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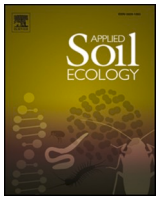

Land cover, plant residue and soil microbes as drivers of soil functioning in temperate agricultural lands. A microcosm study

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ABSTRACT

Feedbacks between plants and soil microbes are critical for ecosystem regulation and restoration. Soil microbial diversity is largely dependent on plant diversity, yet these relationships have received little attention at the landscape scale. In agricultural landscapes, the presence of different plant cover types (landscape elements) can modulate these feedbacks by adding spatial heterogeneity through changes in the amount and composition of plant residues. Furthermore, it can also influence the soil biota. Therefore, the more diverse the landscape elements of farmlands, the higher the increase of their heterogeneity. We investigated the microbial catabolic profiles and respiration rates of soils from different plant cover types through the manipulation of plant residues and microbial communities. In individual microcosms, we incubated sterilized soils sampled from five different cover types of a temperate agricultural landscape: Soybean Monocropping, two crop rotations (Rotation and Intensified Rotation) and two uncropped margins: Herbaceous and Woody spontaneous vegetation. We amended them with each of two plant residues: wheat stubble (Wheat) and a mix of spontaneous vegetation (Mix). Soils were also inoculated with each of two soil microbial communities: Soybean Monocropping and Woody margins. We predict that soils treated with the Mix residue and the Woody margins community will show higher catabolic diversity and respiration than those treated with Wheat stubble and Soybean Monocropping community. In turn, we predict that soils from Woody margins, with higher carbon content, will respire more and amplify the effects of plant residue and microbial community. The microbial catabolic profile changed with plant residue and microbial community whereas the microbial respiration changed with cover type. After 30 days of incubation, soils inoculated with Woody margin community sustained higher diversity than those inoculated with Soybean Monocropping community. Conversely, Wheat stubble increased microbial diversity with respect to the Mix, particularly in soils from Woody margins while Mix residue increased the microbial diversity of soils from Soybean Monocropping. Finally, microbial respiration of soils from Woody margins showed the greatest respiration and Soybean Monocropping the lowest, in correlation with their carbon contents. Despite the complex interactions between soil carbon contents and plant residue composition, our results suggest that internal transfers of soil and plant residue between the different landscape elements might contribute to increasing the resilience of agricultural landscapes.

1. Introduction

In terrestrial ecosystems, plants and soil microbes interact through the reciprocal exchange of carbon and mineral nutrients (Dehlin et al., 2006; Wardle et al., 2006; Fanin et al., 2019). Soil microbes act as both sink and source for carbon and nutrients and can indirectly regulate plant growth through both mineralization and stabilization of soil organic matter (Wardle et al., 2004; Cotrufo et al., 2013). Plants, in turn, provide carbon and nutrients as senescent tissues and root exudates, which are key control factors of the structure, abundance, and activity of soil microorganisms (Kuzyakov and Schneckenberger, 2004; Paterson et al., 2008). Likewise, plant and soil microbial diversity can be positively correlated, particularly in early successional ecosystems, where fresh plant litter is the most abundant source of energy, carbon, and mineral nutrients (Porazinska et al., 2018). Because agriculture reduces species and genetic diversity of plant inputs, in comparison to original

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plant communities, sustaining functional diversity of soil microbial communities in these contexts is challenging. Moreover, in agricultural ecosystems, farming practices cause stronger homogenization of soil bacterial communities at landscape scale (reduced β-diversity), due to the dramatic spatial homogenization of soil physicochemical properties, particularly soil nutrient contents (Wang et al., 2022). However, empirical evidence shows that certain practices at farm and landscape levels, which implies managing uncropped margins for conservation aims, can contribute to increase soil diversity and functioning to a defined extent (McDaniel et al., 2014; Venter et al., 2016; D'Acunto et al., 2016, 2018). Nevertheless, the relative roles of plant residue, microbial composition and soil properties are complex and difficult to predict, which challenge the success of ecological regenerative practices (Callaham Jr et al., 2008; Harris, 2009; Schmidt et al., 2011; Wickings et al., 2012; Cotrufo et al., 2013; Craig et al., 2022).

Restoration practices typically focus on aboveground plant communities while the role of the soil microbial communities is frequently neglected (Callaham Jr et al., 2008; Stanturf et al., 2014). However, aboveground-based restoration does not necessarily result in the recovery of belowground microbial communities and the efforts may then fail to restore the total carbon and nutrient cycling (Fierer and Jackson, 2006; Strickland et al., 2017). An emerging group of restoration strategies focuses directly on reestablishing soil microbial communities and their functions for carbon stabilization and recycling of mineral nutrients through transplanting or removing topsoil to recreate the environmental conditions more favorable for native plant communities (Vécrin and Muller, 2003; Jaunatre et al., 2014; Wubs et al., 2016). Although these restoration techniques are promising, they would not be adequate for large-scale interventions to be implemented in agroecosystems, where the largest proportion of soil cover is continuously cropped. Therefore, in extensive agroecosystems practices provided by cash crop rotation and cover crops, at the plot level, combined with those provided by non-cropped habitats, at the landscape level, might result an effective strategy for achieving productive agroecosystems and resilient to cope with biotic and abiotic adversities (Lauber et al., 2008; Wickings et al., 2012; Venter et al., 2016; D'Acunto et al., 2016, 2018; Iglesias et al., 2021).

In the extensive agricultural landscapes of the Pampas of Argentina, agricultural mosaics coexist with intermingled herbaceous and woody patches of spontaneous vegetation (Poggio et al., 2010; Urrutia Larrachea et al., 2022). The composition and spatial configuration of these landscape elements affect soil through the simultaneous action of different factors. At the landscape level, the uncropped woody elements have more litter fall, soil carbon, a more diverse microbial catabolic community and soil respiration rates than the cropped areas (D'Acunto et al., 2014, 2016). In turn, at the plot level, within the cropped mosaic we observed that more diverse cash crop rotations correlate with more diverse soil microbial communities and showed higher respiration rates (D'Acunto et al., 2018). Respiration rates imply multiple, interacting processes involving complex microbial communities and fauna. Changes in the characteristics and functional properties of these consortia may have subtle effects on transformation pathways that may have long-term implications for microbial diversity and organic matter stabilization. Furthermore, the microbial communities of the different land covers revealed a relatively high resilience under agronomic practices such as fertilization and herbicide application (Iglesias et al., 2021). Even though empiric evidence seems promising for the design of sustainable soil management strategies, we ignore the mechanism underlying those responses, particularly the relative contribution of plant residue, microbial community, and plant cover type.

Here, based on a controlled microcosm experiment, we investigated to what extent it is possible to change soil microbial respiration, catabolic diversity and catabolic profile of five land cover types (two uncropped margins and three cropping systems) by exchanging plant residues and soil microbial communities among neighboring landscape elements. The general objective is to understand the mechanisms that determine the structure and functioning of the detritivorous microbial community of five land cover types that compound the agricultural landscape of the Pampas. We hypothesize that, in extensive agricultural landscapes such as the Pampas, a mix of management practices at plot scale (such us the manipulation of plant residues to a greater extent, and to a lesser extent, soil microbial communities) and at landscape scale (uncropped margins conservation) are a potential ecology-based strategy for the conservation and improvement of agricultural soil biodiversity in an extensive landscape as Pampas. We predict that modifications in plant residue and soil microbial communities will have a greater impact on microbial catabolic profiles and diversity compared to variations in land cover type. Besides, we expect that soil amendments with a combination of residues and microbial communities from Woody margins will exhibit higher respiration rates and greater catabolic diversity than those amended with Wheat residue and microbial communities from Soybean Monocropping. Finally, we predict that soils characterized by higher carbon content, primarily associated with Woody cover type, will demonstrate elevated soil respiration rates and a more diverse catabolic profile compared to other land cover types, regardless of the specific plant residue amendments or soil microbial inoculation.

2. Methods

2.1. Study system and land cover types

The study was performed in soil microcosms obtained from five land cover types of three locations (replicates) from the central portion of the Northeastern pampa grassland in the province of Buenos Aires, Argentina (Bragado: 35°07′S; 60°30′W, Pergamino; 33°55′S; 60°23′W, and Arrecifes: 34°04′S; 60°07′W). This region comprises extensive croplands which are among the most productive agricultural areas in the world, due to favorable climate and fertile soils (Urrutia Larrachea et al., 2022). Climate is temperate subhumid, without a marked dry season but with frequent water deficit during summer. Mean annual rainfall is approximately 1000 mm and mean annual temperature is 17 °C. Soils are mainly Mollisols, characterized by their outstanding aptitude for agriculture. In Arrecifes and Pergamino, typic Argiudolls are the prevalent soil types. This soil type is distinguished by a deep top horizon rich in organic matter (ca. 3 %), and an argillic horizon (usually between 40 and 80 cm depth from the soil surface) with higher clay content than in the above soil layer (38 % clay, Urquiza soil series in Pergamino). Typic Hapludolls are the common soils in Bragado, mostly well-drained soils with sandy-loam texture (Bragado soil series).

The original grassland vegetation was extensively plowed, and nowadays continuous cropping of annual crops dominates the landscape. Annual crops exceed 90 % of the area, 8 % is for feed cattle, and 2 % corresponds to uncultivated areas. Soybean occupies >80 % of the area as a single crop or as a second crop right after Wheat. Maize occupies <10 % of the area and Wheat is the main winter crop, with >20 % of the sown area (Urrutia Larrachea et al., 2022).

2.2. Sampling of soils, plant residues and microbial communities

Soils samples from the three locations corresponded to five cover types: Soybean Monocropping, regular and intensified crop rotation, and Herbaceous and Woody uncropped margins. Soil samples from croplands were obtained in a crop rotation experiment (see details in Iglesias et al., 2021). In each location, two plots were selected for Soybean Monocropping, two plots for Rotation, and two plots for Intensified Rotation. Soybean Monocropping and crop rotations differed in the composition, the total number of different crop types and land occupancy with crops. In each site, monocropping and two different crop rotations were replicated in two plots 24 m wide and 150 m long (3600 m^2 per plot). Monocropping consisted of a long fallow followed by soybean crop during two consecutive years: only one crop per year. Crop

rotation consisted of (i) a short winter fallow period followed by the wheat/soybean double crop in the first year, and a long fallow followed by maize in the second year; three crops in two years (hereafter Rotation); (ii) a short fallow followed by wheat/soybean double crop in the first year, and a short fallow followed by field pea/maize double crop in the second year; four crops in two years (hereafter Intensified Rotation). Sowing dates, plant densities and row spacing were adjusted to each crop according to the regional recommendation. Fertilization was applied at sowing to ensure non limiting nutrient supply, with nitrogen and phosphorus as urea, monoammonium phosphate, or single superphosphate (see also Iglesias et al., 2021). Soybean and field pea seeds were inoculated before sowing with nitrogen-fixing bacteria. Weeds, insect pests, and disease controls were conducted by chemical treatments with the usual protocols following the criteria applied in previous experiments (Andrade et al., 2015; Iglesias et al., 2021). Briefly, for fallow, soybean and maize, total herbicides (glyphosate, paraquat) were applied. Broadleaved weeds in wheat crops were controlled with residual herbicides (Metsulfuron methyl + Dicamba). Insect pests were controlled with chlorpyrifos, and fungal diseases were treated with products based on cyproconazole, tebuconazole, trifloxystrobin and azoxystrobin (see details in Iglesias et al., 2021).

Soil samples from uncropped margins were collected, in each location, from two areas corresponding to each of two cover types, dominated by spontaneous herbaceous vegetation (hereafter Herbaceous margins) or woody vegetation (hereafter Woody margins). The uncropped area represents 1–2 % of the landscape (Urrutia Larrachea et al., 2022). Herbaceous margins are linear environments (5-10 m wide), year-round vegetated by annual and perennial species that account for 80 % of landscape plant diversity (Poggio et al., 2010). The most abundant species are grasses (*Cynodon dactylon*, *Digitaria sanguinalis*, *Lolium multiflorum*, *Poa annua* and *Paspalum dilatatum*) and forbs (*Apium leptophyllum*, *Artemisia annua*, *Anthemis cotula*, *Bidens subalternans*, *Capsella bursa-pastoris*, *Chenopodium album*, *Hypochaeris radicata*, *Matricaria chamomilla*, *Portulaca oleracea*, *Silene gallica*, *Tagetes minuta* and *Trifolium repens*). Woody margins have an average area of 1 ha, are covered by tree species and have also an Herbaceous understory. The most abundant tree species is *Broussonetia papyrifera* (see details in D'Acunto et al., 2014).

Soil sampling took place in spring (November 2016). A total of 500 g of topsoil (0–10 cm) was collected with a manual shovel in six points at least 10 m apart at the center of plots, of the five different cover types of the three locations (two plots of Soybean Monocropping, two plots of Regular, two plots of Intensified Rotation, two uncropped Herbaceous and two Woody margins, by location). Soil samples were immediately transported to the laboratory to be sieved (2 mm mesh size) and mixed to obtain a composite sample of the three locations (Bragado, Pergamino, and Arrecifes) and for each of the five cover types (monocropping, Rotation, Intensified Rotation, Herbaceous and Woody margins). Initial soil properties were measured on sample aliquots (Table 1) and the rest of the soil sample (in the case of Soybean Monocropping and Woody margins, see below) was used for soil microbial inoculum preparation and for the microcosm experiment. Initial total organic carbon and nitrogen contents were determined by dry combustion method (LECO Corporation, 747 series combustion). Soil pH was measured in a 2.5:1 solution of water and soil. The remaining sample was autoclaved in 200 g containers to eliminate its microbial community and preserve only the edaphic properties (organic matter, mineral fraction, pH, nutrients, etc). Soils were placed three consecutive days in an autoclave at 120 °C for 20 min and then kept in a closed container until the beginning of the experiment (Trevors, 1996).

Plant residues were collected from the soil surface in the three locations mentioned above. Two residue types were used: a monospecific residue from Wheat stubble (hereafter Wheat) and a mixed of residues of the vegetation from herbaceous and woody margins (hereafter Mix). Wheat was collected in two wheat cropped plots (in six randomly located frames for each plot, 0.4 × 0.4 m) in each of the three sites and Mix was collected in two uncropped margin types dominated by spontaneous herbaceous vegetation (in six randomly located frames for each margin, 0.4 × 0.4 m) and in two woody vegetation margins in each of the three sites mentioned above (in six randomly located frames for each margin, 0.4 m × 0.4 m). In the laboratory, a composite sample was made by residue type (Wheat and Mix) by each location (Bragado, Pergamino, and Arrecifes). Before incubations, plant residue quality was determined with 10 g of each residue (the contents of carbon, nitrogen, lignin, cellulose). Total plant residue organic carbon and nitrogen were determined by dry combustion. The soluble compounds, hemicellulose and lignin concentration were determined by successive extractions with increasingly acidic detergents (Van Soest et al., 1991). In the laboratory, plant residue was dried at 60 °C and milled to ensure soil contact and microbial degradation. Milled plant residue was autoclaved in a closed container at 120 °C for 20 min for three consecutive days to eliminate its microbial community and was stored at 60 °C until the beginning of the experiment (Howard and Frankland, 1974).

Microbial inocula were prepared from the corresponding soil aliquots by filtering soil and collecting the leachate (Rodríguez Echeverría et al., 2013). The inocula were prepared from 2 kg topsoil (0–10 cm) of each cover type. Sieved soils were Mixed with distilled and sterile water in a 1:2 ratio (v:v). Then, they were stirred for 2 min and left to rest another 15 min. This process was repeated twice. The supernatant was filtered through a 0.5 mm filter to obtain a suspension of the fungi spores, hyphae, bacteria, and soil microfauna (Rodríguez Echeverría et al., 2013). Two microbial communities were used: Soybean Monocropping and Woody margins, based on previous results which showed a metabolic profile and functional diversity different of the soil heterotrophic bacterial community (see D'Acunto et al., 2018).

2.3. Incubation experiment design and analyses

The experiment was designed according to a factorial design, which included the five land cover types (two uncropped margins, monocropping and two different crop rotations), two residue types (Wheat and Mix), two soil microbial communities (Soybean and Woody) from three locations (replicates). Therefore, we obtained 60 experimental units (microcosms), each composed of a glass flask with 50 g of sterilized soil (corresponding to each of the five cover types) + a plant residue amendment + a soil microbial inoculation. In addition, two control

Table 1
Soils properties of five land cover types from an agricultural landscape. Data shows means and 1 standard error ($n = 3$). Different letters indicate significant differences among land cover types from ANOVA tests.

Soil properties	Soil cover types				
	Soybean monocropping	Rotation	Intensified rotation	Herbaceous	Woody
Soil respiration rate (μgC-CO2g soil $^{-1}$d^{-1})***	12.20 ± 0.48a	36.30 ± 4.00bc	27.0 ± 2.40b	27.10 ± 2.21b	40.6 ± 3.60c
Carbon (%)**	3.02 ± 0.18a	3.24 ± 0.14a	2.68 ± 0.09a	2.31 ± 0.70a	9.13 ± 1.30b
Nitrogen (%)**	0.24 ± 0.01a	0.20 ± 0.03a	0.21 ± 0.01a	0.18 ± 0.06a	0.56 ± 0.07b
pH***	5.21 ± 0.10a	5.53 ± 0.15ab	5.36 ± 0.11ab	5.77 ± 0.10bc	6.04 ± 0.06c

*** $p \leq 0.0001$.
** $p \leq 0.001$.

treatments were included which were later discarded to avoid differences due to manipulation and sterilization failures. The first control consisted in measuring soil respiration after sterilization treatment in soils coming from the five cover types without substrate or microbial soil community addition. The second control consisted in measuring soil respiration rate to sterilized plant residue in common sterilized soil.

At the beginning of the experiment, each microcosm received 50 g of soil, 10 ml of the microbial community inoculum and 5 g of plant residue. Then, each microcosm was incubated in darkness at random block scheme. Then, the flasks were closed and gently shaken for a minute. Then, flasks were incubated without cap at controlled temperature conditions (25 °C) and water content was replenished when needed (indicated by daily measure of microcosms weight). Soil respiration rate, soil pH and soil water content were measured at 2, 5, 10, 15 and 30 days from the beginning of the experiment extracting an aliquot of soil. In the Results section, we focus mainly on the 30 days since no different patterns were observed on the previous dates measured and because it is the date where the reported patterns are best visualized. Catabolic physiological profiles and diversity of soil heterotrophic bacteria were estimated at the beginning (day 0) and at the end of the experiment (day 30).

Metabolic profile and functional diversity of the heterotrophic bacterial community were characterized through the community level physiological profile method (Garland and Mills, 1991 adapted by Di Salvo and García De Salamone, 2012). In sterile and single 200 µl microplates, we offered 17 different carbon sources to soil suspension from each microcosm. Carbon sources consisted of different compounds usually present in the rhizosphere. They included amino acids (alanine, arginine, histidine, and proline), carbohydrates (cellobiose, dextrose, mannitol, rhamnose and xylose), carboxylic acids (itaconic, pyruvic and oxalic), two phenolic compounds (salicylic and benzoic acid), a polymer (tween 80), a disaccharide (lactose), monosaccharide (fructose) and a control with distilled water. Each well received 50 µl of a standard basal media, 50 µl of tetrazolium violet for color development under CO_2 production. Finally, each well was inoculated with 50 µl from 10^{-4} soil suspensions obtained from each microcosm. Incubations were carried out at 25 °C for a maximum of 96 h. Well color development was measured at 24, 48 and 590 nm (Multiskan EX Spectrophotometer ®). The optical density for each well was calculated by subtracting the control well values from each plate to the optical density value of the well (Garland and Mills, 1991). Based on absorbance data on single carbon sources, bacterial metabolic richness and diversity were calculated, only considering the cells with absorbance values higher than 0.25 (Garland, 1997). Thus, bacterial metabolic diversity was estimated using the Shannon-Wiener index (H′), which combines richness and evenness, as follows $H' = \Sigma\ pi * (\ln pi)$, where pi is the ratio between the optical density developed in each carbon source and the sum of all activities on the 17 carbon sources. Because H′ provides an estimate of the entropy of the system, instead of diversity, the number D also called the 'effective number of species were computed as follows $D = \exp(-\Sigma\ pi * (\ln pi)) = \exp(H')$ (Jost, 2006).

Soil respiration rate was estimated using a portable respirometer (PPSystems), according to Robertson et al. (1999). Briefly, the measure consisted of soil incubations during 24 h in 250 cm^3 closed flasks. After 24 h, 6 cm^3 of air was extracted with a sterile syringe and injected into the respirometer to determine air CO_2 concentration. The amount of CO_2 respired per dry soil gram was estimated with this value, flask volume, incubation time and soil dry mass (Robertson et al., 1999).

2.4. Statistical analyses

The effects of cover type, soil microbial community and plant residue on soil respiration, microbial metabolic diversity and pH were evaluated by analyses of variance considering a mixed effects model with cover type, soil microbial community, residue and their interactions as fixed factors, and location as a random factor with the nlme package (Pinheiro et al., 2019) of R (R Core Team, 2013). When significant effects of fixed factors were detected, means were compared by Tukey tests, performed with the 'agricolae' package of R (R Core Team, 2013).

Soil microbes were analyzed by a principal component analysis (PCA) from the 'vegan' package in R (Baselga and Orme, 2012). This analysis was conducted based on the catabolic profiles of the heterotrophic bacterial community derived from different land cover types, in conjunction with soil inocula and plant residue. The statistical software used for the analysis was R (R Core Team, 2013). The position on the first axis was compared through an analysis of variance following the model described above. The PCA analysis of the absorbance of microplates at 590 nm was normalized to avoid potential confounding effects of cell density (Garland, 1997).

We also related soil carbon content with soil respiration rate, exp. H′ (diversity) and histochemical properties of plant residue (lignin, carbon, nitrogen) by regression analyses with the car package of R (R Core Team, 2013).

3. Results

3.1. Initial soil microbial communities

The initial communities obtained by filtering differed in their catabolic profile and diversity (Fig. 1). The microbial catabolic profiles revealed differences between soil cover types. The first axis of the principal component analysis explained 59.4 % of the variability and separated Woody margins microbial community from the Soybean Monocropping microbial community. The soil microbial communities occupied different positions on the first axis ($F_{1,5} = 44.32$, $p = 0.002$, Fig. 1). The microbial catabolic diversity also differed between soil microbial community ($F_{1,5} = 14.08$, $p = 0.01$, Fig. 1). Microbes from Woody margins are more diverse and showed a higher consumption of phenolic compounds, benzoic acid, histidine, cellobiose, xylose, rhamnose and Tween 80 than microbes from Soybean Monocropping (Fig. 1).

3.2. After incubation experiment

3.2.1. Plant residue and soil microbial communities

After 30 days of incubation, the microbial catabolic diversity showed an interactive effect between plant residue and soil cover type treatments ($F_{4,59} = 3.93$, $p = 0.01$, Fig. 2, upper panel, Table 3). Overall, soils inoculated with Wheat residue community sustained the greater catabolic diversity (Fig. 2, Table 3). The greater contrast of residue effects on catabolic diversity was given by soils from Soybean Monocropping and Woody margins. Wheat showed greater diversity than Mix in soils Woody margin whereas Mix showed greater diversity than Wheat in soils from Soybean Monocropping (Fig. 2, upper panel, Table 3, residue x cover type interaction). Besides this, Wheat residue substantially differs in lignin content with Mix residue ($F_{1,5} = 266$, $p = 0.0001$, Table 2) and contained 70 % less lignin than Mixed residue. Initial lignin concentration of residue was inversely correlated with catabolic diversity (exp H′) and accounted for 30 % of the variation of catabolic diversity ($p = 0.04$).

The microbial catabolic profiles also revealed differences between plant residue ($F_{1,59} = 4.01$, $p = 0.05$) and microbial biota ($F_{1,59} = 4.33$, $p = 0.04$), whereas they did not differ among cover types ($F_{4,59} = 1.18$, $p = 0.34$) (Fig. 2 lower panel, Table 3). The first axis of the principal component analysis explained 37 % of the variability and separated those soils inoculated with the microbial community from the Woody margins from those inoculated with the soybean microbial community (white vs. black bars). Both microbial communities highly metabolized pyruvic acid and alanine. However, the Woody community metabolized more proline and mannitol, while the soybean community metabolized more tween 80. Soils amended with the Mix residue differed from those amended with Wheat (Fig. 2, lower panel and Table 4). Soil inocula from incubations amended with Wheat metabolized more amino acids

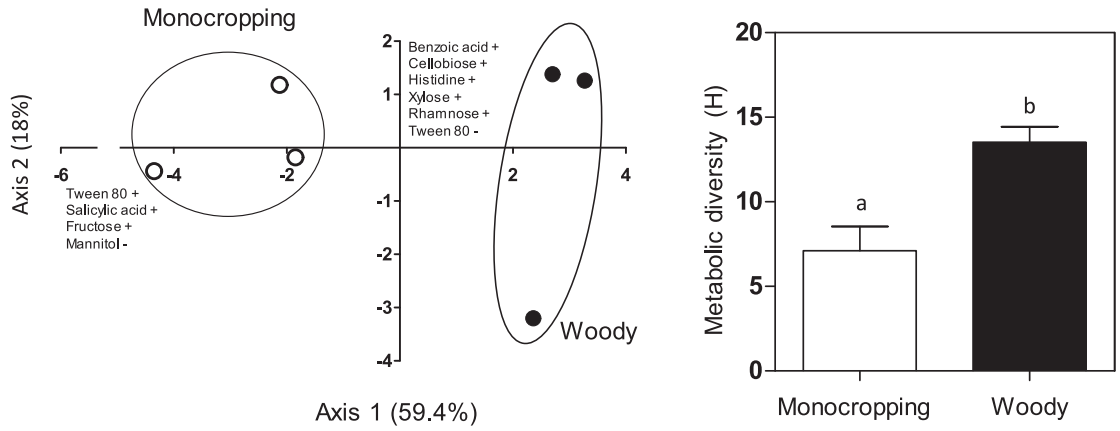

Fig. 1. Principal components analysis of community-level physiological profiles (left panel) and catabolic diversity of soil heterotrophic bacterial community (right panel) of Soybean Monocropping and Woody margins. Samples were obtained in three locations along a SW-NE 120-km transect in the Argentina Pampa. On the left panel, carbon sources on the first and the second axes are those with greater, positive (+) or negative (−), variation in the bacterial activity pattern (larger eigenvectors).

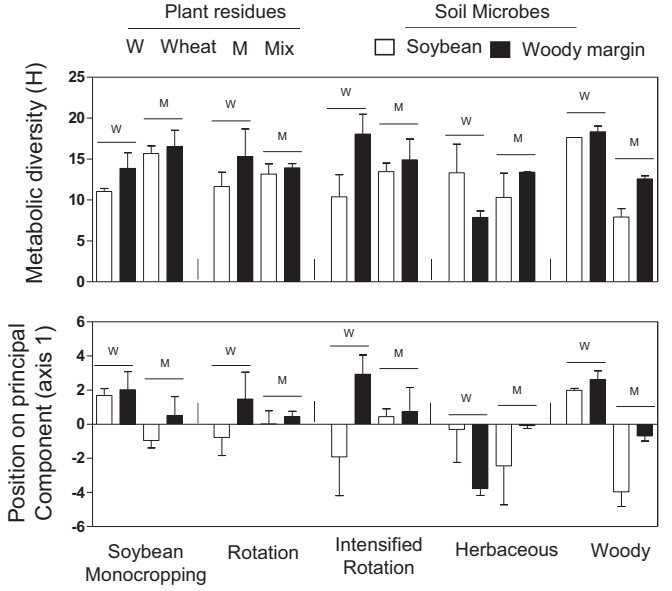

Fig. 2. Catabolic diversity of soil heterotrophic bacterial community (upper panel) and position on Principal Component (axis 1) (lower panel) after 30 days of soil incubation of sterilized soils from different land cover types, plant residue amendment and soil microbes inoculation. Soybean monocropping corresponds to a long fallow-soybean, long fallow-soybean. Rotation corresponds to a short fallow-wheat/soybean, long fallow-maize. Intensified rotation corresponds to a short fallow-wheat/soybean, short fallow-field pea/maize, herbaceous uncropped margins, and woody uncropped margins. Each land cover type was sterilized and inoculated with each of two different microbial communities (soybean monocropping, white bars, and woody margins, black bars), and amended with each of two plant residue types (wheat, W, and mixed of herbaceous and woody margin, M) in a complete factorial design.

(proline and arginine) and mono and disaccharides (rhamnose, xylose and lactose respectively) than those from incubations amended with Mix residue. In turn, inocula from incubations amended with Mix residue metabolized more carboxylic acids (benzoic acid) and a disaccharide (cellobiose) than Wheat residue (data not shown).

3.2.2. Soil respiration rates

After 30 days of incubation, soil respiration only revealed significant effects of the land cover type ($F_{4,\ 59} = 3.80$, $p = 0.01$). Conversely, it was not significantly affected by plant residue ($F_{1,\ 59} = 1.21$, $p = 0.28$) nor by microbial community treatments ($F_{1,\ 59} = 0.09$, $p = 0.77$) (Fig. 3 and Table 3). Respiration of soil from Woody margin was significantly higher than that from Soybean Monocropping, irrespectively of plant residue and microbial biota manipulation (Table 3). In turn, soil from Herbaceous margin and both crop rotations (Rotation and Intensified Rotation) had intermediate respiration rates. Soil carbon content was positively correlated with soil respiration rate and accounted for 58 % of the variation of soil respiration rate ($p = 0.006$).

Table 2
Histochemical properties of the two incubated plant residues. Data show means and 1 standard error in parenthesis (n = 3). Different letters indicate significant differences among residues from a Tukey tests.

Plant residue properties	Plant residue	
	Wheat	Mix
Carbon (%)**	44.0 ± 0.09 b	37.6 ± 0.19 a
Nitrogen (%)**	0.35 ± 0.01 a	1.1 ± 0.01 b
Lignin (%)**	5.39 ± 0.15 a	18.5 ± 0.21 b
Hemicellulose (%)***	22.6 ± 0.15 a	17.2 ± 0.35 b
Soluble (%)*	61.1 ± 0.39 a	60.8 ± 0.53 a

*** $p \leq 0.0001$.
** $p \leq 0.001$.
* $p \leq 0.05$.

Table 3
F and *p* values of microbial metabolic diversity (exp H), position on principal component (axis 1) and soil respiration rate. Details of treatments as in Fig. 2.

Source of variation	Microbial metabolic diversity (exp H)		Position on principal component (axis 1)		Soil respiration rate (μC - CO_2 g soil $^{-1}$ d^{-1})	
	F-value	p-Value	F-value	p-Value	F-value	p-Value
Cover type	1.92	0.13	1.18	0.34	3.80	0.01**
Soil microbes	5.93	0.02**	4.33	0.04*	0.09	0.77
Plant residue	5.88	0.02**	4.01	0.05*	1.21	0.28
Cover:microbes	1.24	0.31	1.42	0.24	0.37	0.83
Cover:residue	3.93	0.01**	1.25	0.31	0.09	0.98
Microbes:residue	0.41	0.52	0.29	0.59	0.29	0.59
Cover:microbes: residue	2.40	0.06 ǂ	1.34	0.27	0.14	0.97

** $p \leq 0.001$.
* $p \leq 0.05$.

Table 4
Soil bacterial utilization of individual carbon sources measured as absorbance at the wavelength of 590 nm. Data shows means and 1 standard error (n = 3). The asterisk (*) in the carbon sources denotes a significant interaction among the three factors: soil cover type, plant residue, and soil microbes.

Treatment	Carbon source	Cover type				
Plant residue/soil microbes		Soybean monocropping	Rotation	Intensified rotation	Herbaceous	Woody
Wheat/soybean	Carbohydrates					
	Cellobiose*	0.89 ± 0.10	0.91 ± 0.03	0.72 ± 0.19	0.77 ± 0.11	0.84 ± 0.01
	Dextrose	0.28 ± 0.14	0.80 ± 0.10	0.75 ± 0.16	0.28 ± 0.15	0.76 ± 0.03
	Mannitol	0.83 ± 0.06	0.88 ± 0.05	0.89 ± 0.12	0.81 ± 0.12	1.04 ± 0.03
	Rhamnose	0.59 ± 0.18	0.63 ± 0.13	0.54 ± 0.18	0.43 ± 0.17	0.74 ± 0.03
	Xylose	0.79 ± 0.05	0.87 ± 0.05	0.65 ± 0.12	0.58 ± 0.20	0.84 ± 0.13
	Amino acids					
	Alanine*	0.67 ± 0.06	0.54 ± 0.03	0.63 ± 0.07	0.69 ± 0.13	0.52 ± 0.01
	Arginine	0.83 ± 0.03	0.57 ± 0.04	0.46 ± 0.14	0.64 ± 0.08	0.67 ± 0.01
	Histidine*	0.75 ± 0.13	0.61 ± 0.04	0.53 ± 0.09	0.88 ± 0.13	1.07 ± 0.01
	Proline*	1.11 ± 0.02	0.65 ± 0.11	0.66 ± 0.23	0.86 ± 0.02	1.07 ± 0.03
	Carboxylic acids					
	Itaconic acid	0.54 ± 0.04	0.19 ± 0.04	0.12 ± 0.01	0.51 ± 0.07	0.60 ± 0.03
	Oxalic acid	0.90 ± 0.04	0.31 ± 0.09	0.28 ± 0.09	0.79 ± 0.03	0.76 ± 0.10
	Pyruvic acid	0.84 ± 0.04	0.66 ± 0.05	0.65 ± 0.04	0.67 ± 0.07	0.71 ± 0.01
	Phenolic compounds					
	Benzoic acid	0.87 ± 0.10	0.55 ± 0.13	0.51 ± 0.13	0.85 ± 0.14	0.93 ± 0.01
	Salicylic acid	0.24 ± 0.05	0.24 ± 0.03	0.19 ± 0.05	0.38 ± 0.15	0.27 ± 0.01
	Polymer					
	Tween 80	0.46 ± 0.08	0.33 ± 0.05	0.33 ± 0.09	0.35 ± 0.03	0.44 ± 0.01
	Disaccharide					
	Lactose*	0.48 ± 0.09	0.26 ± 0.05	0.25 ± 0.08	0.39 ± 0.19	0.35 ± 0.01
	Monosaccharide					
	Fructose	0.83 ± 0.08	0.87 ± 0.04	0.72 ± 0.22	0.54 ± 0.25	1.04 ± 0.01
Mix/soybean	Carbohydrates					
	Cellobiose	0.75 ± 0.18	0.71 ± 0.18	0.96 ± 0.02	0.70 ± 0.27	0.45 ± 0.17
	Dextrose	0.85 ± 0.05	0.86 ± 0.06	0.87 ± 0.10	0.74 ± 0.02	0.65 ± 0.06
	Mannitol	0.80 ± 0.08	0.89 ± 0.05	0.80 ± 0.06	0.76 ± 0.15	0.55 ± 0.11
	Rhamnose	0.61 ± 0.11	0.67 ± 0.10	0.54 ± 0.08	0.56 ± 0.24	0.38 ± 0.10
	Xylose	0.63 ± 0.12	0.58 ± 0.19	0.74 ± 0.08	0.54 ± 0.18	0.39 ± 0.04
	Amino acids					
	Alanine	0.58 ± 0.05	0.70 ± 0.11	0.73 ± 0.06	0.58 ± 0.10	0.52 ± 0.02
	Arginine	0.64 ± 0.04	0.65 ± 0.02	0.69 ± 0.08	0.50 ± 0.02	0.43 ± 0.05
	Histidine	0.56 ± 0.02	0.80 ± 0.15	0.82 ± 0.12	0.38 ± 0.13	0.64 ± 0.15
	Proline	0.83 ± 0.08	1.08 ± 0.07	1.03 ± 0.14	0.60 ± 0.14	0.52 ± 0.06
	Carboxylic acids					
	Itaconic acid	0.50 ± 0.17	0.42 ± 0.09	0.46 ± 0.21	0.58 ± 0.16	0.15 ± 0.03
	Oxalic acid	0.19 ± 0.04	0.52 ± 0.14	0.32 ± 0.12	0.36 ± 0.21	0.36 ± 0.17
	Pyruvic acid	0.67 ± 0.03	0.59 ± 0.23	0.46 ± 0.16	0.51 ± 0.15	0.58 ± 0.05
	Phenolic compounds					
	Benzoic acid	0.66 ± 0.09	0.64 ± 0.05	0.69 ± 0.14	0.47 ± 0.20	0.55 ± 0.16
	Salicylic acid	0.20 ± 0.02	0.25 ± 0.05	0.24 ± 0.10	0.35 ± 0.20	0.30 ± 0.04
	Polymer					
	Tween 80	0.31 ± 0.02	0.46 ± 0.11	0.35 ± 0.01	0.34 ± 0.15	0.31 ± 0.02
	Disaccharide					
	Lactose	0.19 ± 0.02	0.30 ± 0.11	0.38 ± 0.11	0.24 ± 0.09	0.26 ± 0.03
	Monosaccharide					
	Fructose	0.69 ± 0.13	0.67 ± 0.18	0.72 ± 0.19	0.51 ± 0.26	0.39 ± 0.10
Wheat/woody	Carbohydrates					
	Cellobiose	0.93 ± 0.02	0.95 ± 0.03	1.03 ± 0.03	0.41 ± 0.16	0.86 ± 0.02
	Dextrose	0.96 ± 0.04	0.99 ± 0.06	1.08 ± 0.04	0.75 ± 0.05	0.83 ± 0.04
	Mannitol	0.89 ± 0.03	0.92 ± 0.05	0.91 ± 0.02	0.50 ± 0.10	0.93 ± 0.08
	Rhamnose	0.81 ± 0.06	0.74 ± 0.08	0.83 ± 0.05	0.41 ± 0.14	0.70 ± 0.01
	Xylose	0.88 ± 0.03	0.80 ± 0.08	0.86 ± 0.03	0.46 ± 0.13	0.93 ± 0.05
	Amino acids					
	Alanine	0.61 ± 0.07	0.70 ± 0.09	0.77 ± 0.11	0.38 ± 0.15	0.73 ± 0.21
	Arginine	0.63 ± 0.13	0.55 ± 0.21	0.80 ± 0.08	0.42 ± 0.09	0.81 ± 0.14
	Histidine	0.76 ± 0.04	0.71 ± 0.01	0.76 ± 0.08	0.46 ± 0.06	1.04 ± 0.03
	Proline	0.94 ± 0.12	1.03 ± 0.09	0.92 ± 0.18	0.63 ± 0.06	1.12 ± 0.02
	Carboxylic acids					
	Itaconic acid	0.59 ± 0.12	0.61 ± 0.25	0.42 ± 0.16	0.20 ± 0.10	0.66 ± 0.09
	Oxalic acid	0.24 ± 0.03	0.25 ± 0.14	0.37 ± 0.17	0.48 ± 0.12	0.49 ± 0.17
	Pyruvic acid	0.79 ± 0.09	0.65 ± 0.06	0.86 ± 0.04	0.51 ± 0.09	0.74 ± 0.03
	Phenolic compounds					
	Benzoic acid	0.85 ± 0.05	0.75 ± 0.05	0.96 ± 0.05	0.71 ± 0.19	0.89 ± 0.04
	Salicylic acid	0.24 ± 0.03	0.14 ± 0.08	0.17 ± 0.06	0.22 ± 0.18	0.27 ± 0.003
	Polymer					
	Tween 80	0.41 ± 0.11	0.37 ± 0.10	0.48 ± 0.04	0.41 ± 0.13	0.54 ± 0.10
	Disaccharide					
	Lactose	0.70 ± 0.06	0.61 ± 0.23	0.68 ± 0.19	0.17 ± 0.05	0.42 ± 0.06
	Monosaccharide					
	Fructose	0.91 ± 0.02	0.93 ± 0.03	1.01 ± 0.05	0.55 ± 0.15	1.00 ± 0.04

(*continued on next page*)

Table 4 (*continued*)

Treatment	Carbon source	Cover type				
Plant residue/soil microbes		Soybean monocropping	Rotation	Intensified rotation	Herbaceous	Woody
Mix/woody	Carbohydrates					
	Cellobiose	0.89 ± 0.03	0.85 ± 0.02	0.78 ± 0.11	1.19 ± 0.05	0.61 ± 0.18
	Dextrose	0.78 ± 0.12	0.84 ± 0.05	0.77 ± 0.03	0.56 ± 0.17	0.75 ± 0.14
	Mannitol	0.80 ± 0.05	0.84 ± 0.03	0.75 ± 0.14	0.69 ± 0.09	0.63 ± 0.17
	Rhamnose	0.56 ± 0.19	0.70 ± 0.10	0.61 ± 0.10	0.37 ± 0.07	0.57 ± 0.06
	Xylose	0.82 ± 0.06	0.75 ± 0.04	0.64 ± 0.07	0.68 ± 0.26	0.71 ± 0.09
	Amino acids					
	Alanine	0.68 ± 0.11	0.56 ± 0.03	0.64 ± 0.01	0.76 ± 0.16	0.56 ± 0.04
	Arginine	0.67 ± 0.08	0.62 ± 0.07	0.76 ± 0.07	0.66 ± 0.18	0.58 ± 0.03
	Histidine	0.75 ± 0.13	0.73 ± 0.08	0.82 ± 0.14	0.72 ± 0.25	0.62 ± 0.09
	Proline	1.04 ± 0.11	0.98 ± 0.14	1.03 ± 0.10	0.91 ± 0.13	0.78 ± 0.08
	Carboxylic acids					
	Itaconic acid	0.68 ± 0.12	0.58 ± 0.07	0.65 ± 0.07	0.58 ± 0.10	0.66 ± 0.17
	Oxalic acid	0.23 ± 0.14	0.37 ± 0.06	0.35 ± 0.09	0.66 ± 0.18	0.50 ± 0.15
	Pyruvic acid	0.68 ± 0.05	0.70 ± 0.10	0.72 ± 0.08	0.69 ± 0.15	0.68 ± 0.05
	Phenolic compounds					
	Benzoic acid	0.72 ± 0.08	0.79 ± 0.06	0.88 ± 0.10	0.73 ± 0.23	0.61 ± 0.09
	Salicylic acid	0.29 ± 0.07	0.25 ± 0.05	0.29 ± 0.13	0.35 ± 0.03	0.35 ± 0.15
	Polymer					
	Tween 80	0.41 ± 0.06	0.40 ± 0.08	0.36 ± 0.04	0.53 ± 0.19	0.50 ± 0.26
	Disaccharide					
	Lactose	0.21 ± 0.04	0.25 ± 0.04	0.46 ± 0.07	0.41 ± 0.02	0.34 ± 0.07
	Monosaccharide					
	Fructose	0.85 ± 0.04	0.82 ± 0.06	0.76 ± 0.13	0.57 ± 0.16	0.92 ± 0.07

*: $p \leq 0.05$.

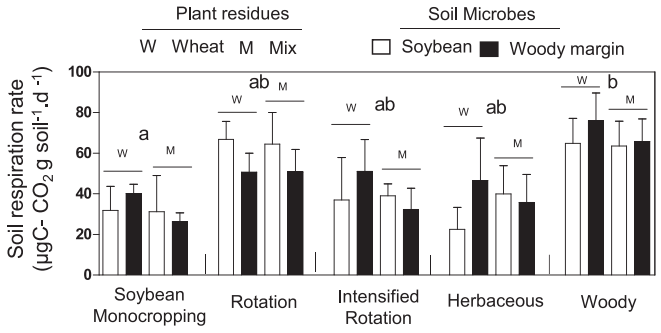

Fig. 3. Soil respiration rate after 30 days of soil incubation of soils under different land cover types. Soybean monocropping corresponds to a long fallow-soybean, long fallow-soybean. Rotation corresponds to a short fallow-wheat/soybean, long fallow-maize. Intensified rotation corresponds to a short fallow-wheat/soybean, short fallow-field pea/maize, herbaceous and woody vegetation in uncropped margins. Each land cover type was sterilized and inoculated with each of two different microbial communities (soybean monocropping, white bars, and woody margins, black bars), and amended with each of two plant residue types (wheat, W, and mixed of herbaceous and woody margin, M) in a complete factorial design. After 30 days of soil incubation, the soil respiration rate only revealed significant effects of the land cover type.

3.2.3. Soil pH

The soil pH after 30 days of incubation was significantly affected by land cover type ($F_{4, 59} = 12.1, p = 0.0001$), plant residue ($F_{1, 59} = 7.74, p = 0.008$) and microbial community ($F_{1, 59} = 7.50, p = 0.009$) (Table 5). The cropped soils (Soybean Monocropping and Rotation) showed slightly more acidic values than uncropped soils (Woody and Herbaceous) and the Intensified Rotation soils. In turn, soils inoculated with Soybean microbial community and amended with Wheat plant residue had a lower pH than the soils inoculated with the Woody microbial community and amended with the Mix residue. Finally, no significant relationship was found between soil pH and microbial functional diversity ($p = 0.84$).

Table 5
Soil pH after 30 days of soil incubation of soils under different land cover types. Results revealed significant effects of the cover type ($p < 0.001$), plant residue ($p = 0.008$) and soil microbes ($p = 0.009$) from an ANOVA test.

Treatment	Cover type***				
Plant residue**/ Soil microbes**	Soybean monocropping	Rotation	Intensified rotation	Herbaceous	Woody
Wheat/ soybean	5.31 ± 0.09	5.62 ± 0.07	5.28 ± 0.10	5.58 ± 0.17	5.89 ± 0.16
Mix/ soybean	5.55 ± 0.11	5.70 ± 0.05	5.33 ± 0.6	5.70 ± 0.15	5.74 ± 0.18
Wheat/ woody	5.36 ± 0.08	5.82 ± 0.23	5.36 ± 0.07	5.61 ± 0.18	5.86 ± 0.14
Mix/ woody	5.45 ± 0.12	6.10 ± 0.17	5.59 ± 0.18	6.01 ± 0.12	6.26 ± 0.17

*** $p \leq 0.001$.
** $p \leq 0.01$.

4. Discussion

Our results revealed complex, non-linear responses of soil microbes to the manipulation of plant residues and microbial communities in sterile soils from different cover types. The effect of plant residue on catabolic microbial diversity largely depended on the cover type, because Wheat stimulated diversity of Woody margin and Mix stimulated diversity of Soybean Monocropping. The soils inoculated with the Woody microbial community, in general, maintained their original greater catabolic diversity with respect to that of Soybean after 30 days, although this response marginally depended on the cover type and plant residue. This experiment was conducted over a 30-day period, considering that the evidence shows a large proportion of organic compounds are respired in the short term. Additionally, selecting a 30-day interval for soil sampling provides sufficient time for microbial communities to establish and exhibit metabolic activities (van Hees et al., 2005). Finally, these effects on catabolic responses were not translated into changes in carbon respiration as we only detected a significantly higher respiration in soils from Woody margins. Our results suggest that the management of land cover, plant residues quality, and the inoculation with soil

microbial solutions have the potential ecologically-based strategies for complementing soil catabolic capabilities. Nevertheless, the complex interactions observed requires a greater understanding, particularly on how they are linked to plant residue quality, soil organic matter content, and microbial community composition.

4.1. Plant residues and soil microbial communities

Plant residue effects on catabolic diversity depended on the cover type. The incubations amended with Mix residue in general had lower catabolic diversity than those amended with Wheat, except in soils from Soybean Monocropping, where Mix residue seemed to have stimulated other catabolic groups of the microbial community. This would suggest that the plant residue created a favorable condition for carbon substrate utilization by soil microbes in the two studied microbial communities (Soybean Monocropping and Woody margins) (Shrestha et al., 2019; Sradnick et al., 2013). In general, it is believed that the contribution of more diverse substrates will determine an increase of the overall catabolic activity (in this case, greater catabolic diversity). However, here the most diversity residue (Mix) had also the highest lignin content in their tissue. Lignin is one of the most recalcitrant substrates which is consistent with its biological functions. Lignin complex organic molecules are normally degraded by fungi (Kaiser et al., 2014). Despite some studies suggesting that microbial carbon use efficiency is higher in fungal-dominated soil communities compared to bacterial-dominated ones, more recent estimates present a contrasting perspective, showing similar microbial carbon use efficiency across different soil communities, including fungi and bacteria (Six et al., 2006; Thiet et al., 2006). Furthermore, in many examined fungal communities, ligninolysis occurs under conditions of nutrient limitation, with greater degradation observed when soil nutrient availability is lower (Hammel, 1997). Therefore, the final contribution of more diverse substrates will depend not only on substrate diversity (residue species diversity) but also on substrate quality and the soil nutrient content. Among them, rich lignin substrates will promote degradation by fungi through the production of exoenzymes. Here, we found that soils amended with Mix residue metabolized more benzoic acid. Phenolic compounds, such as benzoic acid, are used more for energy production, resulting in a lower microbial carbon use efficiency (Gunina and Kuzyakov, 2022).

The structural complexity of the Mix residue may also have affected microbial activity since microbes invest energy in synthesizing extracellular enzymes to break down substrates before they can be taken up. Therefore, such complex substrates produce a relatively low microbial net carbon use efficiency (Agren and Bosatta, 1987). Furthermore, Mix and Wheat amendment promoted the metabolization of different carbon substrates. Soils amended with Wheat metabolized more amino acids (proline and arginine) and carbohydrates (rhamnose and xylose) than those amended with the Mix residue. In turn, soils amended with Mix metabolized more phenolic compound (benzoic acid) and a carbohydrate (cellobiose) than those amended with Wheat. Therefore, a more complex nature of plant residue (and its breakdown products) is thought to result in a lower microbial carbon use efficiency compared to labile and more simple substrates (Cotrufo et al., 2013).The unexpected greater microbial diversity in soils of Woody margins amended with Wheat compared to soils amended with Mix might be due to an interaction with the carbon content of this soil, which tripled that of the other cover types (Table 1). This residue-soil carbon interaction was also documented for alpine successional habitats (Porazinska et al., 2018). They proposed that soils with high carbon contents stimulate microorganisms by complementing with energy and nutrients the substrates offered by fresh litter. Therefore, in soils with high carbon contents, the relationship between plant and microbial diversity would be partly decoupled from fresh litter. In our case, we hypothesize that the large provision of soil carbon in Woody margins might have stimulated other catabolic functions than those stimulated by the fresh plant litter. In turn, because Wheat had lower fiber contents and greater soluble than Mix, soil microbes amended with Wheat would have had more readily energy to respond to this abundant soil sources of carbon.

Soils inoculated with the Woody microbial community in general maintained their original greater catabolic diversity with respect to that of soybean, although this response marginally depended on the cover type and plant residue. Overall, soils inoculated with the Woody microbial community sustained the inherent greater catabolic diversity of this community, except in the Herbaceous margins amended with Wheat (triple interaction marginally significant). Contrary to our predictions, the greater diversity of the Mix residue was not translated into a greater microbial catabolic diversity. Instead, plant residue acted on catabolic diversity in complex interactions with cover type since soils from Woody margins amended with Wheat had a significantly higher catabolic diversity than their counterparts amended with Mix (significant residue x cover type interaction). Besides this, for soil from Woody margins, Wheat residue seemed to amplify the differences between the two microbial communities while Mix seemed to blur them. We hypothesized that the recalcitrance of the more lignified Mix residue determines the less catabolic microbial diversity in Woody margins soil amended with the Mix residue than amended with Wheat. The specificity of this degradation (lignified residues) implies a select small set of microbes capable of degrading the polymer (Cragg et al., 2015) and therefore could explain the less catabolic diversity.

4.2. Soil respiration rates

Regardless of residue quality and soil community added, soil respiration rates only differed between land cover types. Soils from Woody margins respired significantly more carbon than those from Soybean Monocropping presumably through its persistent effect on soil total carbon and nitrogen contents. In Woody soils, plant residue quality is crucial in soil carbon formation, while in croplands and grasslands it is the microbial activity that rules the organic matter formation (Wang et al., 2021). This is attributed to the faster microbial turnover rates, higher bacteria to fungi ratio and more complete decomposition of above and below-ground litter, as well as more rhizosphere activity in cropland and grassland soils than in wood. We hypothesize that Woody margin soils usually contain more partially decomposed plant residues since Woody soils have a larger living fungal biomass than crop or Herbaceous margins soils (Wang et al., 2021). Moreover, the renewal of living microbial biomass in these soils is usually slower and thus able to persist longer in soil (Wang et al., 2021). Since we milled the residues to ensure soil contact and microbial degradation, it might have accelerated their decomposition and, therefore, the respiration rate in Woody soils. Respiration rates involve multiple, interacting processes involving complex microbial consortia and fauna. Changes in the characteristics and functional properties of these consortia may have subtle effects on transformation pathways that may be difficult to detect by measuring gross properties such as respiration, but which may have long-term implications for microbial diversity and organic matter stabilization.

5. Conclusion

In agricultural landscapes, the different land cover types affect the feedbacks between plants and soil microbes. Restoration practices frequently disregard the role played by the soil microbial communities in the regulation of ecosystem processes. Our study reveals complex, non-linear responses of soil microbes to changes of plant residue and microbial community. The effect of plant residue quality on catabolic microbial diversity seems a potential complementary pathway to increase the diversity of microbial catabolic functions in arable soils. In turn, the soils inoculated with the Woody microbial community, in general, maintained their original higher catabolic diversity with respect to that of soybean after an incubation of 30 days, although this response marginally depended on the cover type and plant residue. Finally, these effects on catabolic responses were not translated into

changes of carbon respiration as we only detected significantly higher respiration in soils from Woody margins. Our results suggest that a mix of management practices at plot scale (such as the manipulation of plant residues) and at landscape scale (uncropped margins conservation) are a potential ecology-based strategy for the conservation and improvement of agricultural soil biodiversity. This is due to the complexity of interactions between plant residue quality, soil organic matter content, and microbial community composition, particularly in an extensive landscape like the Pampas.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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