampling date” and “the effect of sampling day for each treatment” on distribution of aggregates size (> 5; 5-2; 2-0.25; > 0.25; 0.25-0.05; < 0.05 mm). D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage. CT: Conventional tillage, RT: Reduced tillage and NT: No tillage. The tests values are given. F: F-value, p: p-value, R2: variance explained by both fixed and random factors. The rejection level was set at  $\alpha = 0.05$ . \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns  $p > 0.05$ . The location of the significant differences is in Appendix C-Figure C4.

		Tillage effect																	
		Aggregates(mm)																	
		> 5			5 – 2			2 – 0.25			> 0.25			0.25 – 0.05			< 0.05		
		F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)
D0		0.17	ns	3.05	0.33	ns	28.3	0.23	ns	3.94	0.59	ns	9.65	0.14	ns	32.0	0.22	ns	15.5
D1		3.33	ns	37.7	3.91	ns	75.5	0.56	ns	9.18	1.84	ns	40.1	0.38	ns	6.38	7.44	*	67.5
D7		2.83	ns	43.2	1.83	ns	50.8	1.04	ns	27.6	7.96	*	80.8	4.74	*	56.5	11.8	**	79.7
D30		8.69	*	61.2	4.84	ns	56.4	2.56	ns	34.7	6.31	*	62.3	3.77	ns	46.4	2.04	ns	49.4
D49		2.08	ns	40.5	0.39	ns	6.61	3.48	*	38.8	3.08	ns	35.9	0.65	ns	26.1	0.47	ns	68.5
D56		6.69	*	62.0	1.81	ns	24.7	1.06	ns	16.2	0.49	ns	8.19	12.1	**	73.3	8.09	*	77.0
D104		36.7	***	88.9	1.77	ns	49.6	6.18	*	64.4	2.23	ns	0.50	111.0	***	97.0	4.79	*	49.9
D210		1.82	ns	24.8	0.08	ns	1.41	1.62	ns	52.3	0.36	ns	6.12	2.82	ns	61.5	1.33	ns	40.5
		Sampling day effect																	
		Aggregates(mm)																	
		> 5			5 – 2			2 – 0.25			> 0.25			0.25 – 0.05			< 0.05		
		F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)
CT		8.54	***	72.6	1.45	ns	24.7	2.76	*	52.2	2.23	**	49.4	6.99	***	63.7	2.57	*	67.9
RT		7.95	***	70.3	0.97	ns	42.8	1.66	ns	29.1	1.01	ns	18.5	0.39	ns	42.4	2.61	*	76.9
NT		2.09	*	35.5	0.46	ns	33.4	1.18	ns	20.7	1.03	ns	20.1	0.53	ns	12.3	0.82	ns	64.1

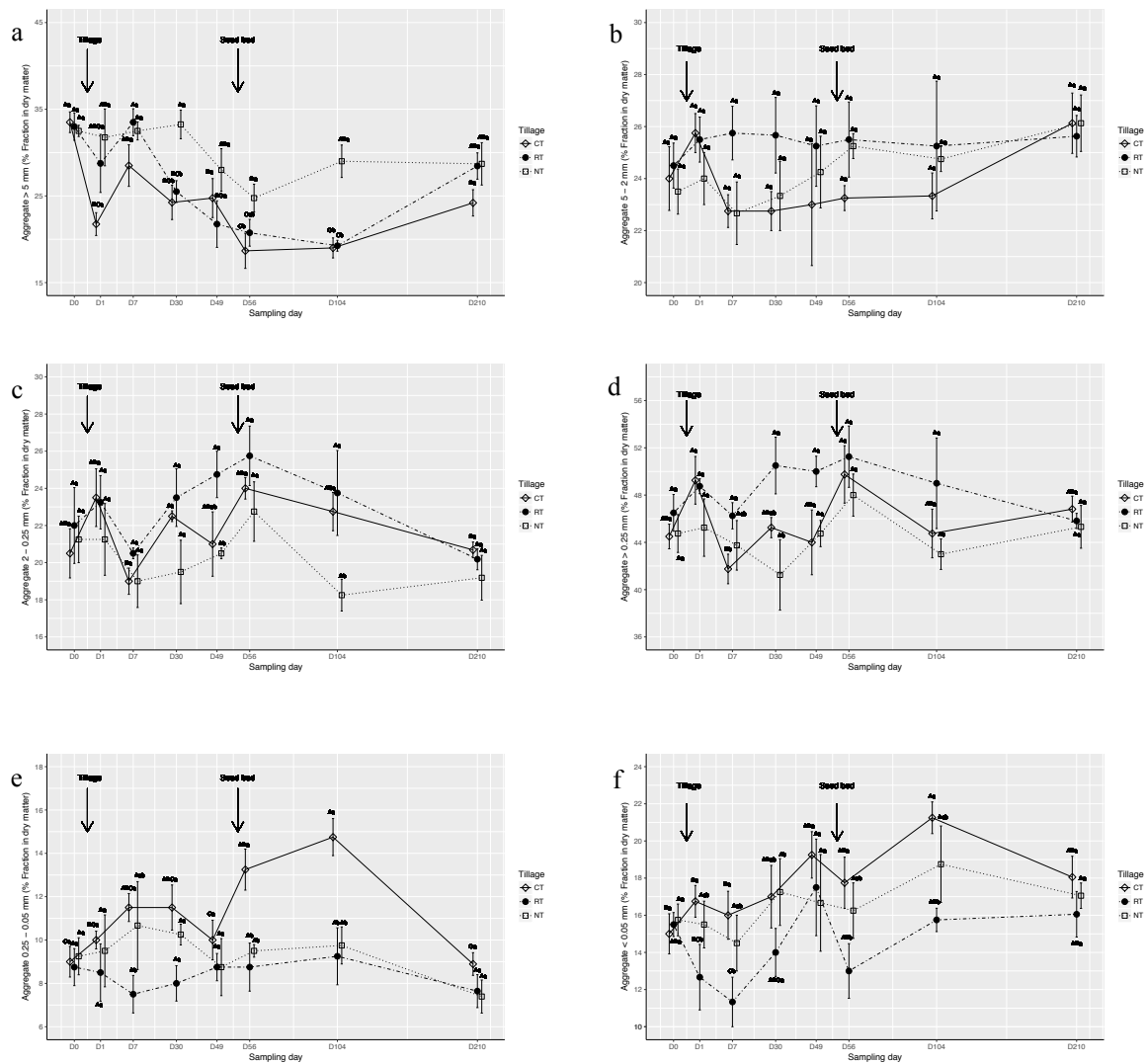


Figure C4: Aggregates size (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment. a) Aggregates > 5 mm; b) aggregates between 5 and 2 mm; c) aggregates between 2 and 0.25 mm; d) aggregates > 0.25 mm. e) aggregates between 0.25 and 0.05 mm; f) aggregates < 0.05 mm.

Table C3: Results of Linear Mixed-Effects Models (LMM) of “the effect of treatment for each sampling date” and “the effect of sampling day for each treatment” on both evenness and Simpson index of Collembola and earthworm. D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage. CT: Conventional tillage, RT: Reduced tillage and NT: No tillage. The tests values are given. F: F-value, p: p-value, R2: variance explained by both fixed and random factors. The rejection level was set at  $\alpha = 0.05$ . \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns  $p > 0.05$ . The location of the significant differences is in Appendix C-Figure C5.

	Tillage effect											
	Collembola						Earthworm					
	Evenness index			Simpson index			Evenness index			Simpson index		
	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)
D0	0.80	ns	12.7	0.52	ns	8.61	0.13	ns	2.28	0.15	ns	2.61
D1	0.14	ns	27.6	0.31	ns	20.6	7.01	*	58.5	14.3	**	72.2
D7	1.05	ns	16.1	0.83	ns	17.1	4.52	*	45.1	29.2	***	84.1
D30	2.37	ns	51.2	2.47	ns	58.3	4.51	*	39.8	18.0	**	77.4
D49	2.65	ns	47.7	3.06	ns	74.7	7.61	*	62.3	36.0	***	87.8
D56	5.42	*	55.1	20.7	**	81.2	3.25	ns	52.6	5.85	*	59.2
D104	9.45	**	63.2	5.49	*	49.9	1.20	ns	46.3	1.09	ns	58.9
D210	0.45	ns	7.56	0.31	ns	5.37	4.71	*	42.3	3.34	ns	37.8
	Sampling day effect											
	Collembola						Earthworm					
	Evenness index			Simpson index			Evenness index			Simpson index		
	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)	F	p	R <sup>2</sup> (%)
CT	2.56	*	36.7	1.63	ns	26.9	4.57	**	50.8	12.8	***	71.1
RT	1.70	ns	31.7	2.69	*	48.9	3.37	*	43.2	12.0	***	68.2
NT	1.48	ns	39.4	1.11	ns	40.5	4.20	**	60.3	11.6	***	78.1

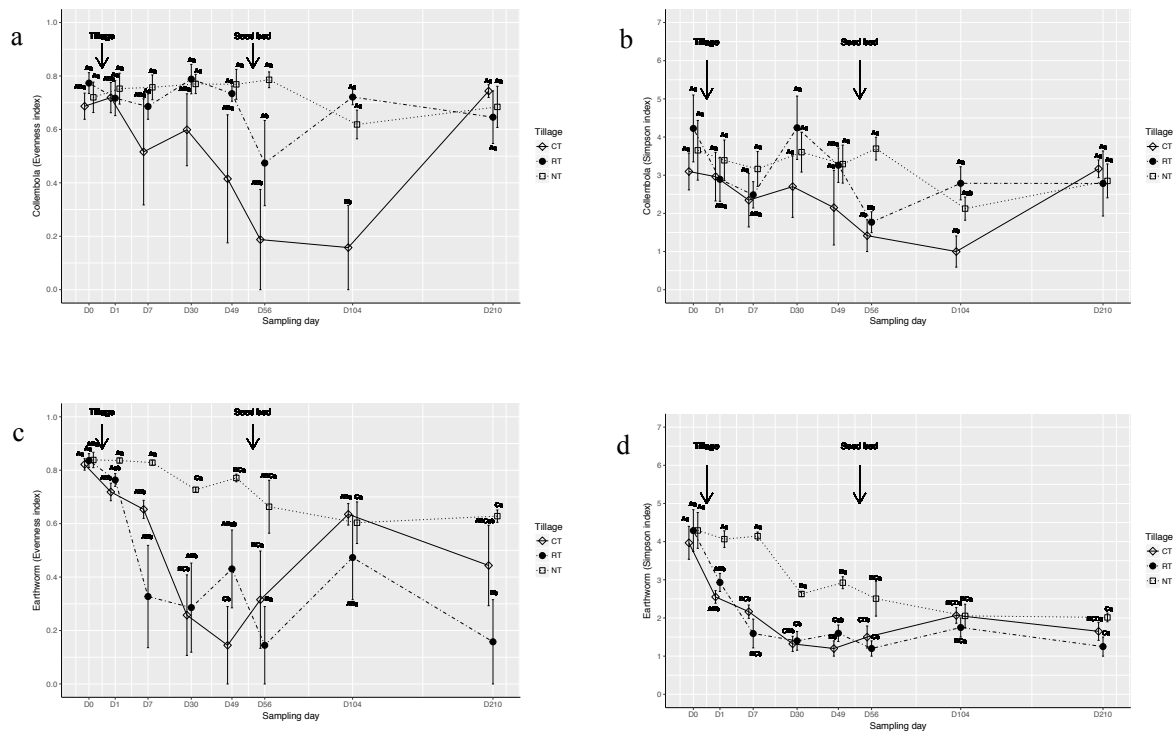


Figure C5: Evenness and Simpson index of Collembola and earthworm (means and standard error) of three tillage treatments (CT: Conventional tillage, RT: Reduced tillage, NT: No-tillage) over a 8 sampling date period (D0: 1 day before tillage, and respectively D1: 1; D7: 7; D30: 30; D49: 49; D56: 56; D104: 104; D210: 210 days after tillage) performed in Estrées-Mons, Picardie, France. For each sampling date, different minuscule letters (i.e. “a”, “b”) indicated significant differences ( $\alpha = 0.05$ ) between treatments. Different capital letters (i.e. “A”, “B”) showed significant differences ( $\alpha = 0.05$ ) between sampling dates within a single tillage treatment. a) Evenness index of Collembola; b) Simpson index of Collembola; c) Evenness index of earthworm; d) Simpson index of earthworm.