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► **To cite this version:**

Claire Ricono, Philippe Vandenkoornhuysse, Stéphanie Aviron, Olivier Jambon, Sophie Michon-Coudouel, et al.. Organic agriculture and field edges uphold endospheric wheat microbiota at field and landscape scale. FEMS Microbiology Ecology, 2022, 98 (3), pp.fiac027. <10.1093/femsec/fiac027>. <hal-03631261>

HAL Id: hal-03631261

<https://hal.science/hal-03631261v1>

Submitted on 8 Aug 2025

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Organic agriculture and field edges uphold endospheric wheat microbiota at field and landscape scale

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One sentence summary: Agricultural intensification affects crop plant root microbiota at landscape scale for bacteria and field scale for fungi.

Editor: Ian Anderson

Abstract

Agricultural intensification has been demonstrated to induce a loss of biodiversity. Despite the key role of symbiotic microorganisms in plant nutrition and protection, the impact of agricultural intensification on these microorganisms is not fully understood. Organic farming and field edges (as semi-natural elements) may promote a higher microbial diversity thanks to lower anthropic disturbance and higher plant diversity. We sampled wheat individuals in pairs of wheat fields (one organic and one conventional) along a distance gradient to the edges (hedgerow vs. grassy), in 20 landscape windows selected along an uncorrelated gradient of organic farming and hedgerow density. We demonstrated that organic farming shaped microbial composition and increased fungal and bacterial richness, while hedgerows had a neutral or negative effect on richness depending on the microbial phyla considered. In contrast to bacteria, fungal communities were heterogeneously distributed within fields, having a higher diversity for some phyla close to field edges. Overall we highlighted that fungi responded more to the field scale while bacteria were more affected by landscape scale. The effect of agricultural intensification on plant microbiota and therefore on the functions provided by microorganisms to the plants has to be considered at a multiple spatial scale—from field to landscape.

Keywords: agricultural practices, bacteria, field edges, field management, fungi, multi-spatial scale analysis

Introduction

Intensive agriculture has been promoted since the green revolution in the 1960s to boost crop yields and satisfy increasing food demand (Mann 1999). Such intensification led to modifications in agricultural practices with higher fertilization, increased pest control and intense varietal selection among others. Additionally, the increase in the overall agricultural land cover led to marked changes in land use (e.g. deforestation) at the expense of natural and semi-natural habitats (Tschamtko et al. 2005). Fields were merged to increase their size to facilitate crop management. Natural linear elements, such as hedgerows formerly used to set borders, were removed leading to homogenized and open landscapes. Because of these changes at local and landscape scale, agricultural intensification strongly shaped ecosystem properties (Matson et al. 1997). More specifically, agricultural intensification resulted into changes, mostly negative, in the diversity and abundance of many taxonomic groups including mammals, birds, insects and plants (e.g. Hole et al. 2005, Gonthier et al. 2014), while it increased soil erosion and reduced soil quality (Foley et al. 2005, Tilman et al. 2011) likely impacting soil microorganisms (De Graaf et al. 2019).

Microorganisms display a large diversity in the soil comprising bacteria, fungi and archaea. Within this huge diversity, endospheric microorganisms are intimately associated with plants,

and involved in many ecological functions for their host plants such as nutrition and resistance to herbivores, pathogens and environmental stresses (Rodriguez et al. 2009, Vannier et al. 2019). The plant endospheric microbiota is both inherited from sexual or clonal reproduction (i.e. vertically transmitted) and recruited from the soil microbial pool (i.e. horizontally transmitted) close to the plant root system (Vandenkoornhuys et al. 2015, Xiong et al. 2021). Agricultural intensification is thus likely to influence the recruitment of microorganisms by plants by influencing the soil microbial reservoir (e.g. Xu et al. 2020), and the potential transmission of microorganisms among plants. Yet, the consequences of agricultural intensification on plant-associated microorganisms have been mostly analyzed at the field level (e.g. Schmidt et al. 2019 on rhizosphere, Banerjee et al. 2019 on endosphere), but overlooked at the landscape scale.

Farming practices including chemical pest control, tillage and fertilization events have a strong impact on soil physical and chemical characteristics and affect the diversity of soil organisms (Mäder et al. 2002, Hartmann et al. 2015, Chen et al. 2019, Sheoran et al. 2019). Alternative practices such as organic farming were developed to promote more efficient soil natural ecosystem services, including organic matter cycling, storage, redistribution of mineral nutrient and prevention of soil leaching (McLaughlin and Mineau 1995). Such practices should be favorable for mi-

Received: September 5, 2021. Revised: February 11, 2022. Accepted: March 3, 2022

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croorganisms. For example, the use of organic amendments, such as manure, improves organic matter content and nutrient cycling (Sheoran *et al.* 2019). Organic farming is also characterized by the absence of pesticides, especially fungicides, which may then favor the occurrence of symbiotic microorganisms such as arbuscular mycorrhizal fungi (Manoharan *et al.* 2017). The overall higher diversity in organic fields, especially of plant species (Ründlof *et al.* 2010, Stein-Bachinger, 2021), can also participate in the enrichment of the soil microbial pool due to the preferential association of plant species with a given microbiota (Berg and Smalla 2009). Overall the positive effect of organic farming on the soil microbial reservoir has started to be demonstrated at the field level (e.g. Chaudhry *et al.* 2012, Hartman *et al.* 2015). At a larger spatial scale, the occurrence of organic fields may constitute microbial reservoirs in agriculture-dominated landscapes. Such reservoirs could provide fluxes of microorganisms that could colonize and enrich areas with limited microbial communities, a process that we call herein a “rescue-effect” (sensu Brown and Kodric-Brown 1977). A higher % cover of organic farming in the landscape may thus have a positive effect on the diversity of microorganisms in crop fields.

In agroecosystems, semi-natural interfaces such as hedgerows and field edges are less disturbed by farming practices than other landscape elements, and consequently provide particular ecological niches. Hedgerows have been seen to provide many ecosystem services in landscapes (Montgomery *et al.* 2020). For instance, hedgerows enable integration of more organic matter thereby increasing carbon storage in the soil (Follain *et al.* 2007). They also influence water infiltration and percolation in the soil (Holden *et al.* 2019) and provide particular microclimatic conditions (Vanneste *et al.* 2020a). Field edge type may then profoundly influence soil characteristics by acting on microbial assemblages (D’Acunto *et al.* 2016). Additionally, they generally harbor a higher diversity of plants compared with crop fields (Marshall and Moonen 2002). Hedgerows in particular are important refuges for plant species owing to their stability in the landscape (Vanneste *et al.* 2020b, Marshall and Moonen 2002). Because plant diversity promotes microorganism diversity, field edges and especially hedgerows may constitute species-rich microbial reservoirs that influence the distribution of microorganisms in crop fields due to edge effects (D’Acunto *et al.* 2014, 2016). At a larger spatial scale, field edges and hedgerows may diversify ecological niches and correspond to biodiversity refuges. The hedgerow network has also been suggested to act as corridors for many organisms (Davies and Pullin 2007), especially plants (Mony *et al.* 2018, Uroy *et al.* 2019), likely promoting the co-dispersal of microorganisms (Correia *et al.* 2019). A dense network of hedgerows in the landscape thus likely improves microorganism diversity in fields.

We investigated the influence of the farming type (organic vs. conventional) and the presence of hedgerows on the diversity of endospheric bacterial and fungal communities inhabiting wheat roots. We hypothesized that the wheat roots in a given crop field would display higher microbiota diversity (i) in organic fields, and near field edges at the field scale; and (ii) in landscapes with a higher % cover of organic farming and hedgerow density at the landscape scale. To check these hypotheses, we used a large-scale experimental design encompassing nested-spatial scale sampling. Using next-generation sequencing we analyzed microbial assemblages in the roots of individual wheat plants sampled in pairs of wheat fields (one under organic and the other under conventional farming) along a gradient of distance to the edge of the field (two edge types considered per field, hedgerow vs. grassy edges), in 20 landscapes selected along two independent gradients of organic farming % cover and hedgerow density.

Methods

Field selection

We sampled winter wheat roots from 40 fields in the Long-Term Socio-Ecological Research (LTSER) site “Zone Atelier Armorique”, Western France, Rennes (48°06’43”N 1°40’27”W). The 40 fields were located in a bocage landscape (i.e. a mosaic of agricultural fields partly surrounded by hedgerows), characterized by mixed crop-livestock farming. The sampling design comprised 20 landscape windows selected along an independent gradient of hedgerow density and % cover of organic farming. The 20 landscape windows corresponded to a 500 m buffer zone around each pair of fields (Fig. 1A). In each landscape window, one organic and one conventional field located close to each other were selected (Fig. 1B). The fields in a given pair were always less than 1000 m apart.

Hedgerows were mapped by photographic interpretation of aerial maps produced by the French National Geographical Institute. The distribution of organic fields in the buffer area was mapped based on interviews with farmers. For each landscape window, we calculated the hedgerow density, i.e. the total length of hedgerows divided by the total used agricultural area (UAA) and the % cover of organic farming (the surface area of crop fields and grassland under organic agriculture divided by the UAA) in the landscape window (Fig. 1C). Calculations were made using QGIS (2.18). The % cover of organic farming (7.9–40.7%) and hedgerow density (1.3–8.1 km/km²) were not significantly correlated (Pearson correlation test, $R^2 = 0.004$, $P > .05$), indicating that they might be considered afterwards as independent variables. The % cover of organic farming and of grassland were not significantly correlated (Pearson correlation test, $R^2 = 0.160$, $P > .05$). At the landscape scale, the effect of organic farming on plant microbiota was therefore not corresponding to an indirect grassland effect.

To characterize the sampled fields and edges, we conducted interviews with farmers to get information on their management. Farmers did not use irrigation because of the oceanic weather conditions. Conventional farmers managed their fields with tillage (12 out of 19 fields, others with no tillage, data missing for one field), used pesticides (all fields) and mostly mineral amendments (16 out of 19 fields, others with organic amendments). Organic farmers managed their fields with tillage (18 out of 20 fields) and mechanical weeding (14 out of 20 fields). They did not use phytosanitary products, but added organic amendments (11 out of 20 fields) or nothing (9 out of 20 fields). Farmers did not use pesticides to manage hedgerows whatever the farming type of the nearby field. We selected sampled fields having a similar hedgerow size, width and tree composition (only deciduous tree, no ornamental species). Field size was in general ~1.6 times higher when conducted in conventional farming compared with organic farming (Table 1).

Root sampling

Wheat individuals were sown in October 2018. We sampled individual wheat plants in March 2019 corresponding to a vegetative phenological stage. Individuals were sampled every 10 m along two 30-m transects, one starting from the hedgerow and one from a grassy edge to the center of the field to measure similar effects independently of the size of the field (eight individuals; Fig. 1B). In most cases, the points located at 30 m were close to the center of the field. The root system was removed from the sampled plants within 12 h. Roots were washed for ~5 min with tap water, 10 min with a Triton × 100 5‰ solution and then twice with sterile 18 mΩ of purified water. Because differences in root morphology could

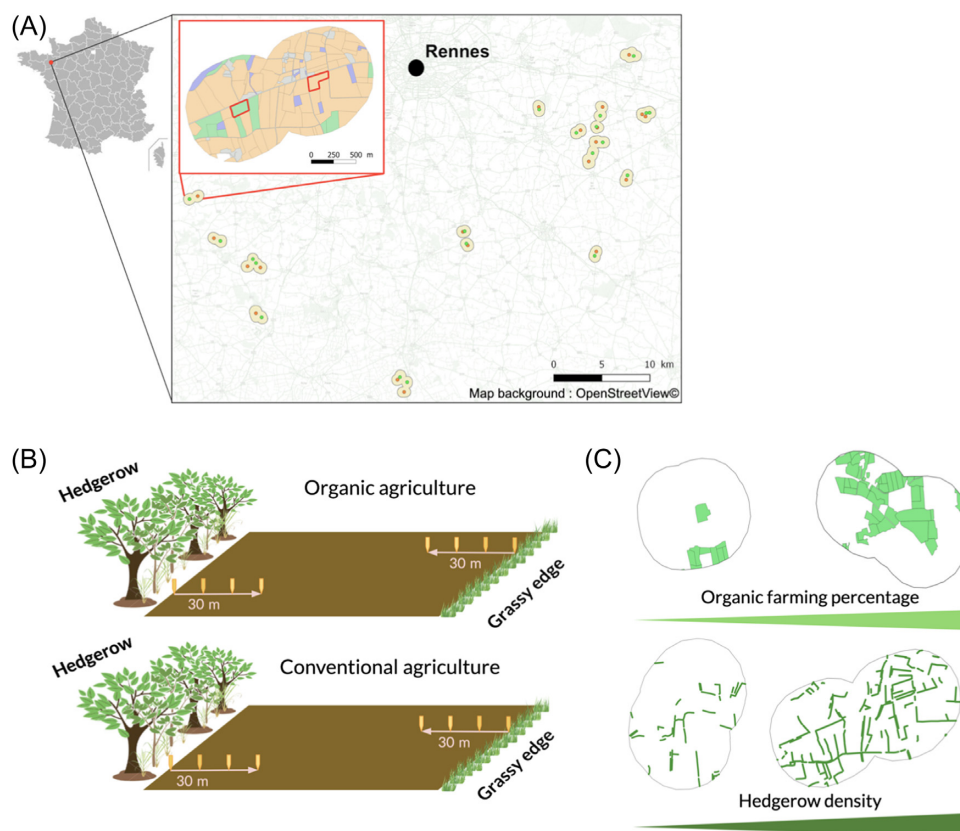


Figure 1. Experimental design rationales to assess the wheat microbiota impact of landscape. **(A)** Geographical location of the selected landscape windows. Black ellipsoids represent the 500-m radius buffers (i.e. landscape windows) within the LTSE site “Zone Atelier Armorique”. The orange and green dots correspond respectively to the centroids of the conventional and organic fields. In the red box: the orange and green polygons stand for fields under conventional and organic agriculture, respectively, the blue polygons stand for natural areas and gray polygons for artificial areas. **(B)** Variables at the field scale. Individual wheat plants were sampled along two 30-m transects per field (pastel pink arrows) starting from two edge types (hedgerow vs. grassy edge) and going toward the center of the field for each farming type (organic vs. conventional). **(C)** Variables at the landscape scale. Black ellipsoids represent the 500-m radius buffers. Landscape windows were characterized by their % cover of organic farming and the hedgerow density. Percent cover was calculated as the proportion of the area covered by crop field and grassland under organic farming (light green gradient). Hedgerow density was measured as the ratio of the length divided by the area of the landscape window (dark green gradient). These two gradients are uncorrelated.

Table 1. Field information depending on the farming type. Mean, standard error (SE) and the minimum and maximum values are shown.

	Conventional farming		Organic farming	
	Mean (SE)	Range	Mean (SE)	Range
Field surface (ha)	5.1 (0.9)	1.8–15.7	3.2 (0.3)	1.1–5.4
Length of field (m)	163.7 (18.5)	60.0–410.0	116.8 (7.5)	64.0–179.0
Hedgerow width (m)	1.6 (0.2)	0.8–3.0	2.1 (0.2)	1.0–4.2
Hedgerow height (m)	10.1 (0.7)	4.2–16.0	9.0 (0.7)	2.1–14.8

lead to modification in the microbiota composition (e.g. Saleem et al. 2018, Ianucci et al. 2021), comparable root-tips were only sampled (i.e. approximately similar diameter and shape). Small pieces of root (<1 cm) were sampled from different parts of the root system of each individual wheat plant. Eighty mg aliquots of roots were placed in 1.5-ml Eppendorfs® tubes and stored at -20°C until root total DNA extraction.

DNA extraction and Illumina sequencing

Root samples were ground to powder. DNA was extracted by magnetic beads (sbeadex mini plant kit, LGC Genomics; Berlin, Germany) using a standard protocol performed with a robot (oK-topure robot, LGC Genomics). DNA concentrations were mea-

sured by fluorimetric quantification (Hoeschst). DNA was extracted from roots at the Gentyane platform (<http://gentyane.clermont.inra.fr/>; Clermont-Ferrand, France). For all the extracted DNAs, sample concentrations were normalized at $7\text{ ng}/\mu\text{l}$ (Bravo-Agilent®), of which $3\text{ }\mu\text{l}$ was used for each PCR. We used 18S rRNA (fungi) and 16S rRNA (bacteria) to analyze the wheat endospheric microbiota. Fungal amplification was performed using the NS22b (5'-AATTAAGCAGACAAATCACT-3') and SSU817 (5'-TTAGCATGGAATAATRAATAGGA-3') primers for specific amplifications of the fungal V4 and V5 18S rRNA gene region (Lê Van et al. 2017 after Borneman and Hartin 2000) leading to a 530 pb amplicon. The primers 799F (5'-AACMGGATTAGATACCKG-3') and 1223R (5'-CCATTGTAGTACGTGTGTA-3') (Vannier et al. 2018) were

used to amplify the bacterial V5-V6-V7 16S rRNA gene region without amplification of plant DNA. All the primers contained the Illumina® adaptors necessary for multiplexing at their 3' region. The PCRs were performed with Illustra™ PuReTaq Ready-to-go beads (GE Healthcare®).

Fungal PCRs consisted in an initial denaturation step at 95°C for 4 min followed by 35 cycles of 95°C for 30 s, 53.5°C for 30 s, 72°C for 1 min and a final extension step at 72°C for 10 min. Bacteria PCRs started with an initial denaturation step at 94°C for 4 min followed by 35 cycles of 94°C for 30 s, 53.5°C for 30 s, 72°C for 1 min and a final extension step at 72°C for 10 min. All PCR products were then purified with AMPureXP magnetic beads (Agencourt®) using an automated liquid platform (Bravo-Agilent®) and quantified (Quant-iT PicoGreen™ dsDNA Assay Kit) to allow normalization at the same concentration. A second PCR was performed using the Smartchip-system (Takara) to achieve multiplex tagging (up to 384 amplicons in one-step PCR); the resulting tagged-amplicon pool was purified (AMPureXP, Agencourt®) and quantified using Kapa Library Quantification Kit Illumina® platforms (KAPA BIOSYSTEMS®) on a LC480 LightCycler qPCR instrument (Roche®). Pair-End 2 × 250 cycles sequencing runs (MiSeq instrument, Illumina) and Pair-End 2 × 300 cycles for bacterial and fungal sequencing, respectively, were performed. The DNA concentration was normalized, the amplicon library constructed and sequencing was performed at the 'EcogenO' platform (<https://osur.univ-rennes1.fr/ecogeno>; Rennes, France).

Data trimming and affiliation

Data trimming consisted of removing primer and degenerated bases and dereplicating sequences (Cutadapt) resulting in 9110 420 reads for bacteria and 11 893 842 reads for fungi. Trimmed sequences were then analyzed using the FROGS pipeline (Escudié et al. 2018). The FROGS standard pre-process was used for bacteria and fungi. This pipeline uses SWARM for cluster formation. SWARM is an adaptive sequence agglomeration based on aggregation parameters rather than on a global similarity threshold (Escudié et al. 2018) to produce "sequence-cluster". In comparison to the ASV approach, the main advantage of clustering in FROGS is avoiding overestimation of sequence diversity (e.g. multicopy artifacts). Sequence clustering was combined with a rigorous chimera removal step (Escudié et al. 2018) and removal of all clusters detected in less than three samples and with a threshold of 0.005% of reads. Silva132 (16S) (Quast et al. 2013) which is already in reference list but with 2012 instead of 2013 and PhymycoDB (Mahé et al. 2014) databases were used to implement taxonomic data onto each bacterial and fungal sequence cluster respectively. Sequence cluster affiliations were filtered with a threshold of at least 95% coverage and 95% BLAST identity. Sequence data are available at the European Nucleotide Archive under the accession number PR-JEB43151. Contingency matrices were normalized to the minimum number of sequences per sample, i.e. 5000 and 7913 sequences for bacteria and fungi, respectively. By drawing rarefaction curves, we checked that this number of sequences per sample described both the root endospheric bacterial and fungal communities in sufficient depth (Fig. S1). All statistical analyses were performed on these two normalized contingency matrices.

Beta diversity

A principal coordinate analysis was performed on the Bray–Curtis dissimilarity distance matrix for bacteria and fungi. Dissimilarity analyses ("adonis", which performs a multidimensional analysis of variance on distance matrices, with 999 permutations) were

performed on bacterial and fungal community using the "vegan" R package (; Oksanen et al. 2011). At the local scale, we tested the effect of farming type, edge type and edge distance on sequence cluster composition among samples. At the landscape scale, we defined four modalities based on the quartile values (1, 2, 3 and 4 from the minimum to the maximum values) for organic farming % cover (quartiles: 7.9–16.9, 16.9–24.8, 24.8–32.7 and 32.7–40.7%) and hedgerow density (quartiles: 1.3–4.3, 4.3–5.6, 5.6–6.9 and 6.9–8.1 km/km²).

Analysis of indicator species

We used a taxon group association analysis to determine sequence clusters that were indicators of each condition. We analyzed indicator species for each farming type (organic or conventional) and within each farming type depending on field edge type (grassy or hedgerows) and extreme field edges distance (0 and 30 m). We assessed the degree of fidelity ($P \leq .05$) of each sequence cluster with one given condition or combination of conditions with correlation indices (point biserial correlation coefficient) using the multipath function of the "indicspecies" R package (De Cáceres et al. 2010).

Calculation of diversity indexes

From the normalized contingency matrices, we calculated root-endosphere microbial species diversity metrics including richness (hereafter sequence-cluster richness), Shannon diversity index and Pielou's evenness index. These metrics were calculated for the "all fungi" and "all bacteria" assemblages as well as for the phyla representing the most important sequence-cluster numbers. Richness, Shannon diversity and evenness indices were calculated using the microbiome R package (Lahti et al. 2017). Richness and Pielou's evenness were correlated less than 0.70 confirming the non-redundancy of these response variables (Dormann et al. 2013). However, Shannon index was always correlated to Pielou's evenness or sequence cluster richness (Table S1), and was then not included in further analysis.

Trophic guild assignment

We classified the identified sequence clusters into ecological guilds using the FUNGuild database (Nguyen et al. 2016) for fungi, and the Faprotax database (Louca et al. 2016) for bacteria. We assigned for each fungal sequence cluster one of the following functional groups: pathogen, saprotroph, symbiotroph, unassigned. We assigned for each bacterial sequence cluster one of the following functional groups: denitrification, hydrocarbon degradation, iron respiration, pathogen, photoautotrophy, others, unassigned. A majority of the microorganisms found in the root endosphere could not be assigned to a given clear trophic group (55% for bacteria and 72% for fungi are unassigned). In bacteria, 32 out of the 955 sequence clusters recorded were removed from the dataset because they were assigned to two or more functional guilds. We then calculated the relative richness and relative abundance of the sequence clusters by trophic guild. The effect of explanatory drivers on functional guilds with low numbers of sequence clusters (e.g. denitrification, iron respiration, photoautotrophy for bacteria) were not tested statistically.

Statistical analyses

We tested the effect of agricultural intensification on microbial diversity at field and landscape scales for "all fungi" and "all bacteria" and the dominant fungal and bacterial phyla. At the field scale, we used a linear mixed model for each diversity index and

the relative richness and relative frequency per trophic guild were used as the explained variables, and farming type (organic vs. conventional), edge type (grassy vs. hedgerow) and distance from the edge, and their interactions, as the explanatory variables. At the landscape scale, we used a linear mixed model for each diversity index and the relative richness and relative frequency per trophic guild were used as the explained variables, and % cover of organic farming and hedgerow density, and their interactions, as the explanatory variables using the lme4 R package (Bates et al. 2015). Because of our nested sampling design (Fig. 1), we added a nested random factor to each model to control for data dependency (landscape/field/edge). We checked the normality and homoscedasticity of the model residuals using a graphical representation of the residuals. The data were log or square-root transformed when necessary to meet linear model requirements. Then we calculated the Akaike information criterion corrected for small sample sizes (AICcs) of all the models with the combination of the three factors and their interactions. We calculated the marginal (R^2_m) and conditional (R^2_c) values of R^2 for the model with the lower AICc value. These R^2 correspond to the variance explained by the fixed effects and the addition of fixed and random effects, respectively. The models were ranked by their AICcs. All models having an AICc value between the smallest AICc value + 2 were averaged (Burnham and Anderson 2002). All statistical analyses were performed using R software (R Development Core Team 2013) version 4.0.0.

Results

Wheat root endosphere bacterial and fungal taxonomic composition

The wheat root endospheric bacterial assemblage in the total pool (955 sequence clusters) was mainly composed of *Proteobacteria* (587 sequence clusters, 67% of the sequences) and the *Bacteroidetes* (153 sequence clusters, 22% of the sequences) phyla (Fig. S2a). The wheat root endospheric fungal assemblage in the total pool (291 sequence clusters) was composed of 65% of *Ascomycota* (130 sequence clusters), 5% of *Basidiomycota* (61) and 14% of *Chytridiomycota* (36), 2% *Glomeromycota* (18) and 11% *Zygomycota* (42) (Fig. S2b). Bacterial trophic guilds were composed of sequence clusters involved in denitrification (2), hydrocarbon degradation (341), iron respiration (5), pathogen (37) and photoautotrophy (6). Fungal trophic guilds included pathogens (21 sequence clusters), saprotrophs (30) and symbiotrophs (18).

Effect of farming type and edge type at the field scale

At the local scale we found significant effects of farming type and edge distance on the wheat root endosphere bacterial and fungal taxonomic composition despite low R^2 (Table 2; Fig. S3). The explanatory variables were also significantly related to fungal richness and to some phyla of bacteria (Table 3), while it was not related to Pielou's evenness. Indeed, the model averaging selection on Pielou's evenness always converged to the null model or showed no significant result.

In bacteria, sequence cluster richness for 'all bacteria' and for all phyla except *Acidobacteria* was not related to any of the variables tested (Table 3). The sequence cluster richness of *Acidobacteria* was significantly higher in organic than in conventional farming ($P < .01$) (Fig. 2). In fungi, the sequence cluster richness for "all fungi" ($P < .01$), *Glomeromycota* ($P < .001$) *Chytridiomycota* and *Zygomycota* ($P < .05$) depended on the farming type but not on the

Table 2. Multidimensional analysis test (adonis) on dissimilarity distance matrices (Bray Curtis) of bacterial and fungal communities depending on local (farming type, edge type and edge distance) and landscape factors (% cover of organic farming and hedgerow density).

	Bacteria		Fungi	
	P	R ²	P	R ²
Farming type	*	0.01	***	0.03
Edge type	ns	0.01	ns	0.01
Edge distance	**	0.01	**	0.02
Organic farming %	*	0.01	***	0.02
Hedgerow density	ns	0.01	**	0.02

ns: non significant, **: $p < 0.01$; ***: $p < 0.001$

edge type (Table 3). In these groups, we recorded higher richness in organic fields than in conventional ones. *Ascomycota* were not linked to either farming type or edge type. In "all fungi" and in two out of the five phyla tested, sequence cluster richness decreased from the edge to the 30-m sampling point (Fig. 2).

The "indicator species" analysis identified 250 bacterial sequence clusters significantly more related to a given farming type (i.e. 137 to organic and 113 to conventional farming) (Table 4). Sequence clusters indicative of farming type were more related to *Proteobacteria* in conventional and organic fields with a higher number of indicator sequence clusters in conventional fields (Fig. S4). We found also a higher number of indicator sequence clusters in *Acidobacteria*, *Actinobacteria* and *Bacteroidetes* in organic fields compared with conventional ones (Fig. S4). Within organic fields, we found a higher number of indicator species related to hedgerow than to grassy edges. Within conventional fields, similar numbers of indicator species were detected between grassy and hedgerow types (Table 4). For both farming and edge types, there was a higher number of indicator sequence clusters close to the edge compared with the 30-m sampling point. For fungi, 91 sequence clusters were identified with 46 sequence clusters significantly more related to organic and 45 to conventional farming (Table 4). Sequence clusters indicative of farming type were strongly related to *Ascomycota*, but differed in sequence cluster number for *Glomeromycota* and *Basidiomycota* among organic and conventional fields (Fig. S4). Within organic fields, there were more indicator species related to hedgerow edge than to grassy edge, and to closer distance to the edge compared with the 30-m sampling point (Table 5).

The relative guild type richness and abundance were both not related to any of the local variables tested for bacteria, except for the guild of hydrocarbon degradation, and for fungi, except for the guild of fungal symbiotrophes. The number of sequence clusters involved in hydrocarbon degradation depended on edge distance ($P < .001$). Interestingly, the fungal symbiotroph showed higher relative richness in organic compared with conventional fields ($P < .001$; Org (0.045) > Conv (0.030)).

Effect of the % cover of organic farming and hedgerow density at the landscape scale

At the landscape scale, the % cover of organic farming modified the wheat root endosphere bacterial and fungal composition while hedgerow density only influenced fungal microbiota despite low R^2 (Table 2; Fig. S3).

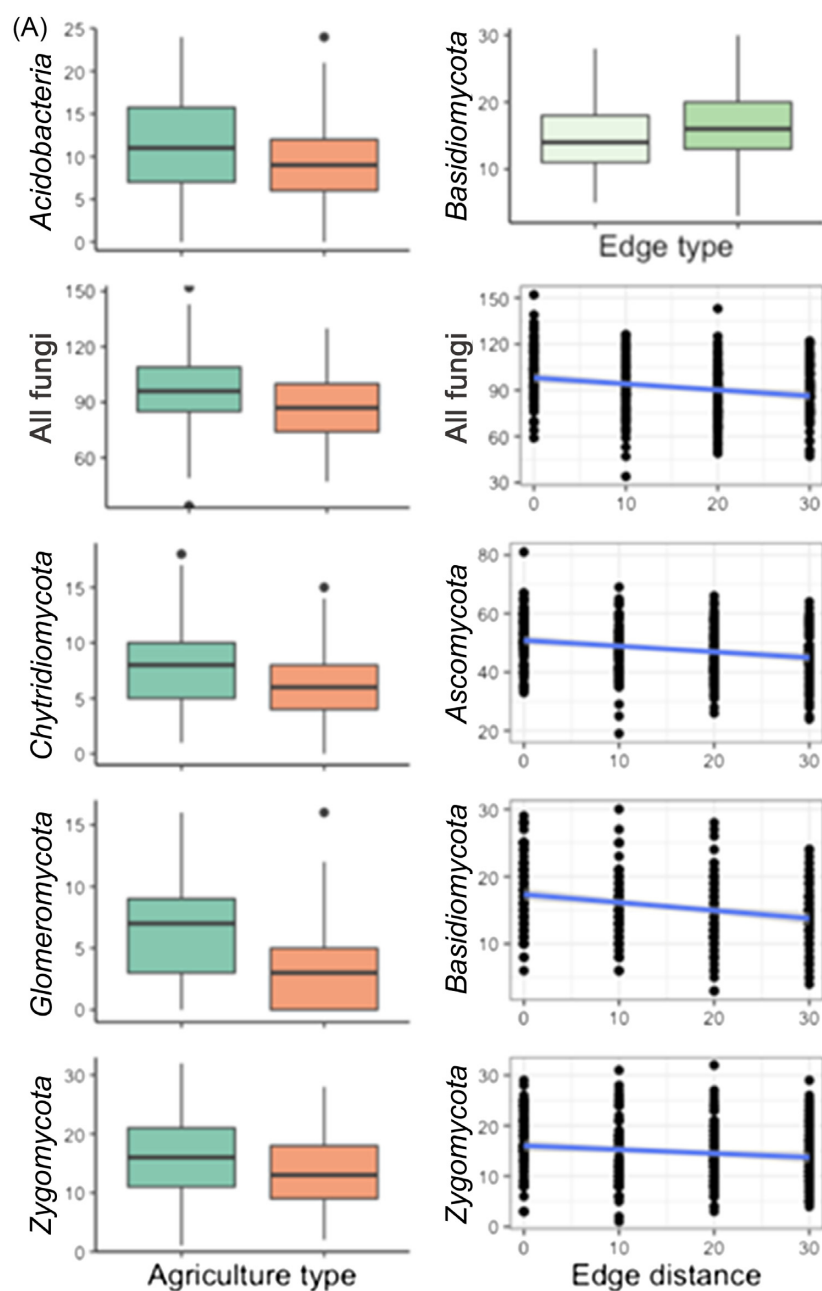


Figure 2. Data for significant richness variation at local (A) and landscape scale (B). Richness variation depending on farming type (organic in teal and conventional in orange), edge type (grassy edge in light green and hedgerow in green) and edge distance from the edge (A). Richness variation depending on % cover of organic farming and hedgerow density (B).

In bacteria, the sequence cluster richness of “all bacteria” and of three out of the five phyla tested was related to the % cover of organic farming (Table 5). Sequence cluster richness of “all bacteria”, *Actinobacteria*, *Firmicutes* and *Proteobacteria* increased with the % cover of organic farming in the landscape (Fig. 2). In addition, the sequence cluster richness of “all bacteria” and of two out of the five phyla tested was related to hedgerow density (Table 5). The sequence cluster richness in “all bacteria”, *Actinobacteria* and *Proteobacteria* decreased with hedgerow density (Fig. 2). In fungi, the sequence cluster richness of “all fungi” and of all phyla except *Chytridiomycota* was not related to the % cover of organic farming or to hedgerow density in the landscape. By contrast, the sequence cluster richness of *Chytridiomycota* increased with the % cover of organic farming and decreased with hedgerow density (Table 5; Fig. 2).

For bacteria and fungi, the relative guild type richness and relative guild type abundance were not related to any of the landscape variables tested, except for the guild of hydrocarbon degradation in bacteria. The number of sequence clusters involved in hydrocarbon degradation increased with the % cover of organic farming in the landscape ($P < .05$) and decreased with hedgerow density ($P < .01$).

Discussion

We investigated the effect of agricultural intensification on wheat root endospheric microbiota by analyzing more specifically the effect of organic farming and hedgerow density for two spatial scales: field and landscape scales. We demonstrated that the wheat root endosphere taxonomic composition and diversity of

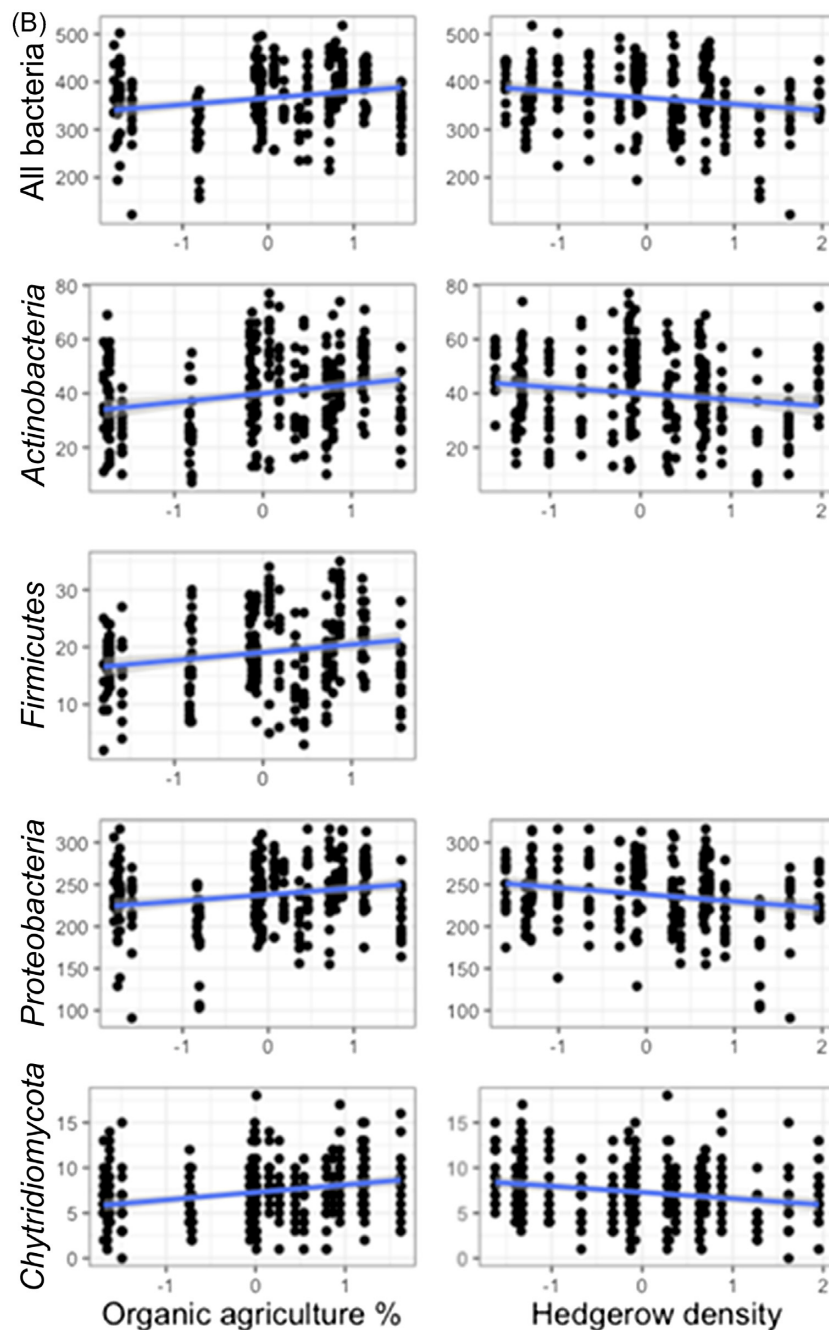


Figure 2. Continued.

bacterial and fungal assemblages were influenced by farming type (organic vs. conventional), edge type (hedgerow vs. grassy) and the distance from the field edge, with contrasting scales of effect (*sensu* Miguet et al. 2016) depending on the taxonomic group and phyla considered.

Influence of organic compared with conventional agriculture at the field and landscape scales

Organic farming induced a shift in root endosphere taxonomic community composition with a promoted diversity in both bacteria and fungi.

In bacteria, wheat developing in organic fields displayed a higher richness in *Acidobacteria* but similar richness in the other

phyla compared with conventional fields, while at the landscape scale, a higher % cover in organic farming was related to higher overall bacteria, *Actinobacteria*, *Proteobacteria* and *Firmicutes* richness. Changes in root endosphere bacterial composition were statistically significant, and corresponded to shift in specific sequence clusters. These changes could be related to modifications in the soil microbial reservoir in response to changes in soil characteristics. Indeed, organic fields display higher soil fertility (Mäder et al. 2002), especially linked to increased soil water content, soil porosity, humic matter and higher content in extractable carbon and nitrogen (Liu et al. 2007). These particular characteristics have been shown to drive higher microbial activity and bacterial functional diversity (Liu et al. 2007). We demonstrated herein a positive effect of organic farming at the landscape scale on par-

Table 3. Effect of farming type, edge type, edge distance and their interactions on bacterial and fungal sequence cluster richness. The farming type—organic and conventional—are abbreviated as “Org” and “Conv”, the hedgerow and grassy edges as “H” and “G”, and the variation in richness as ‘/’ and ‘\’ for increasing and decreasing values respectively. R² m and R² c correspond reciprocally to marginal and conditional R² of the best model. N values correspond to the number of samples for each model tested. Variable values that were not included in the averaged models are not shown here.

	Model			Farming type			Edge type			Edge distance			Farming type: Edge type			Edge type: Edge distance		
	N	R ² c	R ² m	P	Richness		P	Richness		P	Richness		P	Richness		P	Richness	
All bacteria	268	0.25	0.01	ns	-		ns	-		ns	-		ns	-		ns	-	
Acidobacteria	268	0.23	0.05	**	Org>Conv (11.2>9.0)		ns	-		ns	-		ns	-		ns	-	
Actinobacteria	268	0.24	0.01	ns	-		ns	-		ns	-		ns	-		ns	-	ns
Bacteroidetes	268	0.50	0.01	ns	-		ns	-		ns	-		ns	-		ns	-	-
Firmicutes	268	0.35	0.00	ns	-		ns	-		ns	-		ns	-		ns	-	-
Proteobacteria	268	0.27	0.01	ns	-		ns	-		ns	-		ns	-		ns	-	-
All fungi	310	0.28	0.10	**	Org>Conv (96.3>88.0)		ns	-		***	↘ (98.0–86.3)		ns	-		ns	-	-
Ascomycota	310	0.16	0.08	-			-	-		***	↘ (50.8–45.0)		***	↘ (17.3–13.8)		ns	-	-
Basidiomycota	310	0.18	0.09	Ns			ns	-		***	↘ (17.3–13.8)		ns	-		ns	-	-
Chytridiomycota	310	0.33	0.05	**	Org>Conv (8.0>6.5)		ns	-		ns	-		ns	-		ns	-	-
Glomeromycota	310	0.46	0.15	***	Org>Conv (6.4>3.5)		ns	-		ns	-		ns	-		ns	-	-
Zygomycota	310	0.31	0.06	*	Org>Conv (16.0>13.7)		ns	-		ns	-		ns	-		ns	-	-

ns: non significant, ***: P<0.001

ticular bacteria phyla suggesting that in addition to providing particular habitat conditions, organic fields act as reservoirs of sequence clusters for the other fields, or promote dispersal by reducing isolation among organic fields. Further work is needed to validate this hypothesis by analyzing more specifically the dispersal process in the bacterial and fungal groups responding at the landscape scale.

In fungi, wheat developing in organic fields harbored a higher richness in overall fungi, and more specifically in *Glomeromycota*, *Chytridiomycota* and *Zygomycota*, impacting the root-endosphere sequence clusters composition. The effect of organic farming was detected only for *Chytridiomycota* at the landscape scale with higher richness found in fields surrounded by a high % cover of organic farming. The positive effect of organic farming may be linked to the lower presence of pesticides in soils (Riedo et al. 2021). Indeed, the use of pesticides and especially fungicides to protect plants from fungal pathogens can have harmful collateral effects on symbiotic fungi (Johnsen et al. 2001, Hussain et al. 2009), and a lasting effect on soil fungal diversity (Riedo et al. 2021). It can be linked also to the higher diversity in plants in organic crop fields (Ründlof et al. 2010, Stein-Bachinger 2021). Higher plant diversity might ensure higher richness of the total pool of fungal propagules in the soil through a fingerprint effect on the soil reservoir (Vannier et al. 2020), and enhanced transmission through root contacts (Mony et al. 2021). In the present study, these positive effects seem to override the negative effects of higher frequency of tillage and mechanical weeding found in organic fields (see the Methods section on Field Description) on endospheric and rhizospheric fungi (Jansa et al. 2003, Alguacil et al. 2008, Säle et al. 2015).

The overall positive effect of organic farming at the field and/or at the landscape level could have several implications on key ecological functions for the plant. Some phyla promoted by organic farming may be involved in plant growth. For instance, the increase of symbiotic fungi, such as *Glomeromycota*, could enhance plant resource uptake and protection from stresses (van der Heijden et al. 2008), while *Acidobacteria* improved the increase in plant biomass likely through acting on hormone production and iron acquisition (Kielak et al. 2016). Other phyla interplay with plant resistance to diseases. For instance, *Actinobacteria* were dominated by *Streptomyces*, which are often described as antibiotic producers (Liu et al. 2013). In addition, in the *Gammaproteobacteria* phylum, we detected a high proportion of *Pseudomonadaceae*, *Burkholderiaceae*, and *Xanthomonadales*, *Gammaproteobacteria* that have been associated with disease-suppressive activity governed by nonribosomal peptide synthetases (Mendes et al. 2011). Organic farming might hence promote microorganisms that could help wheat to better resist pathogens.

Influence of hedgerows at the local and landscape scales

Hedgerow presence at the edge of the field had a limited impact at the field scale on both bacteria and fungi, while hedgerow density affected microbial assemblages at the landscape scale. Indeed, high hedgerow density modified root endosphere fungal taxonomic composition in wheat, and negatively affected richness in *Chytridiomycota*, and in the overall group of bacteria with a more specific effect on *Actinobacteria* and *Proteobacteria*. In bacteria, edge types and distance from the edge were not linked to sequence cluster richness in any phylum, suggesting an overall homogenization of assemblages at the field level. However, wheat developing within landscapes with a high hedgerow density displayed a lower richness in overall bacteria, and more specifically in Acti-

Table 4. Counting of the “indicator species” detected. Numbers correspond to “indicator species” richness per phylum for organic and conventional farming types; and within each farming type, close (0 m) or far (30 m) from the field edges (grassy or hedgerow).

	Organic farming				Conventional farming			
	Grassy		Hedgerow		Grassy		Hedgerow	
	0	30	0	30	0	30	0	30
Acidobacteria	0	0	1	0	0	0	0	0
Actinobacteria	1	1	2	1	4	0	1	3
Bacteroidetes	1	0	4	0	1	9	4	0
Fibrobacteres	0	0	0	0	1	0	0	0
Firmicutes	0	0	0	0	1	0	0	0
Proteobacteria	6	2	12	5	11	7	11	9
Ascomycota	1	0	5	1	3	0	7	0
Basidiomycota	0	0	3	0	0	0	2	1
Chytridiomycota	0	0	0	0	0	0	1	0
Zygomycota	0	0	0	0	0	0	1	0
Unknown	0	0	0	0	6	0	1	0

Table 5. Effects of the % cover of organic farming, hedgerow density and their interactions at the landscape scale on bacterial and fungal sequence cluster richness. Variations in sequence cluster richness are shown respectively as ‘↗’ and ‘↘’ for increasing and decreasing values. R² m and R² c correspond reciprocally to marginal and conditional R² of the best model. N values correspond to the number of samples for each model tested. Variable values that were not included in the averaged models are not shown here.

	Model			Organic farming %		Hedgerow density		Organic farming %: Hedgerow density	
	N	R ² c	R ² m	P	Richness	P	Richness	P	Richness
All bacteria	268	0.24	0.08	**	↗ (342.4–387.1)	**	↘ (386.7–342.6)	ns	-
Acidobacteria	268	0.22	0.02		-	ns	-	ns	-
Actinobacteria	268	0.24	0.07	**	↗ (34.2–45.0)	ns	↘ (43.5–35.7)	ns	-
Bacteroidetes	268	0.49	0.02	ns	-	ns	-	ns	-
Firmicutes	268	0.35	0.07	*	↗ (16.4–21.1)	ns	-	ns	-
Proteobacteria	268	0.26	0.07	*	↗ (225.8–249.0)	**	↘ (251.1–223.2)	ns	-
All fungi	310	0.22	0.01	ns	-	ns	-	ns	-
Ascomycota	310	0.09	0.00	ns	-	ns	-	ns	-
Basidiomycota	310	0.08	0.00		-	ns	-		-
Chytridiomycota	310	0.33	0.10	**	↗ (5.9–8.6)	**	↘ (8.3–6.0)		-
Glomeromycota	310	0.46	0.00		-	ns	-		-
Zygomycota	310	0.28	0.00	ns	-	ns	-	ns	-

ns: non significant, **: P<0.01

nobacteria and *Proteobacteria*. This suggests the importance of landscape openness (landscape with numerous and/or large herbaceous habitat patches) for the dispersal of bacteria. By acting as barriers to wind and water, a high density of hedgerows in the landscape could reduce dispersal fluxes, and hence the probability of the establishment of bacteria in crops (Plantegenest et al. 2007). In addition to these possible dispersal-limiting processes, the decrease in *Actinobacteria* and *Proteobacteria* richness could also be explained by their ecological requirements. Santos-Medellín et al. (2017) reported an increase in *Actinobacteria* in rice root microbiota exposed to drought stress and more particularly in the *Thermophililla* genus, which was the main component of *Actinobacteria* in our dataset (79% of sequence clusters). In agreement with these results, the climatic effect of hedgerows on their immediate vicinity may limit drought stress through better control of water distribution and shading effect (Vanneste et al. 2020a) and thus explain the lower richness of *Actinobacteria* in landscapes with a high density of hedgerows.

In fungi, a similar negative effect of hedgerow density was found on one of the phyla: *Chytridiomycota*. As this phylum disperses predominantly in water via zoospores (Gleason and Lilje

2009), we can speculate that hedgerows might act as barriers to water flow occurring after rainfalls, and reduce the dispersal capacity of *Chytridiomycota*. In contrast to bacteria, whatever the type of field edge (hedgerow or grassy), individual wheat plants located close to field edges displayed a higher sequence cluster richness of overall fungi and in most of the fungal phyla, suggesting that field edges are biodiversity reservoirs for fungal communities. First, wheat individuals were sampled at a few centimeters of the edge border. This area might correspond to reduced farming activity (i.e. less tilling or spreading of fertilizer and phytosanitary products) or specific abiotic conditions, especially of soil characteristics and local microclimate. Edges also display high plant diversity (Aude et al. 2003) that may influence root-endosphere microbial composition through the neighborhood effect. In this work, we assumed that the edge effect assessed from distances to the edge was similar among fields. Because our sampling design was along a similar distance to the edge, we expect that no other indirect effect of farming type could influence the decrease of fungal diversity observed along the transect, but a bias related to the field size could not be excluded.

Contrasted scales of response between bacteria and fungi

The present work revealed that bacteria and fungi do not respond to agricultural intensification at the same spatial scales. While fungal assemblages mainly responded at the field scale, bacteria mainly responded at the landscape scale. Because we studied endospheric microbiota at the individual plant scale, the differences in responses cannot therefore be related to differences in the specific recruitment of plants, but rather to the factors that govern the accessible pool of soil microorganisms to be recruited. This suggests that mechanisms operating at large scale, such as dispersal, may be involved. Indeed, most endospheric fungi may be dispersed below-ground over short distances, in a fraction of them, through hyphal development (Smith and Read 2008) and by spore dispersal (Reddell and Spain 1991), while bacteria are assumed to disperse over greater distances (Bell 2010, Constanças *et al.* 2015), especially through rainfall flow within the landscape. This hypothesis needs to be tested because, at present, little is known about how microorganisms disperse and about the relative importance of short versus long dispersal distances in these groups. Further sampling campaigns over time should be undertaken to confirm these results to cover the whole life cycle of the crop plant and to account for seasonal changes in microbial assemblages due to plant phenology and agricultural management.

Conclusion

Studies investigating the effect of landscape structure on the distribution of microorganisms associated with crops are rare, and those that do generally focus on pathogen species (Margosian *et al.* 2009, Biek and Real 2010, Reisen *et al.* 2010). To our knowledge, this study is one of the very few demonstrations of the effect of landscape drivers, and especially of agricultural intensification, on the root endosphere microbiota in agrosystems. Overall, our results showed the enrichment effect of organic agriculture at both field and landscape scales on the wheat endophytic richness providing evidence that agricultural management needs to be considered at several spatial scales. More especially, we provide here the evidence that increasing the percentage of organic agriculture at the landscape scale can maintain higher bacterial richness even in conventional fields, thus could contribute to a microbial richness “rescue effect”. In contrast to our expectations, hedgerow density at the landscape scale did not promote microbial richness but rather negatively affected some fungal and bacterial phyla, potentially because of their role in dispersal fluxes. More detailed analyses are now required to understand exactly how they interact in microorganism dispersal. Lastly, our work stresses the important role of field edges, whatever their grassy or woody plant cover, as a source for disseminating fungi in the crop field. This work provides new evidence of field margin benefits for agrosystem diversity and productivity via their associated ecosystem functions (here, endophyte richness). Endospheric microorganisms provide various functions to crop plants and strongly affect plant fitness and hence crop productivity. Maintaining a rich microbial pool associated with plants, to ensure a wide range of ecological functions, is a key issue in the current transition toward more environmentally friendly agricultural practices. In this sense and as supported by this study, considering the multiscale responses of microbial communities to drivers of agricultural intensification is of primary importance.

Funding

This work was supported by both Fondation de France and by the Agence française pour la biodiversité.

Supplementary data

Supplementary data are available at [FEMSEC](https://femsec.org) online.

Author contributions

CR, CM, SA and PV conceived the project and all the authors contributed to the methodology of the study. CM, PV, OJ and CR collected the data. SM-C, RC-V, SM and CR performed the sequence analyses. CR and CM analyzed the data statistically and CR, CM and PV wrote the manuscript. All authors contributed critically to the interpretations of results and to the drafts and gave their final approval for publication.

Acknowledgements

We thank the farmers who gave us permission to sample wheat in their fields. This work used landscape databases built in the LTSER site “Zone Atelier Armorique”. Hedgerow network maps were drawn by Kermap. We are grateful to the GENTYANE (<http://gentyane.clermont.inra.fr/>) and the EcogenO ([https://geh.univ-rennes1.fr/?\[en\]](https://geh.univ-rennes1.fr/?[en])) and the Genotoul (<https://www.genotoul.fr/en/>) platforms for DNA extraction, amplicon sequencing and bioinformatics analyses, respectively. We are also grateful to ANAEE-France (<https://www.anaee-france.fr/en/>). We thank Sébastien Boinot and Eloïse Couthouis for providing information on hedgerows. We also want to thank Sarah Leclerc, Noémie Poulain, Marine Biget and Ning Ling for assistance during the sampling campaigns.

Conflict of interest statement. None declared.

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